REVISION OF SOME DWARF CHAMELEONS (SAURIA: CHAMAELEONIDAE: *BRADYPODION*) FROM EASTERN SOUTH AFRICA

By

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requirements for the degree of
Master of Science
in the
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PREFACE

The research described in this dissertation was carried out at my home and in the former Department of Zoology and Entomology, Pietermaritzburg, under the supervision of Professor Denis J. Brothers.

The research described is the original work of the author, except where duly acknowledged to others in the text, and has not been submitted, in part or in whole, to another university for any degree or diploma.

As provided by Article 8.2 of the International Code of Zoological Nomenclature, 4th edition (1999), this dissertation is not to be considered a publication for the purposes of zoological nomenclature; new names included here are therefore not available and must not be cited prior to their formal publication (to be done elsewhere at the first opportunity).

Lynn Roy Graham Raw

Denis J Brothers

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Last but not least, my wife, Leslie, and children, Gareth, Darrell, Rowan, Paula and Kerry, who went without many of the normal benefits of family life due to my herpetological interests, but who have, nevertheless, supported my activities and readily assisted with fieldwork, often under rather unpleasant conditions.

To all of the above and to all whose names may have escaped me, my heartfelt gratitude for your contributions to the progress of this study.

ABSTRACT

This dissertation has the object of re-examining the taxonomic status of the dwarf chameleons related to *Bradypodion melanocephalum* and *Bradypodion caffrum* from eastern South Africa. The historical context of previous taxonomic treatments is reviewed. The basis of the taxonomic interpretation was established after a review of available alternatives. Cladistic analysis is used to elucidate the relationships of the taxa. The number of separate taxa that can be distinguished has been increased by the revival of one previously described taxon, the discovery of heretofore unknown populations and by the detection of the composite nature of some of the previously described taxa. Diagnoses and descriptions of the taxa under review are provided along with a key to their identification.

The geographic distribution of these *Bradypodion* taxa is reviewed in the context of present ecological parameters and in terms of the historical evolution of the study area. Comparison is made with the distributions of other taxa of plants, invertebrates and vertebrates occurring in the same general area. This appears to indicate a shared evolutionary history with a number of localised areas of endemicity.

The conservation status of these Red Data Book and CITES-listed dwarf chameleons is discussed with discussion of threats and priorities for further action. The use of these dwarf chameleon species as indicators for the identification of endemic areas should have important implications for conservation strategies in eastern South Africa.

This dissertation is not to be considered as a publication for the purposes of zoological nomenclature.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF TREE DIAGRAMS

1 INTRODUCTION

1.1 Justification of research

The taxonomy of the South African dwarf chameleons has presented problems for herpetologists for many years. Their generic status, whether separate from the rest of the chameleons or as part of the catch-all genus *Chamaeleo* and the status of the component taxa, either as separate species or as subspecies of *Bradypodion pumilum,* has been subject to various interpretations.

A recent classification (Klaver & Böhme, 1997) assigns these chameleons to 5 species within the genus B*radypodion.* These are as follows (in alphabetical order): *dracomontanum* Raw, 1976; *nemorale* Raw, 1978; *pumilum* (Gmelin, 1789); *setaroi* Raw, 1976 and *thamnobates* Raw, 1976. *Bradypodion pumilum* is considered to consist of 10 subspecies, viz., *caffer* (*sic*) (Boettger, 1888), *damaranum* (Boulenger, 1887), *gutturale* (Smith, 1849), *karrooicum* (Hewitt, 1930), *melanocephalum* (Gray, 1865), *occidentale* (Methuen & Hewitt, 1915), *pumilum* (Gmelin, 1789), *taeniabronchum* (Smith, 1831), *transvaalense* (FitzSimons, 1930) and *ventrale* (Gray, 1845). This is contrary to the views of Raw (1976, 1995 and 1997) who regarded all the taxa as species and Branch (1988) who regarded them as species except for *occidentale* and *karrooicum* that were placed as subspecies of *ventrale.*

Branch (1988) has suggested that *Bradypodion* species may be separated into two species groups. He states "The first, composed of the larger species, is associated with montane forests in Natal (e.g. *B. thamnobates*), Cape (e.g. *B. damaranum*) and Transvaal (e.g. *B. transvaalense*), but occurs in a wider variety of habitats in the Cape (e.g. *B. pumilum* and *B. ventrale*). The second group is restricted to coastal or fynbos vegetation and consists of small species (e.g. *B. taeniabronchum*, *B. setaroi* and *B. melanocephalum*)." In an unpublished paper presented to the Herpetological Association of Africa Symposium in Stellenbosch in April 1987, Raw (1989: abstract only) suggested that *Bradypodion* might comprise seven species groups. These were the *pumilum* group of the south-western areas of the Western Cape; the *damaranum* group of the Knysna Forest region of the Western and Eastern Cape Provinces; the widespread *ventrale* group of the Eastern, Northern and Western Cape Provinces and adjoining areas, and the *transvaalense* group of the KwaZulu-Natal Midlands and Drakensberg and the eastern escarpment of Swaziland, Mpumalanga and Northern Province. These groups as a whole correspond to Branch's group of larger species. The *taeniabronchum* group from just south of Port Elizabeth in the Eastern Cape; the *caffrum* group of KwaZulu-Natal and the Transkei region of the Eastern Cape and the *melanocephalum* group of the same areas correspond to Branch's group of smaller species.

The present study examines the taxonomic status of *B. melanocephalum* and *B. kentanicum*, *B. caffrum*, *B. nemorale* and *B. setaroi.* The first two taxa comprise the *melanocephalum* group and the second three taxa the *caffrum* group as proposed by Raw (see above), i.e., Branch's second group excluding *B. taeniabronchum*. The latter is not included as it is morphologically distinct, geographically widely separated from the other species under consideration and occurs in fynbos habitat, a very different habitat compared to the forest and forest-grassland ecotones inhabited by the species considered here.

During and preceding the present study a number of previously unknown populations have been discovered. The status of *B. melanocephalum kentanicum* (Hewitt, 1935) has also been uncertain (Branch, 1988, p. 18). The relationships and status of the various populations as members of the *B. melanocephalum* and *B. caffrum* groups needed to be determined satisfactorily. The question was whether they consist of a number of geographically isolated species, a number of subspecies belonging to the two nominate species or are merely geographic variants of two subspecies of *Bradypodion pumilum*.

The aim of this study is to attempt to delimit the various populations assigned to these two groups, to investigate their relationships and to formulate a hypothesis of their taxonomic status. Ultimately, the hypotheses and methods derived from this study should enable further clarification of the status of the remaining taxa of *Bradypodion* in southern Africa. This will be of great value in assessing the biodiversity of the region, in guiding conservation management and in identifying the critical areas which will need to be set aside as formally conserved or protected areas.

1.2 Description of study area

The study area is in the southeast of the continent of Africa, between the great escarpment of the Drakensberg range on the west and the coastal littoral fringing the Indian Ocean on the east. It is bordered in the south by the Kei River and in the north by the unnatural boundary of the Mozambique border. The land rises rapidly in a series of scarps deeply incised by the courses of numerous relatively short, fast-flowing rivers. Dwarf chameleon populations have been discovered on the higher-lying areas between these incised river valleys (Raw, 1976, 1978, & 1995) and, although each isolated population is considered distinct, they are also obviously closely related. Since most of these populations remain undescribed and the taxonomy of this particular geographical area is particularly complex, it was considered an appropriate region for detailed study.

1.3 Taxonomic review

When undertaking any survey of the literature on the South African dwarf chameleons it is soon obvious that two major controversies dominate the field. One of these is the question of whether they merit recognition as a distinct genus; the other is the question of whether the described taxa are all members of a single variable species. The following sections will discuss these topics in more detail.

1.3.1 Generic nomenclature and status

Fitzinger (1843) described two new subgenera and a new genus of chameleons. One of these was the genus *Bradypodion.* He designated *Cham. pumilus* Latreille (= *Lacerta pumila* Gmelin in Linnaeus, 1789), as the type species (Fitzinger, 1843, p. 15). J. E. Gray (1865), after discussing Fitzinger's attempt at dividing the chameleons into genera, then proceeded to ignore *Bradypodion* when he, himself, proposed a number of new genera. These included, among many others, two genera which are now regarded as synonyms of *Bradypodion*, namely *Lophosaura* and *Microsaura*.

Despite the availability of these generic names, most workers in the years that followed, e.g., Boulenger (1887, 1910) and Werner (1902, 1911), included the southern African dwarf chameleons with most other chameleons in the genus *Chamaeleon* Gronovius, 1763. Methuen & Hewitt (1915) reconsidered the separate generic status of the southern African dwarf chameleons and revived *Lophosaura* (Gray, 1865) to accommodate them. Broom (1925) subsequently accepted *Lophosaura* for these chameleons and Power (1932) and Hewitt (1935) also followed this path. FitzSimons (1943) then pointed out that *Lophosaura* (Gray, 1865) was preoccupied by Gray's own earlier genus of iguanids, described in 1852, and indicated that in any case Gray's *Microsaura* had page precedence over *Lophosaura.* As he had placed *Bradypodion* Fitzinger, 1843 as a synonym of *Chamaeleo* Laurenti, 1768, he proceeded to assign all the South African species to Gray's *Microsaura*.

Loveridge (1957: 197, footnote 38) preferred to regard the southern African dwarf chameleons as members of *Chamaeleo s. l.*, tentatively as the sub-genus, *Bradypodion*, but advised those who preferred a separate genus that *Bradypodion* (Fitzinger, 1843) took precedence to *Microsaura* (Gray, 1865). Hillenius (1959) adopted Loveridge's choice of arrangement but only recognised a single species, *Chamaeleo pumilus*, with the other described taxa being relegated to subspecies. Mertens (1966) followed Hillenius's arrangement in his checklist of the family.

Raw (1976) resurrected *Bradypodion* as a distinct genus in a review of the dwarf chameleons of Natal (now KwaZulu-Natal). This step was criticised by Klaver (1981) who, while acknowledging that the recognition of further genera of chameleons was warranted, thought that further studies were necessary before this could be accomplished. He believed that phylogenetic evidence was needed to establish the absolute rank of sister groups. Subsequently various authors including Branch (1981, 1988a & 1988b), Rieppel (1981, 1987), Billett, Gans & Maderson (1985), Shine (1985) and Yaron (1985) also adopted the genus *Bradypodion.*

Later Klaver & Böhme (1986, 1988 & 1997) eventually accepted the genus *Bradypodion* but then added several East African species on rather dubious grounds. Broadley & Howell (1991) subsequently followed this arrangement uncritically. The biochemical studies of Hofman *et al* (1991) did not confirm the inclusion of these East African species.

1.3.2 Species nomenclature and taxonomic status

Gray (1865) described the first species known from KwaZulu-Natal, *Microsaura melanocephala*, from Port Natal (Durban). Later, Boettger (1889) described a new species, *Chamaeleon caffer*, from Pondoland, now in the Eastern Cape. Power (1932) reviewed the South African dwarf chameleons and considered specimens of what is here regarded as *B. caffrum* to be *Lophosaura pumila taeniabroncha*. Later Hewitt (1935) described a new subspecies, *Lophosaura melanocephala kentanica*, from Kentani, Transkei.

FitzSimons (1942) recognised three species as occurring in KwaZulu-Natal and Transkei, these being *Microsaura melanocephala*, *M. caffer* and *M. pumila transvaalensis*. He placed *Lophosaura melanocephala kentanica* in the synonymy of *M. melanocephala*. His KwaZulu-Natal specimens of *M. p. transvaalensis* were a composite of the species now regarded as *Bradypodion dracomontanum* and *B. thamnobates*.

Hillenius (1959), in his major revision of the chameleons (excluding *Brookesia* and *Rhampholeon*), re-examined the *Chamaeleo pumilus* species group and assigned the ten recognised taxa including *melanocephalus* and *caffer* to subspecies of *Chamaeleo pumilus*. Mertens (1966) subsequently followed this arrangement in his checklist of the family.

Raw (1976) described three new species from KwaZulu-Natal. These included a member of the *caffrum* group, *Bradypodion setaroi*, from St Lucia Estuary. Two years later, he described another new species of this group, *Bradypodion nemorale*, from Qudeni Forest (Raw, 1978). Having revived *Bradypodion*, Raw (1976) preferred to regard all the described species and subspecies, as recognised by FitzSimons (1942), as full species rather than as several subspecies within a single species, *B. pumilum*. He also suggested the same treatment for *kentanicum* if that taxon was really valid and later, after collecting additional topotypic specimens, included *kentanicum* as one of the 15 described species of South African *Bradypodion* (Raw, 1995, 1997).

Klaver & Böhme (1997) provide an odd treatment of the South African taxa. They follow Hillenius (1959) and Mertens (1966) in regarding most of the taxa as subspecies of *B. pumilum*, since this is in accordance with the last comprehensive study of the "*pumilum*" group by Hillenius (1959). They do, however, regard the four most recently described by Raw, i.e., *B. dracomontanum, B. nemorale, B. setaroi* and *B. thamnobates*, as full species. Strangely, they ignored the fact that Raw (1976) had also raised *B. melanocephalum* to species level.

2 MATERIALS AND METHODS

2.1 Specimens used in study

A total of 687 preserved *Bradypodion* specimens were examined for this study. Some were borrowed from other collections while many were collected specifically for this project. The acronyms used for collections housing these specimens are listed below: -

AJL – A. J. L. Lambiris Private Herpetological Collection, Hillcrest, South Africa

AMG – Albany Museum, Grahamstown, South Africa (transferred to PEM in 1993)

BM – The Natural History Museum, London, United Kingdom

LR – L.R.G. Raw Private Herpetological Collection, Durban, South Africa and Greenford, Middlesex, United Kingdom (Note: The original catalogues of the collection were lost in transit from South Africa to the United Kingdom and only an incomplete photocopy previously provided to the former Natal Parks Board is now available. As a result collection data for specimens numbered 2671-2855 were lost except for locality data held on a separate computer database file. All data for those specimens subsequent to 2855 have been entirely lost.)

MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States of America

MMK – McGregor Museum, Kimberley, South Africa

NMP – Natal Museum, Pietermaritzburg, South Africa

NMSR – National Museums of Southern Rhodesia (now in NMZB)

NMZB – National Museums of Zimbabwe, Bulawayo (also listed as NMSR & UM)

OB – Field label for Ortwin Bourquin (most specimens subsequently deposited in TM)

PEM – Port Elizabeth Museum, Humewood, Port Elizabeth, South Africa

SAM – South African Museum, Cape Town, South Africa

TM – Transvaal Museum, Pretoria, South Africa

UM – Umtali (now Mutare) Museum (now in NMZB)

2.2 Choice of characters

The choice of suitable descriptive characters forms the basis of any taxonomic study. These may relate to external or internal anatomical morphology, cytology, biochemistry or even behaviour. The analysis of unique character states allows the diagnosis of the different Operational Taxonomic Units or OTUs (i.e., groups comprised of individuals that resemble each other on a phenetic level). Shared character states indicate the relationships of these OTUs to each other and to other related taxa and, as a result, provide some idea of their evolution. Characters that are useful for the first are usually not suitable for the second and vice versa.

In the present case the characters available have all been morphological although it has been possible to gain some insight into their relative importance from observations of behaviour (see below). Characters need to be evaluated to establish whether they are useful for delimiting taxa. Those that do not vary between taxa and those varying randomly within or between taxa will not provide useful information. By assessing the work of previous investigators, one can often establish which characters are of little use and those requiring further investigation.

Accelerated progress in taxonomy often results from the use of 'new ' or under-utilised characters (Wiley, 1981). This study has attempted to make use of 'new' characters to resolve problems encountered which could not be solved using accepted characters. The presence of allometry in the development of certain characters hampered the investigation, particularly where most of the available specimens were juvenile or sub-adult. Other specimens appeared to have retained the juvenile condition that was often more simple than that of fully developed adults.

2.2.1 Behavioural indicators of significant characters for species recognition

Personal observations of many interactions between dwarf chameleons, both in natural and captive situations, show that when male dwarf chameleons come into proximity to other chameleons of their own or other species they usually react by turning and flattening the body to give a greater lateral exposure while revealing their brightest colour patterns. They also expand their throats ventrally to expose the interstitial skin of the gular region. This action also emphasises the lobes of the gular crest. At the same time, the chameleons move the head and forepart of the body in a rhythmic lateral shaking movement (described as 'bobbing' by Burrage, 1973). While females will respond to the displays of males with corresponding head shaking, they will either darken their overall colouration to indicate a passive mating response or display an emphasised body pattern and react aggressively to drive off the approaching male.

Observations also indicate that the frequency of head shaking differs in different species. This behavioural complex stresses certain morphological characters, e.g. casque profile, body pattern, body colouration and colours of the expanded gular region, as being important species recognition characteristics. This is similar to the way differences in frog calls serve as species recognition signals in nature and also serve as convenient tools to enable taxonomists to distinguish morphologically similar species. It was interesting to observe that *Bradypodion* species appear to use lateral flattening of the body, expansion of the throat and head shaking in both male-to-male and male-to-female interactions.

In contrast, the Central African species, *Chamaeleo (Trioceros) johnstoni* uses the first two actions in male-to-male territorial interactions while head shaking is only mentioned in the male-to-female courtship behaviour. Receptive females retain their dark passive colouration while shaking their heads in response to the males' head shaking. Non-receptive females, in contrast, will expand their throats, flatten their bodies, display a warning colour pattern and rock from side to side (Annis, 1992).

While the frequency in terms of cycles per unit time could possibly be of some use in distinguishing taxa, the present study lacked the simultaneous availability of live chameleons of the various OTUs concerned and access to facilities for controlled experiments to record and make full use of this feature. The morphological characters that are emphasised in display are, nevertheless, likely to be significant as species recognition features.

2.2.2 Precedence in the use of characters

FitzSimons (1943) used a number of characters in his treatment of the taxa now referred to *Bradypodion*. These included the following: gular crest structure; casque shape; lateral cranial crests; dorsal crest structure; size of tubercles on body and tail; size and shape of tubercles on sides of throat; relative length of body compared with head-and-body length; size and arrangement of tubercles on side of body; condition of scales on top of head; head-and-body length; tail length; mandible length; head length; head width at widest point; depth of head including mandible and tibia length.

Raw (1976) commented on the paucity of reliable specific characters. He introduced the gular and dorsal counts as well as drawing attention to the gular groove colours and the casque profile in the hope of introducing characters that are more reliable. This study examined many more potential characters. These are discussed below. The problems of allometric growth and intra-population variation continue to present difficulties with many of the characters examined.

Some 685 preserved specimens of *Bradypodion* were examined and data recorded where possible for several measurements and character states. The rigid and fragile nature of many of the specimens made it necessary to measure some features using a flexible fibreglass-reinforced metric tape measure while stainless steel metric vernier slide callipers were used for the others. Counts were made using a Zeiss DR binocular dissecting microscope.

2.3 Characters used for statistical analysis

Both measurements and counts were recorded for further analysis. Details of how these data were collected are given below.

2.3.1 Measurements

Specimens were measured with either a fibreglass-reinforced tape measure (tm) or a stainless steel vernier calliper (vc). The measurements are defined and measured as follows:

Head length – distance from anterior tip of snout to posterior edge of casque (vc).
Head width – greatest width of head, usually measured across the raised tubercles of the lateral crest in the post-ocular region (vc).

Mouth length – distance from the anterior tip of snout to the posterior edge of the enlarged sub-ocular tubercle (corresponding to the posterior edge of the maxilla) (vc).

Casque height – vertical distance between a line projected posteriorly along the line of the upper lip and the highest point of the casque (vc).

Head-and-body length – distance from anterior tip of snout measured along the dorsal surface of head and body to a point directly opposite the cloaca (tm).

Tail length – distance from cloaca to extremity of tail (tm).

Because it is difficult to measure juveniles accurately and because these measurements do not contribute useful information regarding species characters, particularly since the salient features only develop with maturity, not all measurements were taken for many juvenile specimens. Head-and-body measurements at least were recorded for all except 19 of the specimens of the taxa covered in this study.

2.3.2 Scale counts

Counts were recorded for the following features: -

Gulars – all enlarged lobes and scales of the central gular crest (enlarged scales or tubercles of accessory rows were excluded).

Dorsals – all enlarged scales of the central dorsal row between the nape and the point immediately opposite to the cloaca (figure 14).

2.4 Qualitative data

Qualitative data were collected where possible; in some cases preserved specimens had already lost some significant characters such as colour, while juveniles also lack many of the features that are useful for adults. The characters examined are external and were used in diagnosing and describing taxa and in a cladistic analysis of the relationships of these species of *Bradypodion*. The plesiomorphic states (0) in the following character state list have been set in accordance with the states found in the chosen outgroup species, i.e., *C. tigris*. The apomorphic states (1, 2, 3, etc.) may either form a linear sequence (ordered character states) or be non-sequential (unordered character states, indicated below by *).

1. Snout length (distance from tip to anterior border of orbit): greater than or equal to diameter of orbit (0); less than diameter of orbit (1).

2*. Casque profile (adult) (Figure 1): slightly raised (0); distinctly raised posteriorly (1); not raised (2). Note that this feature only develops fully in mature adults.

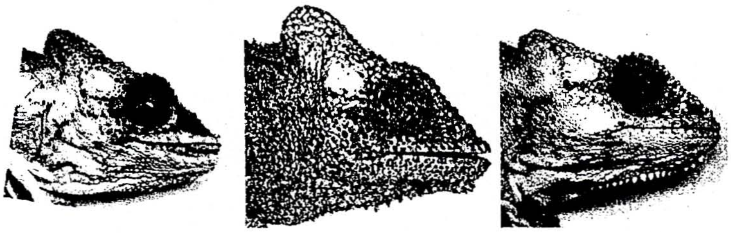


Figure 1: Examples of casque profile

3. Posterior temporal (squamosal) crest (figure 2): meets lateral parietal crest at side of casque (0); continues parallel to lateral parietal crest (1); replaces lateral parietal crest (2).

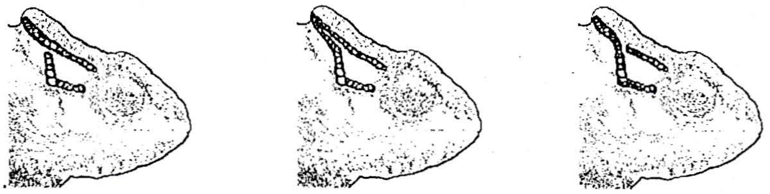


Figure 2: Variations in junction of temporal and parietal crests

4. Median parietal crest (figure 3): raised to form an abrupt-edged keel (0); raised to form a less-distinct ridge (1).

Figure 3: Location of median parietal crest

5*. Temporal crests (figure 4): distinctly developed (0); with posterior crest tubercles reduced or absent (1); lower temporal crest not or poorly developed (2); posterior crest and lower temporal crest not or poorly developed (3). (NB. Posterior tubercle of lower temporal crest is usually well developed in all cases and should not be taken into account).

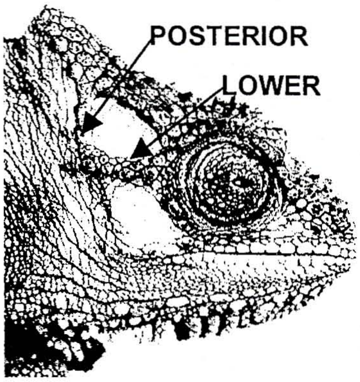


Figure 4: Location of temporal crests

(Original photograph courtesy of J.-P. Gasc, MNHN, Paris)

6. Subocular tubercle (Figure 5): not or slightly raised (0); distinctly raised (1).

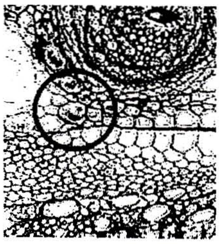


Figure 5: Location of subocular tubercle below and behind eye

7. Subocular tubercle (figure 5): does not contact mouth (0); borders mouth (1).

8*. Gular groove colour in population (on interstitial skin between scales, see figure 6): unpigmented, white or flesh coloured (0); white or yellow (in populations having both colours) (1); yellow (2); brown (3); red (4); blue-grey (5); black (6); purple-brown (7). (N.B. Needs living or freshly preserved specimens that still retain their colours.)

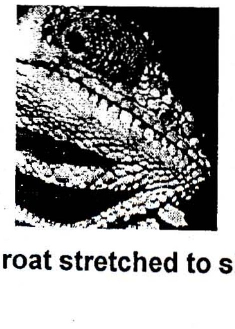


Figure 6: Skin of throat stretched to show gular grooves

9*. Gular lobes (figure 7): first or second lobes largest (0); median lobes largest (1); more or less equal in size (2).

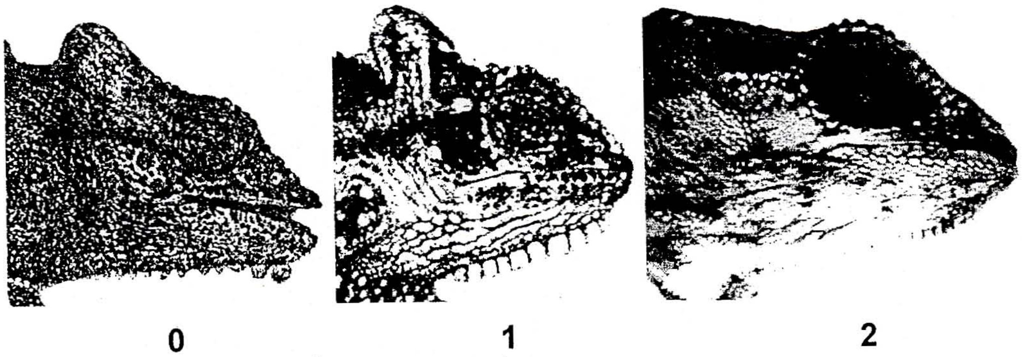


Figure 7: Examples of gular crest arrangements

10. Gular lobes (figure 8): mostly triangular (0); mostly rounded (1).

Figure 8: Examples of gular lobe shapes

11*. Gular lobe distal tip (figure 9): with denticulate edges (0); sharply papillate (1); smooth (2).

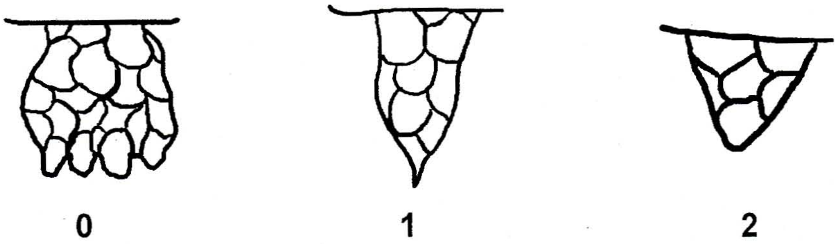


Figure 9: Examples of gular lobe distal tips

12*. Longitudinal flank grooves (figure 10): absent (0); red (1); black (2); blue (3). (N.B. Usually needs living or freshly preserved specimens that still retain their colours although black may be retained permanently.)

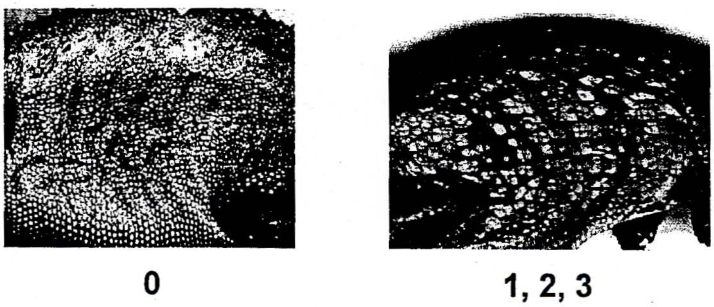


Figure 10: Longitudinal flank grooves

13. Posterior dorsolateral scales (figure 11): equal or sub equal (0); with a slightly differentiated pattern of alternating larger and smaller scales (1); with a distinct barred pattern (2).

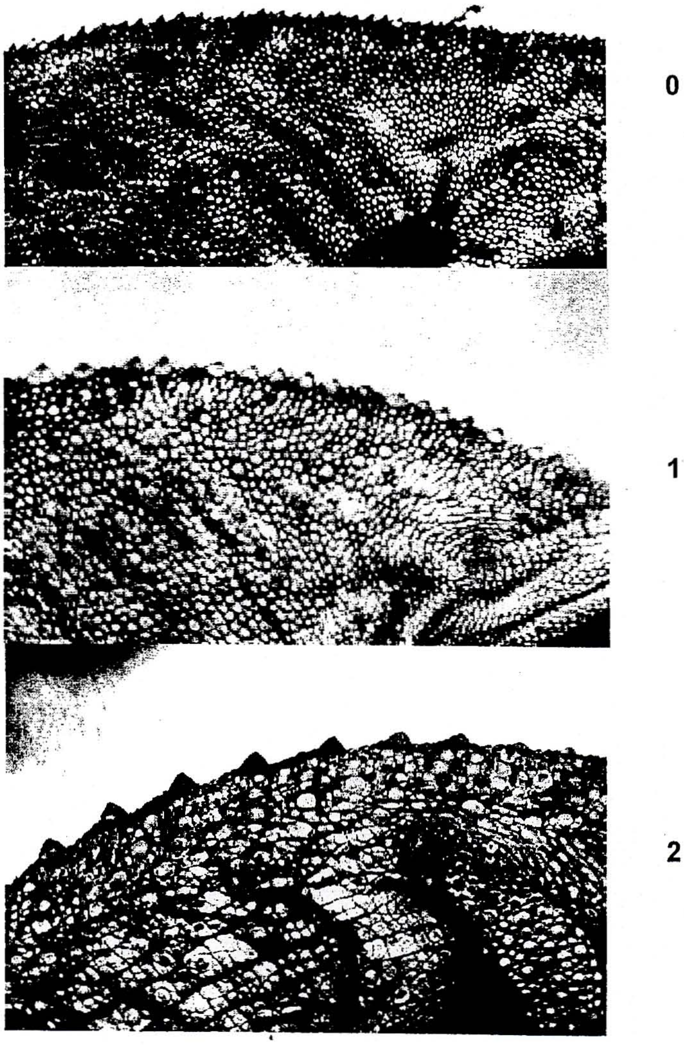


Figure 11: Posterior dorsolateral scale patterns

14. Flank tubercles: not enlarged (0); slightly enlarged (1); distinctly enlarged (2).

15. Flank tubercles: absent (0); form a single row only (1); one or two rows (2); two or more rows (3).

16. Dorsal crest: extends along tail (0); does not reach tail (1).

17. Dorsal tubercles (figure 12): form an interrupted series (0); form a continuous series without gaps between them (1).

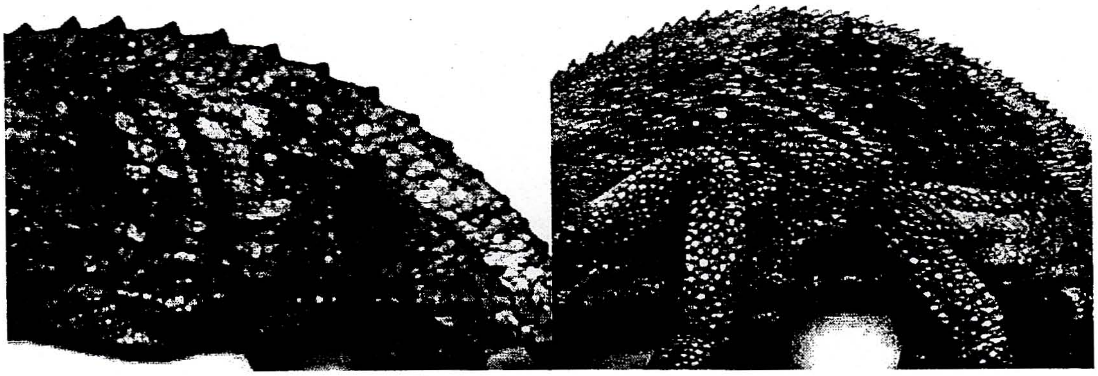


Figure 12: Examples of dorsal tubercle arrangements

18. Tail length in males: more or less equal to or less than head-and-body length (0); longer than head-and-body length (1).

19*. Head-and-body length in adults: between 75 mm and 85 mm (0); less than 75 mm (1); greater than 85 mm (2).

20. Maximum gular lobe count (figure 13): 20 or less (0); 21 or more (1).

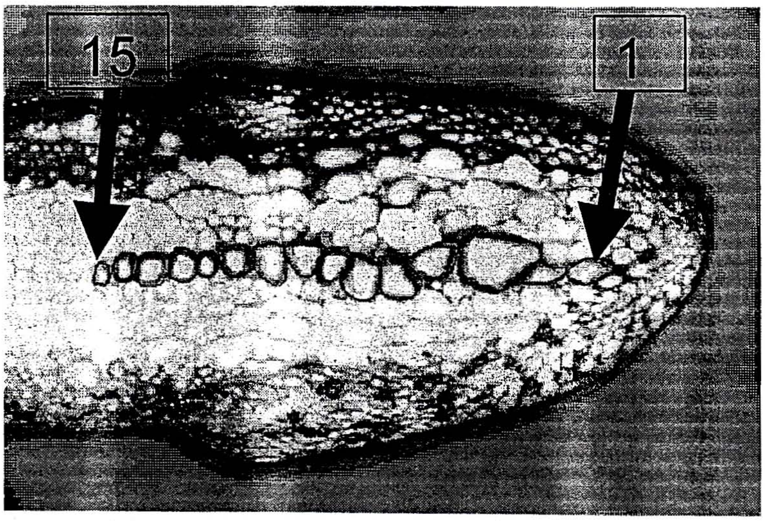


Figure 13: Counting lobes of gular crest

21. Maximum dorsal tubercle count (figure 14): 20 or less (0); 21–30 (1); 31–40 (2); 41–50 (3); 51–60 (4). (Note that the last dorsal tubercle is usually indicated by a change in size and shape of the dorsal tubercles, those of the tail differing from those of the dorsum.)

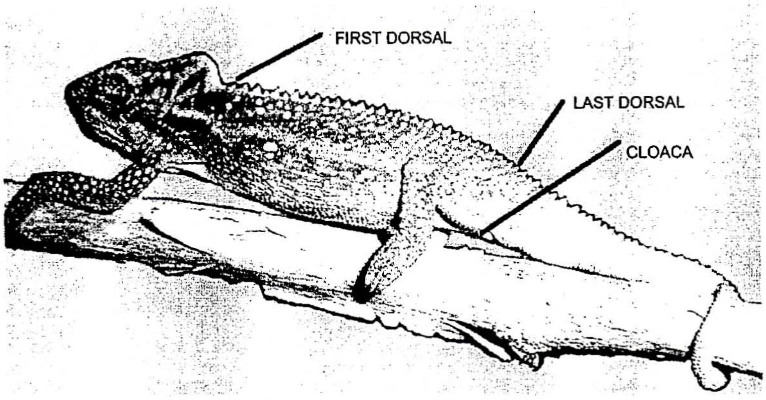


Figure 14: Limits of tubercles of dorsal crest

22. Parietal structure: parietal narrowed posteriorly, not projecting beyond juncture with squamosal, lateral processes, if present, small and confined to distal tip of parietal (0); parietal broad and rooflike, projecting beyond juncture with squamosal, lateral processes extend ventrolaterally to meet squamosal in temporal region (1).

23. Reproductive mode: oviparous (0); ovoviviparous (1).

24. Lung structure - diverticula: with at least an indication of diverticula (0); without any sign of diverticula (1). Note: Diverticula are elongate pouches or air sacs, often branched, extending from the ventral and posterior walls of the main body of the lung.

25. Lung septation: lungs without internal septa (0); lungs with short internal septa (1). Note: septa are walls of thin tissue that occur on the anterior, dorsal and ventral interior walls of the lungs.

26. General scalation: Scales homogeneous, more or less equal in size (0); Scales heterogeneous, scales often differ in size significantly (1).

27. Scales on side of body: flanks covered with irregular flat polygonal scales forming linear or island-like groupings (0); flanks covered with irregular centrally-raised polygonal scales forming linear or island-like groupings (1); flanks covered with regular centrally-raised rounded scales forming linear or island-like groupings (2); flanks covered with regular rounded granular scales distributed more or less uniformly (3).

2.5 Hemipeneal features

The descriptions of the hemipenes examined in this study basically follow the terminology developed by Klaver and Böhme (1976). Figure 15a (after Klaver & Böhme, 1986) illustrates the features and current terminology used to describe chameleon hemipenes. Figure 15b shows a posterior view of the typical *Bradypodion* hemipenes structure with short, thick hemipenes, four apical rotulae, calyculate sides and the sulcus spermaticus traversing the base posteriorly before turning abruptly lengthwise to terminate on the lateral surface below the apex. Descriptions, where available, are provided under the species descriptions as a basis for further study. Too little material was available to enable any comparative analysis of intra- or interspecific variation.

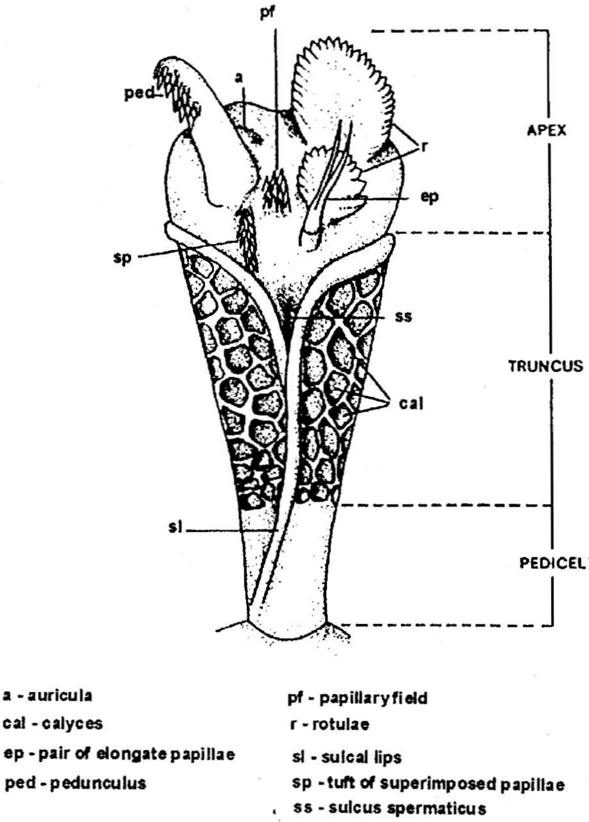


Figure 15a. Hemipeneal structures and terminology (after Klaver & Böhme, 1986)

Figure 15b: Posterior view of typical *Bradypodion* hemipenes

2.6 Geographic co-ordinates used to identify localities

Geographic localities listed in this study have been identified using a quarter-degree grid description system as follows: The location 3227AC refers to a quarter-degree cell within the degree grid cell having the top left corner with the degree co-ordinates 32° South and 27° East. Each degree grid cell is divided into 4 half-degree grid cells labelled A, B, C and D and these in turn into 4 quarter-degree cells labelled AA, AB, AC, and so forth to give a total of 16 quarter degree grid cells. The shaded cell in figure 16 below indicates the cell 3227AC, i.e., a point within the area enclosed by the co-ordinates 32° 15' 0" S and 27° 0' 0" E; 32° 30' 0" S and 27° 0' 0" E; 32° 15' 0" S and 27° 15' 0" E; and 32° 30' 0" S and 27° 15' 0" E.

The quarter-degree grid cell system forms the basis for the 1:50 000 map series for South Africa and is therefore useful for locating and mapping the distributions of organisms that occur throughout South Africa.

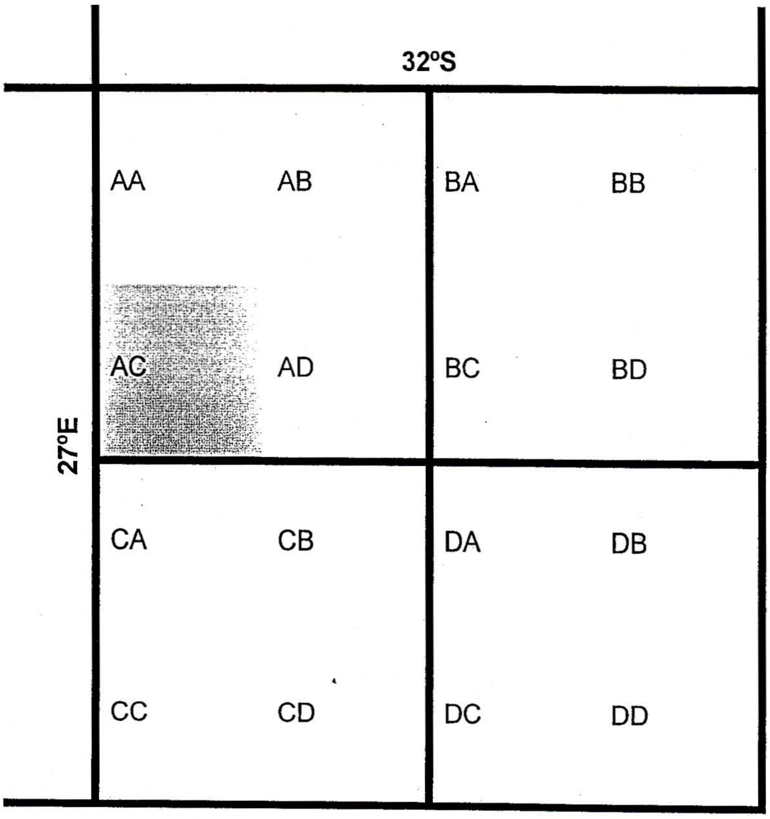


Figure 16: Codes for individual quarter degree grid cells

(Shaded cell is 3227AC)

3 TAXONOMIC ANALYSIS

3.1 Species concept and taxonomic units used for this study

The problem that requires resolution at this point does not initially concern the classification of taxa but rather the recognition of distinct taxa at the species level. In order to decide the taxonomic status of the various OTUs dealt with in this study some consideration was given to various species concepts.

Mayr (1969) distinguished three species concepts, namely the Typological, the Nominalistic and the Biological species concepts. He rejected the first two concepts and defined the Biological species as follows: "*Species are groups of interbreeding natural populations that are reproductively isolated from other such groups*". Unfortunately, this definition is beset with problems of a practical nature. In the case of the geographically isolated OTUs under consideration here, it is obvious that the populations cannot interbreed in nature since they do not come into contact but at the same time, it is impossible to predict whether they will interbreed and merge should they eventually make contact.

A further species definition is that of Wiley (1978) that is a modified version of that proposed by Simpson (1961). This states "*An evolutionary species is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate*". The second part of this definition would suggest that the OTUs considered here are more properly regarded as species. This definition has been modified yet again to allow the inclusion of clones (in asexually reproducing animals) and allopatric demes (in sexually reproducing animals) within the concept of the definition. The modified definition states "*A species is a single lineage or minimal monophyletic group of lineages of ancestor-descendant populations which maintains its identity from other such lineages or groups of lineages and which has its own evolutionary tendencies and historical fate*" (Brothers, 1985).

Paterson (1978, 1985) has proposed yet another concept, the Recognition Concept. In this case he argued that species are maintained by a common Specific Mate Recognition System (SMRS) and that speciation results from changes to this system. Paterson does not believe that changes in SMRS could result from natural selection reinforcing incipient species differences in sympatry. His definition would also include geographically isolated populations in the same species as long as they shared a common SMRS.

Ax (1987), in a detailed review of the phylogenetic system, defined the species taxon as "*being equivalent to a closed reproductive community in Nature in which evolution can occur and which, by splitting, can enter the process of phylogenesis*".

Some other Phylogenetic Species definitions have been: "*A species is a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind*" (Eldredge and Cracraft, 1980). This was later modified to: "*A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent*" (Cracraft, 1983) and *"A species is the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)"* (Nixon and Wheeler, 1990).

The interpretation of various populations as species, subspecies or merely taxonomically insignificant variants will depend on both the species concept chosen for use and the evidence available at the time. In evolutionary terms, it would seem that any isolated population acts as a species since its immediate evolutionary history, present and future, differs from that of all other populations (or species). For the purposes of this study where the identification of taxonomic diversity is a major objective, the species taxon is regarded, for practical purposes, as including any population which can be distinguished in some consistent way from other populations, whether sympatric, parapatric or allopatric. This may mean that some subspecies may be incorrectly elevated to species rank but, until more detailed studies are possible, it is not feasible to apply subspecific rank with any certainty.

In many respects this concept is very similar to the Phylogenetic Species Concept (also known as the Practical or Diagnostic Species Concept) discussed by de Queiroz & Donoghue (1988, 1990). A recent e-mail exchange with de Queiroz indicates that more recently (1998, 1999) he has argued that all modern biologists have the same general concept of species (species are segments of population level evolutionary lineages). They differ, however, with respect to the secondary criteria that they use for conferring species status on a lineage. Some use reproductive isolation between species, others the ability to diagnose the species, others ecological distinctiveness of the species, and so forth. He argues that all these properties can give evidence that entities are separate 'species, but none of them should be viewed as necessary properties of species.

In the absence of sympatric taxa, the question of the specific or subspecific status of the various OTUs is impossible to determine other than by the subjective assessment of visible differences. As the literature shows, this has resulted in conflicting views of how these species (or subspecies) should be defined (FitzSimons, 1943; Hillenius, 1959; Klaver & Böhme, 1997; Mertens, 1966; Raw, 1976).

In this study a pragmatic approach is applied which follows two basic premises. The first is that all OTUs showing either geographic or genetic isolation need to be recognised in practice if the extent of biological diversity is to be established. The second is that, if isolated taxa are to be recognised taxonomically, then the lowest taxon level that can be realistically applied is that of species. The use of subspecific rank would imply more knowledge of the relationships these taxa have with other taxa than is currently available. In any case, the use of the rank of subspecies implies that some genetic interchange is taking place, while this is patently not the present case. As with every taxonomic hypothesis the arrangement presented here will be subject to review as additional evidence becomes available.

3.2 Choice of operational taxonomic units (OTUs)

The populations under investigation occur in discrete geographical areas (Figure 17). This situation has been useful in determining operational taxonomic units for this study. Specimens from contiguous or adjacent localities were included in the same OTU unless gross morphology indicated that a different OTU was more appropriate, e.g., specimens of *B. thamnobates*, not included in this study, occur adjacent to populations of the *melanocephalum* group. The initial grouping of specimens into OTUs was by intuitive assessment of gross morphology and geographic separation. The names applied to each OTU are derived from the specific epithet of already described taxa falling within the OTU or have been coined specifically for the purpose.

Delimitation of OTUs was as follows: -

OTU 1 (*kentanicum*) – Specimens from the vicinity of Kentani, southern Transkei. This OTU resembles OTU 6 (*melanocephalum*) superficially and has white gular grooves and no lateral grooves.

OTU 2 (*wezae*) – Specimens from southern KwaZulu-Natal in the Ingeli Forest and Weza district as well as from near Port Edward (believed to have resulted from a translocation). Also fairly similar to OTU 6 (*melanocephalum*) but differs in that all specimens have red gular grooves, a character unique to this OTU. There are no lateral grooves.

OTU 3 (*melix*) – Specimens collected near Ixopo and from near Donnybrook. Very similar to the preceding OTU but has white rather than red gular grooves. There are no lateral grooves.

OTU 4 (*bourquini*) – Specimens collected from Pietermaritzburg, Hilton, Boston and Deepdale. Resembles OTU 6 (*B. melanocephalum*) but often larger. Many individuals with greenish colouration and orange tinges on the dorsal crest and some of the raised tubercles of the body, limbs and tail. This colouring is more conspicuous in males. The gular grooves are white or sometimes yellow and there are no lateral grooves.

OTU 5 (*tilburyi*) – Specimens collected from the Greytown area. Resembles OTU 4 but never with green or orange colouration. The gular grooves are white and there are no lateral grooves.

OTU 6 (*melanocephalum*) – Specimens from the Durban area, extending from Warner Beach and Amanzimtoti in the south through to Mt Edgecombe in the north. There is also a single specimen from an apparently isolated population near Darnall (Zinkwazi River). These are smaller than the preceding two OTUs with white gular grooves and no lateral grooves.

OTU 7 (*caffrum*) – Specimens collected from Port St Johns. May be distinguished by black lateral grooves and yellow gular grooves.

OTU 8 (*mkambatiense*)- A female specimen collected from Mkambati had blue gular grooves and no lateral grooves.

OTU 9 (*angustiarum*) – One female specimen collected from Oribi Gorge had brownish gular grooves and black lateral grooves.

OTU 10 (*nebula*) – Specimens from the Karkloof range north of Howick. These had yellow or white gular grooves and no lateral grooves.

OTU 11 (*nemorale*) – Specimens from the Qudeni Forest near Ekombe in Zululand. These had white gular grooves and no lateral grooves.

OTU 12 (*nkandlae*) – Specimens from the Nkandla Forest inland of Eshowe had white gular grooves and red lateral grooves.

OTU 13 (*caeruleogula*) – Specimens from the Entumeni, Dlinza and Ngoye Forests near Eshowe. This OTU is distinguished by blue gular grooves and red lateral grooves.

OTU 14 (*setaroi*) – Specimens collected from the Zululand coastal belt, from Richards Bay in the south to near Mseleni in the north. These had blue-white gular grooves and pale blue lateral grooves.

In addition to these OTUs, some specimens are not indicated on Figure 17 or assigned to any specific taxon but will be discussed after the closest related taxon. One specimen collected at Ngqeleni, Transkei, Eastern Cape closely resembles OTU 1 but was regarded by Hewitt (1935) as a possible subspecies of OTU 7. The gular grooves are white and there are no lateral grooves. One specimen collected some distance inland from Port St Johns that is similar to OTU 7 in having black lateral grooves but has white rather than yellow gular grooves. One specimen collected at Waterfall near Hillcrest by Lambiris (pers. comm.) who records that this specimen was green with orange gular grooves when living, which seems to exclude it from OTU 6. There are no lateral grooves. Specimens from Southport resemble OTU 6 but have far fewer dorsals. The gular grooves are white and there are no lateral grooves.

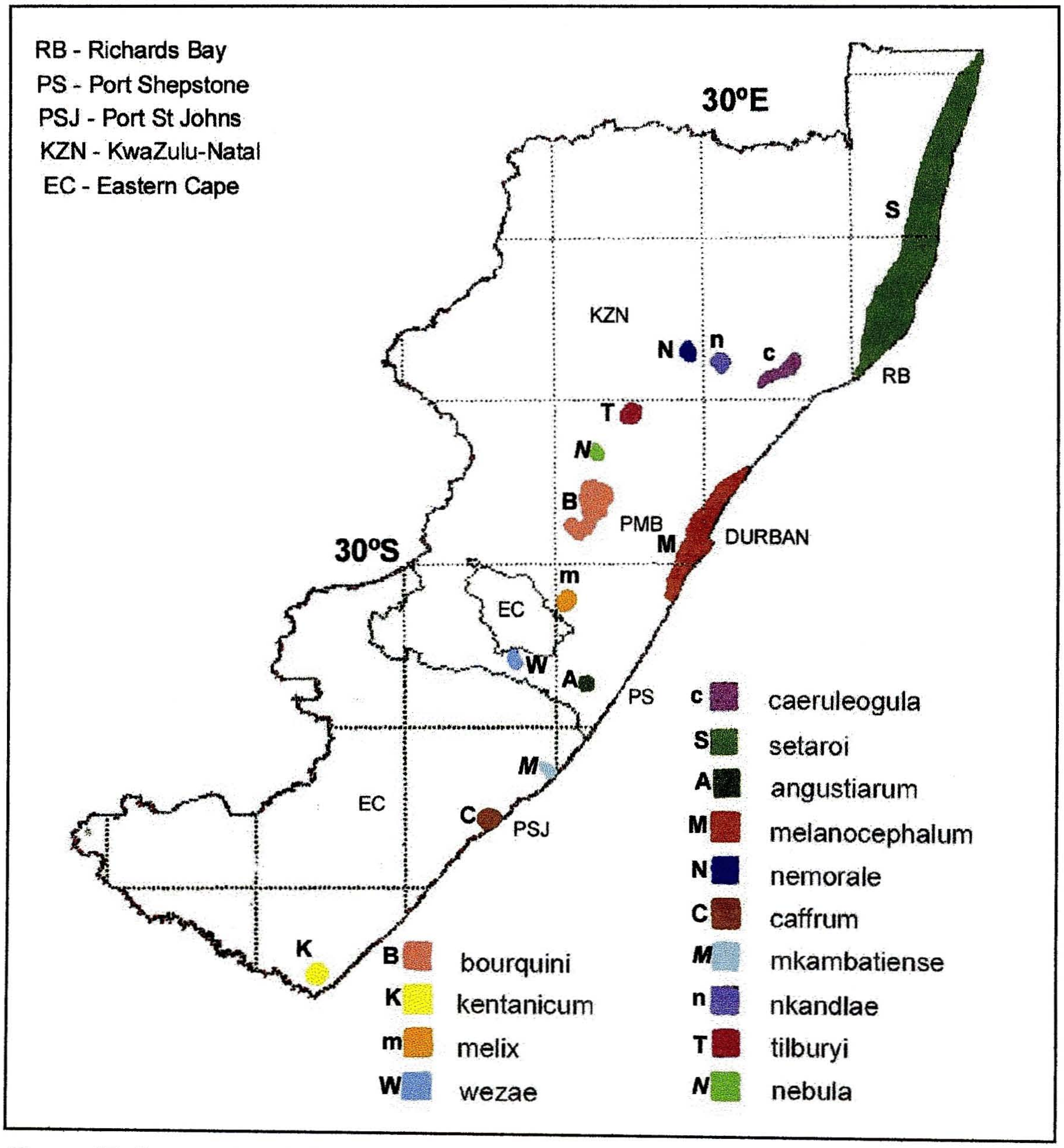


Figure 17: Geographical distribution of some *Bradypodion* taxa in eastern South Africa

3.3 Meristic data analysis

Two data sets were examined, namely, gular counts and dorsal counts. The statistical analysis of gular and dorsal counts obtained from 676 specimens of *Bradypodion* was prepared using a standard computer spreadsheet (Microsoft Excel 2000). The results are recorded in tables 1 and 2 below.

The Kraskal-Wallis H test was performed on the dorsal counts and gular counts listed in tables 1 and 2 above and included those of the undetermined OTUs. The test was used in order to determine the probability of the differences of the means between OTUs resulting by chance. The results are recorded in table 3. Note that the zero probability recorded for dorsal counts and the very low probability recorded for gular counts indicates that differences in the means of these OTUs have not resulted by chance. This non-parametric test was run using Microsoft Excel 2000 with WinSTAT version 2000.1.

Table 1: Basic statistics – gular counts of *Bradypodion* species

CHARACTER	GULARS					
STATISTIC	N	MIN	MAX	MEAN	MEDIAN	S.D.
angustiarum	1	17	17	17	17	N/A
bourquini	57	10	25	16,44	16	3,27
caeruleogula	15	14	20	16,67	17	1,85
caffrum	35	12	22	16,94	17	2,50
kentanicum	16	17	32	24,00	25	3.72
melanocephalum	62	13	24	18,26	18	2,30
melix	9	16	21	18,56	18	1,94
mkambatiense	1	14	14	14	14	N/A
nebula	18	8	16	12,56	13	2,09
nemorale	21	9	15	11,71	12	2,05
nkandlae	42	8	20	14,69	15	2,78
setaroi	57	13	25	17,70	17	2,78
tilburyi	18	10	25	17.56	19	3,99
wezae	14	15	23	20.00	21	2,42

Table 2: Basic statistics – dorsal counts of *Bradypodion* species

CHARACTER	DORSALS					
STATISTIC	N	MIN	MAX	MEAN	MEDIAN	S.D.
angustiarum	1	24	24	24	24	N/A
bourquini	57	15	57	38,95	38	7,70
caeruleogula	15	11	22	15,27	15	2,81
caffrum	35	12	20	16,09	16	1,58
kentanicum	16	40	57	48,38	49	5,80
melanocephalum	62	32	55	42,03	42	6,30
melix	9	43	55	48,56	48	3,91
mkambatiense	1	17	17	17	17	N/A
nebula	18	25	44	31,77	32	4,65
nemorale	21	14	29	21,62	21	4,43
nkandlae	42	11	28	18,02	18	4,48
setaroi	57	10	20	13,50	14	2,71
tilburyi	18	30	49	37,28	37	6,04
wezae	14	46	60	53,21	53	4,56

Table 3: Results of H-Test (Kruskal-Wallis) on dorsal and gular counts

	DORSALS		GULARS	
	N	Mean Rank	N	Mean Rank
bourquini	57	515.34	57	360.26
caffrum	35	93.92	35	395.81
caeruleogula	16	74.81	16	386.44
tilburyi	18	489.81	18	420.81
nebula	18	374.33	18	140.39
kentanicum	15	632.53	15	646.33
melanocephalum	62	562.85	62	472.37
mkambatiense	1	113.50	1	207.00
melix	9	636.56	9	495.39
nemorale	21	171.98	21	100.50
nkandlae	42	120.52	42	268.06
angustiarum	1	192.50	1	413.50
setaroi	57	52.65	57	434.72
wezae	14	661.68	14	554.46
H	Degrees of Freedom	P	Degrees of Freedom	P
566.9087249	30	0	30	5.33771E-59

3.4 Classification and relationships

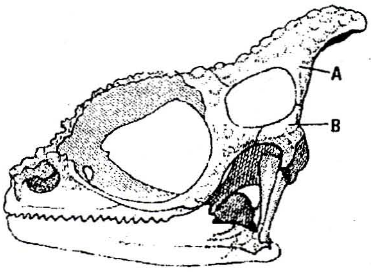
Until fairly recently, all taxonomic decisions were made on the basis of intuitive belief in the importance or irrelevance of certain characters in the assignment of taxa to groups at various levels. With the advent of simplified and speedy means of calculating complex algorithms using large data sets many taxonomists resorted to using numerical methods of preparing classifications, e.g. the 'NT-SYS' program (Rohlf, 1986). The advantage of numerical taxonomy is that, provided that as many characters as possible were used, the results should always be repeatable. However, these classifications, based on phenetic resemblances, which could reflect adaptive homoplasy rather than synapomorphy, do not necessarily reflect phylogenetic descent and evolutionary history. Other computer algorithms are available which enable taxonomists to obtain phylogenetic or cladistic classifications based on shared synapomorphy, e.g. the 'Hennig 86' program (Farris, 1988) and others. Both the phenetic and cladistic procedures produce tree diagrams that still need to be interpreted subjectively. Integrating intuitive, phenetic and cladistic information may assist in giving a more balanced evolutionary classification by combining the branching patterns of evolutionary descent with overall estimates of morphological similarity and dissimilarity.

3.4.1 Cladistic analysis

The usual procedure for undertaking a cladistic analysis of any taxonomic group is to first establish whether it is monophyletic; if this is so, to select a suite of as many characters as can be found to show different states within the group with synapomorphic or shared derived character states, allowing the assessment of relationships; and, finally, to select an outgroup to use in deciding which character states are plesiomorphic by means of the outgroup rule (Wiley, 1981).

3.4.1.1 Monophyly of the South African *Bradypodion*

While the South African species of *Bradypodion* have been characterised by their unique combination of character states (Raw, 1976) these, on their own, are not sufficient for the recognition of the genus. However, although most of the character states (e.g. scaly gular lobes, ovoviviparity) are shared with other taxa, there is one unique feature that distinguishes the genus. This is the structure of the parietal bone (A) that is produced posteriorly to form a unique roof-like casque over the back of the head. The parietal also has lateral processes that descend to meet the squamosals (B) on each side of the skull. These processes are present in the Rhynchocephalia, as well as the Iguanidae and Agamidae and may therefore be regarded as plesiomorphic. Most other chameleons have lost these processes but they are retained in *Brookesia* and a few *Rhampholeon*. *Bradypodion* differs from these latter taxa in having extended lateral processes rather than the plesiomorphic postero-lateral processes. This synapomorphic character state defining *Bradypodion* may be



stated as 'parietal broad, produced posteriorly beyond the extended lateral processes to form a roof-like bony casque with a median and two lateral crests comprised of bony tubercles'. As discussed previously, the East and Central African taxa included in *Bradypodion* by Klaver and Böhme (1986, 1997) do not have this parietal structure and instead resemble the typical chameleons in this feature and therefore should be excluded from *Bradypodion*.

3.4.1.2 Monophyly of the *Bradypodion caffrum* and *B. melanocephalum* groups

The actual monophyly of these OTUs was not originally considered when choosing to study these two groups. It was presumed (Raw, 1989) that these OTUs made up two groups of similar species, i.e., those related to and including *B. caffrum* and those related to and including *B. melanocephalum*. The chameleons that belong to these two groups, together with *B. taeniabronchum*, are the smallest in size of the *Bradypodion* taxa. Those previously considered to make up the species *B. caffrum*, *B. setaroi* and *B. nemorale* are similar in general body pattern, in having uniquely low dorsal counts and raised casques. Those previously considered to be *B. melanocephalum* are usually even smaller, have the casques of the head virtually level and undeveloped in adults, unlike any other *Bradypodion* species except *B. taeniabronchum*, while their dorsal counts are usually much higher. *Bradypodion taeniabronchum* appears to be evolutionarily distinct both in its distinctive black-lined gular grooves and its biogeographical and ecological separation from the other species considered here. It was also excluded from this study out of consideration for an independent study being carried out on its taxonomy by Dr W.R. Branch of the Port Elizabeth Museum (Branch, 1988b). Ecologically, the *B. caffrum* relatives tend to be associated with forest canopy or high forest while those related to *B. melanocephalum* favour forest ecotones, shrubs and tall grass or reedbeds and do not seem to enter high forests. So, while these two groups of dwarf chameleons are probably closely related and likely to form two monophyletic lineages, there was no formal evidence of their joint monophyly in the form of obvious shared derived character states, although their position as members of a monophyletic *Bradypodion* in the strict sense proposed here is not questioned.

3.4.1.3 Choice of outgroup

The use of a closely related outgroup is useful as it allows the determination of plesiomorphic character states, those shared with the outgroup being regarded as plesiomorphic within the ingroup. In this case, the species *Calumma tigris* has been chosen on the basis of an earlier study on the influences of outgroup selection (Raw & Brothers, 1994). In that study it was found that, when this species was used as an outgroup to *Bradypodion*, the trees produced were always shorter and therefore more parsimonious than those produced using any of the other putatively suitable outgroup species.

3.4.1.4 Cladistic analysis

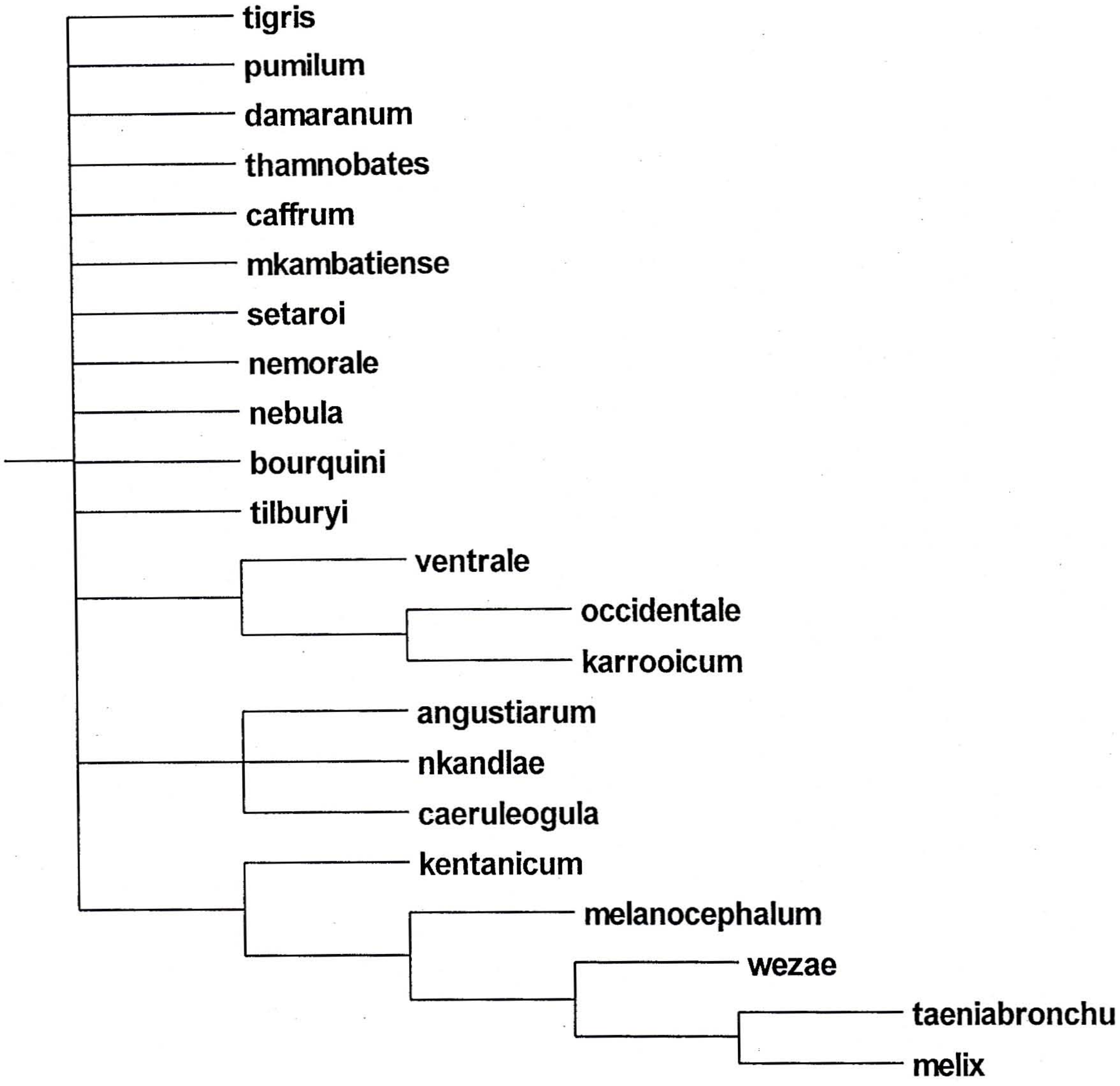
The data for each OTU (table 4) were determined using the character-state list in section 2.3.1 above. These were analysed using the computer program 'Hennig 86' (Farris, 1988). The *mhennig** and *bb** tree-calculating commands were used after setting characters 2, 5, 8, 9, 11, 12, and 19 to non-additive, while the rest were treated as additive.

Table 4: Taxon character state codes used for cladistic analysis

Characters:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
C. tigris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. pumilum	1	1	1	0	0	0	1	2	0	1	0	0	2	1	3	1	0	1	2	1	3	1	1	1	1	1	2
B. ventrale	0	0	1	1	0	0	0	2	0	1	0	0	2	2	3	1	0	0	2	1	2	1	1	1	1	1	2
B. occidentale	0	2	1	1	0	0	0	7	0	0	0	0	1	2	3	1	0	0	1	1	2	1	1	1	1	1	2
B. karrooicum	0	2	1	1	0	1	0	2	0	0	2	0	2	2	3	1	0	0	2	1	2	1	1	1	1	1	2
B. damaranum	0	1	1	0	0	0	1	0	0	1	0	0	2	1	1	1	0	1	2	0	2	1	1	1	1	1	2
B. thamnobates	1	1	2	0	0	0	1	0	0	1	2	0	1	2	2	1	0	1	2	0	3	1	1	1	1	1	1
B. taeniabronchum	1	2	0	1	1	0	0	6	0	0	1	0	0	0	0	1	1	1	1	1	4	1	1	1	1	1	3
B. caffrum	0	1	0	0	1	0	1	2	0	1	0	2	1	2	2	1	0	1	0	1	0	1	1	1	1	1	0
B. mkambatiense	0	0	0	0	0	0	1	5	0	1	0	0	2	1	1	1	0	-	1	0	0	1	1	1	1	1	2
B. angustiarum	0	0	2	0	3	0	1	3	2	1	2	2	1	1	1	0	0	-	1	0	1	1	1	1	1	1	1
B. setaroi	0	0	1	0	0	0	1	0	1	0	0	3	2	1	1	0	0	1	1	1	0	1	1	1	1	1	0
B. nemorale	0	1	1	0	0	0	0	0	2	1	2	0	1	1	1	1	0	-	1	0	1	1	1	1	1	1	1
B. nkandlae	0	0	2	0	3	0	0	0	2	1	2	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1
B. caeruleogula	0	0	2	0	3	0	0	5	2	1	2	1	0	1	1	0	0	1	1	0	1	1	1	1	1	1	0
B. nebula	0	0	2	0	1	1	0	1	2	1	2	0	1	1	1	1	0	1	1	0	3	1	1	1	1	1	2
B. melanocephalum	0	2	0	0	3	0	0	0	2	0	2	0	0	2	1	1	0	1	0	1	4	1	1	1	1	1	3
B. bourquini	0	2	1	0	0	0	1	1	1	1	0	0	1	1	1	1	0	1	0	1	4	1	1	1	1	1	2
B. tilburyi	0	2	2	0	0	1	1	0	2	0	2	0	0	0	0	1	0	1	0	1	3	1	1	1	1	1	1
B. kentanicum	0	2	1	0	1	0	1	0	2	0	2	0	0	1	1	1	1	1	0	1	4	1	1	1	1	1	3
B. wezae	0	2	0	0	1	0	0	4	2	0	2	0	0	1	1	1	1	0	1	1	4	1	1	1	1	1	3
B. melix	0	2	0	1	1	0	0	0	2	0	2	0	0	1	1	1	1	1	1	1	4	1	1	1	1	1	3

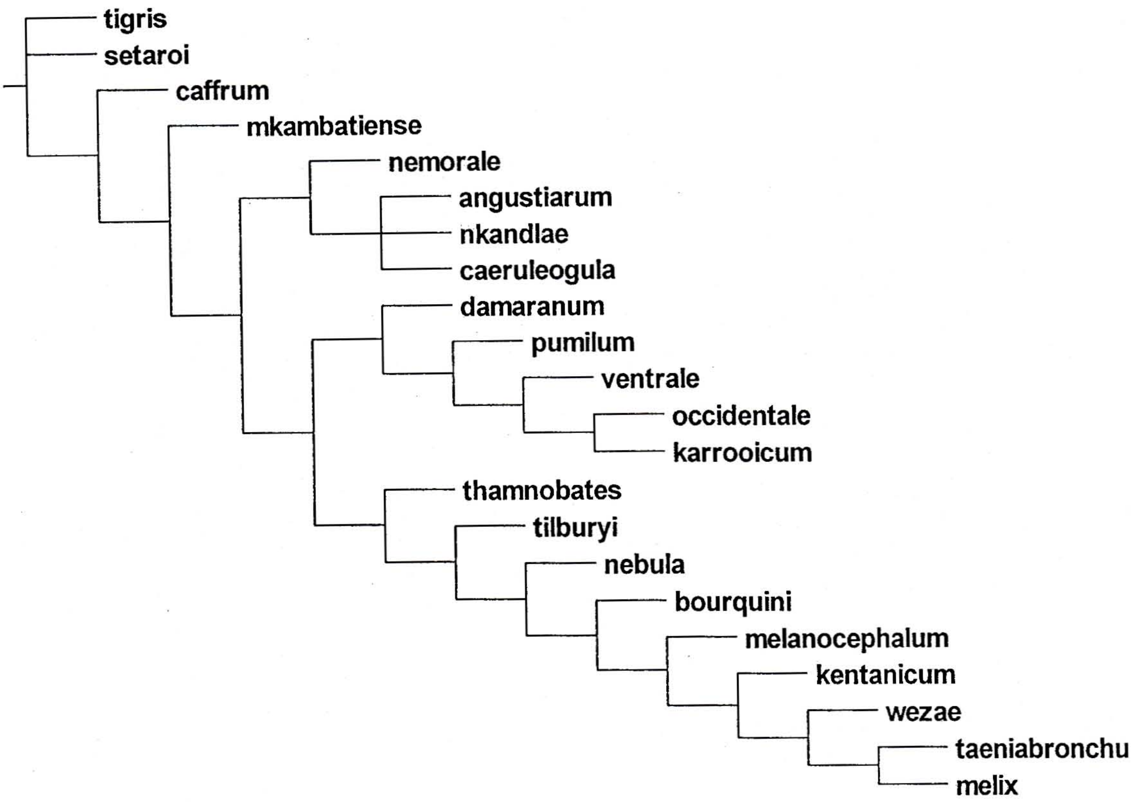
In the first iteration, 303 most-parsimonious trees were found. Tree statistics are: length = 118, CI = 42 and RI = 62. A strict-consensus tree was derived from these 303 trees using the *nelsen* command, to generate Tree 1.

Successive-approximations character weighting was applied (command *xs w*) until a stable result was obtained after 5 iterations. This resulted in a total of 3 trees of equal shortest weighted length. Tree statistics were length = 257, CI = 62 and RI = 78. The length of these trees after resetting the character weightings back to 1 is 120. A further strict-consensus tree was then generated (Tree 2). The tree files were viewed and plotted using the program Winclada (Nixon, 1999).



Tree 1: Strict-consensus tree based on the 303 most-parsimonious trees found.

Tree 1 does not provide an informative picture of the relationships of these chameleons. Although based on the most parsimonious trees found in the analysis, it has the fault that the relationships of 11 of the species are totally unresolved. Also, while the others form 3 monophyletic groups, one of these is still a trichotomy.



Tree 2: Strict-consensus tree from successive-approximations character weighting.

Tree 2, although based on trees that were 2 steps longer and therefore not the most parsimonious, is much better resolved, with only 2 trichotomies. This tree is likely to be further improved through the addition of further characters and taxa to the data matrix as more information becomes available. Nevertheless, it seems suitable as a best first approximation. It shows great similarities to Tree 1 in the clades resolved, with only *B. melanocephalum* and *B. kentanicum* having their relative positions on the one tree reversed on the other.

The results of this analysis must be regarded as very preliminary and were not essential to the delimitation of the new taxa proposed in this study. However, they do give an indication of possible relationships and evolutionary pathways and provide an indication as to which characters will need to be re-evaluated during a revision of the entire genus.

One significant outcome of this analysis is that neither of the species-group hypotheses of Raw (1989) or of Branch (1988b) appears to be supported.

4 SYSTEMATIC ACCOUNT

4.1 Classification of taxa

4.1.1 Status and composition of *Bradypodion*

As detailed above in Chapter 1, the revival of *Bradypodion* as a distinct genus by Raw (1976) has been generally accepted. Klaver & Böhme (1986 & 1997) subsequently extended the genus to include several east and central African species. This decision needs further evaluation.

Examination of specimens of "*Bradypodion*" *f. fischeri*, *f. multituberculatum*, *tavetanum* and *mlanjense* showed that the external morphology of these species has little in common with that of the South African *Bradypodion* species. In particular they lack the broad roof-like parietal of typical *Bradypodion* and instead resemble *Chamaeleo* in this feature. Descriptions in the literature of other species assigned to *Bradypodion* by Klaver & Böhme (1986, 1997) appear to confirm these observations. As a result it is considered that the genus *Bradypodion* should be restricted to the South African species allied to *pumilum*. The synapomorphies regarded as diagnosing the genus are as follows:

(1) Broad, roof-like parietal with lateral processes and pointed posterior extension of the casque beyond the parieto-squamosal intersection (although it may be argued that a broad parietal with lateral processes is plesiomorphic, the roof-like posterior extension is unique);

(2) Ovoviviparous mode of reproduction (considered here to be independently derived from that found in *Chamaeleo (Trioceros) jacksonii* and its subspecies, the members of the *C. (T.) bitaeniatus* group and *C. (T.) fuelleborni* (Davison, 1997) and its relatives); and

(3) The presence of a gular crest consisting of scaly lobes (the single anterior lobes found in *Calumma tigris* and the multiple lobes of *Chamaeleo (Trioceros) eisentrauti* appear to have evolved independently).

In contrast, the east and central African species included in *Bradypodion* by Klaver & Böhme show the following characteristics:

(1) Skull has narrow parietal without lateral processes and with the parieto-squamosal intersection at the posterior tip of the parietal in the typical arrangement found in *Chamaeleo s.s.*;

(2) In those species in which reproduction is known, e.g., *Bradypodion fischeri* and *B. tavetanum* (Schmidt, Tamm & Wallikewitz, 1994; Le Berre, 1995; Davison, 1997), *B. tenue* and *B. xenorhinum* (S. James & E. J. Edwards, pers. com.), this is oviparous rather than ovoviviparous. Nečas (1999) also records all of the east African species included in *Bradypodion* as egg-laying.

(3) All these species lack the typical gular crest arrangement of the southern African species and, moreover, do not possess any form of gular crest.

Considering the above factors, the decision to add the East and Central African taxa appears to be unjustified since including these species does not produce a monophyletic assemblage. Broadley (2000, pers. com.) has suggested that these species are more appropriately included in the Madagascan genus *Furcifer* due to the resemblances between the species *Furcifer bifidus* and *Bradypodion fischeri multituberculatum.* This does not seem particularly appropriate for the species "*Bradypodion*" *tenue* and *oxyrhinum*, which appear to show closer affinities with *Calumma nasutus* and its relatives. For the moment this may be a solution but I suspect that this old radiation of east and central African chameleons may eventually be placed in more than one new genus.

4.1.2 Species groups

The species of *Bradypodion* in South Africa may be classified into a number of morphologically similar and geographically cohesive groups. These are as follows: -

"*Pumilum"* group – comprising *B. pumilum* and probably some undescribed allies occurring in the southwest Western Cape province (Raw, 1995). These are essentially fynbos species.

"*Damaranum*" group – consists of the single species *B. damaranum*. This species is found only in the Knysna forest region.

"*Ventrale*" group – comprising *B. ventrale, B. gutturale, B. occidentale* and *B. karrooicum*, These species occur in dryer areas than the other members of *Bradypodion* and occur along the western littoral of the Western and Northern Cape provinces, in the mountains to the interior, in the dry valleys of the Cape fold mountains and Karoo, in the drier fynbos of these mountains, in the valley bushveld of the Eastern Cape and even in parts of highland sourveld of Transkei (Branch, 1988; FitzSimons, 1943; and personal observation).

"*Taeniabronchum*" group – consisting of *B. taeniabronchum* and a recently discovered undescribed species (Branch, 1988). These are poorly known but appear to occur in montane fynbos on the mountains just south of Port Elizabeth (Branch, 1981, 1988).

"*Transvaalense*" group – contains *B. transvaalense, B. dracomontanum, B. thamnobates* and perhaps nine additional new species (Jacobsen, 1990). These species are essentially associated with the Drakensberg escarpment from southern KwaZulu-Natal in the vicinity of Underberg northwards through Swaziland and Mpumalanga to the northeastern Northern Province. *Bradypodion thamnobates* is found at somewhat lower altitudes in the KwaZulu-Natal Midlands (Raw, 1976). Specimens resembling but not identifiable with *B. thamnobates* were discovered in southern KwaZulu-Natal during the fieldwork for this study.

The following two groups form the subject of this study and are therefore accorded a more detailed treatment than those above.

"*Caffrum*" group – including *B. caffrum, B. setaroi, B. nemorale* and some undescribed new species (Raw, 1995). This group is found in coastal and riverine forests associated with the Pondoland Plateau Sourveld in Transkei and southern KwaZulu-Natal and also in both the higher forests of the Zululand Mistbelt and the dune forests of the northeastern coast.

"Melanocephalum" group – includes *B. melanocephalum* and *B. kentanicum* and is found from the Kentani area in the south northwards through the KwaZulu-Natal Midlands to at least Greytown and along the coast to the Sinkwazi River. At present the known populations of the *melanocephalum* group comprise the populations occurring around Pietermaritzburg and along the coast north and south of Durban, currently referred to *B. melanocephalum*, and isolated populations in southern Transkei at Kentani and Ngqeleni referred to *B. kentanicum* (Raw, 1976). Other more recently discovered populations represent additional undescribed species (Raw, 1995). The type species is restricted to low altitudes, usually not higher than 100 metres, on the central KwaZulu-Natal coastal belt. The other species are found in higher altitudes in forests along the escarpment that lie at approximately 1000 metres a.s.l. from south of the Tugela River through the KwaZulu-Natal Midlands south into the Transkei region of the Eastern Cape where they occur at lower altitudes. Similar specimens have been found at Southport.

Additional populations in other localities seem possible. Further areas that need to be investigated include a number of isolated forests along the Drakensberg escarpment and the fringes of the Tugela basin. The absence of these chameleons from apparently suitable areas such as Kloof and Hillcrest (except for a single specimen from Waterfall) as well as Vernon Crooks Nature Reserve, as shown by Bourquin & Sowler (1980), remains a biogeographical puzzle.

4.2 Identification key to known species of *Bradypodion*

(Note. This key should only be used to identify living or freshly preserved specimens that still retain their colours. The presence of additional, as yet undescribed, taxa could lead to incorrect determinations.)

1 Casque low and strongly produced posteriorly.. **2**
Casque not strongly produced posteriorly relative to height.. **5**

2 Posterior temporal crest replaces lateral parietal crest at side of casque..................... **3**
Posterior temporal crest does not replace lateral parietal crest.................................... **4**

3 Gular grooves coloured purple-brown; gular lobes usually large, very broad anteriorly. .... ***occidentale***
Gular grooves coloured orange-yellow; gular lobes small to moderate, narrower to just wider than long anteriorly .... ***karrooicum***

4 Gular lobes broader than long, in a single row .... ***ventrale***
Gular lobes longer than broad, spiny, in more than one row .... ***gutturale***

5 Casque with parietal strongly raised posteriorly **6**
Casque with parietal not or feebly raised posteriorly **14**

6 Larger chameleons, adults with head and body length over 75 mm **20**
Smaller chameleons, adults with head & body length less than 75 mm **7**

7 Flanks with irregular longitudinal grooves **8**
Flanks without irregular grooves **9**

8 Flank grooves coloured blue .... ***setaroi***
Flank grooves coloured red or black **11**

9 Subocular tubercle not or only slightly raised; throat grooves white or dark blue-grey ... **10**
Subocular tubercle distinctly raised; throat grooves yellow to white .... ***nebula***

10 Throat grooves white .... ***nemorale***
Throat grooves blue-grey .... ***mkambatiense***

11 Grooves on flanks of body black **12**
Grooves on flank of body red **13**

12 Throat grooves yellow .... ***caffrum***
Throat grooves brownish .... ***angustiarum***

13 Throat grooves white .... ***nkandlae***
Throat grooves dark grey-blue .... ***caeruleogula***

14 Throat grooves coloured red or black **15**
Throat grooves unpigmented (white or flesh-coloured) or, rarely, yellow **16**

15 Throat grooves coloured red .... ***wezae***
Throat grooves coloured black .... ***taeniabronchum***

16 Posterior temporal crest continues parallel to lateral parietal crest.............................. **17**
Posterior temporal crest does not continue parallel to lateral parietal crest................ **18**

17 Both temporal crests distinctly developed .... ***kentanicum***
Posterior temporal crest with tubercles reduced or absent .... ***bourquini***

18 Posterior temporal crest replaces lateral parietal crest .... ***tilburyi***
Posterior temporal crest meets lateral parietal crest at side of casque........................ **19**

19 Both temporal crests distinctly developed .... ***melanocephalum***
Posterior temporal crest with tubercles reduced or absent .... ***melix***

20 Throat region coloured white, without markings, cranial crests horn yellow **21**
Throat region not white or with markings, cranial crests not horn yellow.................... **22**

21 Posterior temporal crest meets lateral parietal crest .... ***transvaalense***
Posterior temporal crest replaces lateral parietal crest .... ***thamnobates***

22 Area around base of forelimb covered with smooth skin............................ ***damaranum***
Area around base of forelimb not covered with smooth skin.. **23**

23 Posterior temporal crest continues parallel to lateral parietal crest..... ***dracomontanum***
Posterior temporal crest replaces lateral parietal crest .... ***pumilum***

4.3 Species accounts

The accounts that follow include the re-description in a standardised format of several described species of *Bradypodion* together with the descriptions of several new taxa that have been discovered during the course of investigations into this fascinating genus of chameleons.

4.3.1 *Bradypodion caffrum s.l.*

The following taxa include *Bradypodion caffrum* and several other taxa that show some resemblance to *Bradypodion caffrum.* These taxa appear to occur from Port St Johns (or possibly Dwesa) in the south through to Oribi Gorge in the north. There are possible sight records from Dwesa (H. Thomas, 1994, pers. com.) and Mbotyi (I. Hertogs, 1985, pers. com.). It seems that suitable habitat exists near Lusikisiki while chameleons, possibly of this group, have been reported from Flagstaff (Z Mgeyene, 1992, pers. com.).

4.3.1.1 *Bradypodion caffrum* (Boettger, 1889)

Chamaeleon caffer Boettger, 1889: 292.

Lophosaura pumila taeniabroncha (Smith); Power, 1932: 215-216. (Part, Port St. Johns specimens).

Lophosaura caffer (Boettger); Hewitt, 1935: 300, pl. XXVIII, figs. 1, 4 & 6; Hewitt, 1937: II, 27, text-fig.

Microsaura caffer (Boettger); FitzSimons, 1943: 161-162. (Port St Johns specimens.)

Chamaeleo pumilus caffer (Boettger); Hillenius, 1959: 56-64; Mertens, 1966: 23.

Bradypodion caffrum (Boettger); Raw, 1976: 149.

Bradypodion caffer (Boettger); Klaver & Böhme, 1986: 59.

N.B. Power (1932) misidentified a specimen from Dargle as *Lophosaura caffer* (Boettger, 1889). This specimen is a member of the subsequently described *Bradypodion thamnobates* Raw, 1976.

Holotype:

Not located, presumed lost (FitzSimons 1943). Over 50 years later the specimen had still not been located (Klaver & Böhme, 1997). Recent communications with the curators of the Senckenberg Museum, Frankfurt am Main (Gunther Köhler, March, 2001) and Humboldt Museum, Berlin (Rainer Günther, April, 2001) herpetological collections have confirmed that neither collection presently has the type specimen. There is also no record of the specimen ever being deposited in either of these collections or in any other collection.

Neotype:

In order to stabilise this name with the species most associated with it, a specimen in the Transvaal Museum collection, TM 15015 from Port St Johns, Transkei, Eastern Cape, South

Africa, (pres. A.O.D. Hogg, 25 January 1933) is here designated as the neotype (figure 18). Hewitt (1935, plate XXVIII, fig. 4 and 1937, illustration on p. 28) and FitzSimons (1943, plate XX, fig. 4) have both illustrated this specimen as representing this species.

Type locality:

Pondoland, here restricted to the vicinity of Port St Johns, Umzimvubu River Mouth, Transkei, Eastern Cape, South Africa.

Diagnosis:

A medium sized, fairly slender species with a high casque, yellow gular grooves and black lateral flank grooves.

Description:

Snout sharp, distance from tip to anterior border of orbit greater than diameter of orbit. Casque distinctly raised; not produced posteriorly; median parietal crest convex. Posterior temporal (squamosal) crest replaces lateral parietal crest at side of casque; median parietal crest raised to form an abrupt-edged keel; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests distinct with the posterior tubercle of the lower temporal crest very distinct. Subocular tubercle slightly raised, not bordering mouth. Interstitial skin of gular grooves coloured yellow. Gular lobes with first and second lobes larger than remaining lobes. Gular lobes mostly rounded, distal tips with denticulate edges. Flanks have black longitudinal grooves or striations. Posterior dorsolateral scales form a distinct barred pattern of alternating larger and smaller scales. Flank tubercles enlarged, forming a single row. Dorsal crest extends along tail; tubercles strongly differentiated to form a very distinct pattern. Tail length more or less equal to head-and-body length in males, less to much less in females, slender without a distinct tip region.

Counts:

Gular lobe range: 12-22 (mean 16,94, median 17).

Dorsal tubercle range: 12-20 (mean 16.09, median 16).

Measurements:

Largest male (MMK unlabelled) : head and body length 78 mm and tail length 81 mm.

Largest female (MMK unlabelled): head and body length 84 mm and tail length 65 mm.

Mass:

LR 2753 had a live mass of 6,7g and LR 2750 a live mass of 4,4g.

Hemipenes:

Everted left hemipenis of LR 1801 short, broadening towards apex. Four inward curving, denticulate rotulae on apex grouped in anterior and posterior pairs. The outermost of each pair is largest. A small spiny ridge lies between the anterior rotulae. Basal surfaces smoothly calyculate. Sulcus spermaticus passes along posterior base of organ before turning sharply length-wise between enlarged, fleshy lips to end on outer side of organ. Right hemipenis not everted.

Colouration in life (see figure 19):

Light grey with variable darker hourglass markings on flanks, black longitudinal striations on flanks, interstitial skin of gular grooves coloured yellow.

Reproduction:

Live-bearing, LR 2750 contained 12 embryos and LR 2753 contained 13 embryos.

Field notes:

Specimens were seen during the day at the caravan park at Second Beach, Port St Johns. Individuals were extremely wary and hid by moving to the opposite side of the branch or twig to which they were clinging in order to keep out of sight of intruders. Night searches at Port St Johns and the neighbouring area showed that this species tends to sleep high in the canopies of trees. This species was presumably abundant in the past since Power was able to collect 24 specimens on one occasion prior to or during 1935 and 21 on another during January 1937.

Distribution:

Known only from the immediate vicinity of Port St Johns, Transkei (figure 20). Reports from Mbotyi (I. Hertogs, 1985, pers. com.) and Dwesa (H. Thomas, 1994, pers. com.) may involve this species but remain unconfirmed.

Recorded localities and specimens examined:

Thirty-seven specimens were examined from:

Port St Johns (3129DA): AMG 7095 (2 specimens, no other data), LR 1909 (coll. C.R. Tilbury, 2 November 1980); MMK F807 (24 specimens, coll. J.H. Power, note: Hewitt, 1935, refers to these specimens as "recently collected".); SAM 5998, 5997; TM 15015 (pres. A.O.D. Hogg, 25 January 1933), OB n/n (2 specimens, coll. O. Bourquin).

Port St Johns, 5km S (3129DA): LR 1801 (coll. L.R.G. Raw, 29 November 1982); LR 2753, 2758, 2795 & 2796 (coll. L.R.G., L.A. & D.R.J. Raw, December 1991).

Additional records:

Twenty-one specimens collected by J.H. Power in January 1937 from Port St Johns are in the collection of the Museum of Comparative Zoology, Harvard, Boston, U.S.A. but have not been examined. These are specimens MCZ R-42630-33 and MCZ R-162340-56.

Etymology of specific name:

The original specific name *caffer* refers to the region east of the Cape Colony that was known as Kaffraria (land of the Kaffirs) in earlier times. The word is an adjective, meaning "pertaining to the Kaffirs" or "from Kaffraria", with the various gender renderings of *caffer* (m), *caffra* (f) and *caffrum* (n) (Brown, 1956). However, Power (1932), Hewitt (1935, 1937), FitzSimons (1943) and Klaver & Böhme (1997) treated the name, incorrectly, apparently as a noun in apposition, with the feminine genera *Lophosaura* and *Microsaura* and the neuter genus *Bradypodion*.

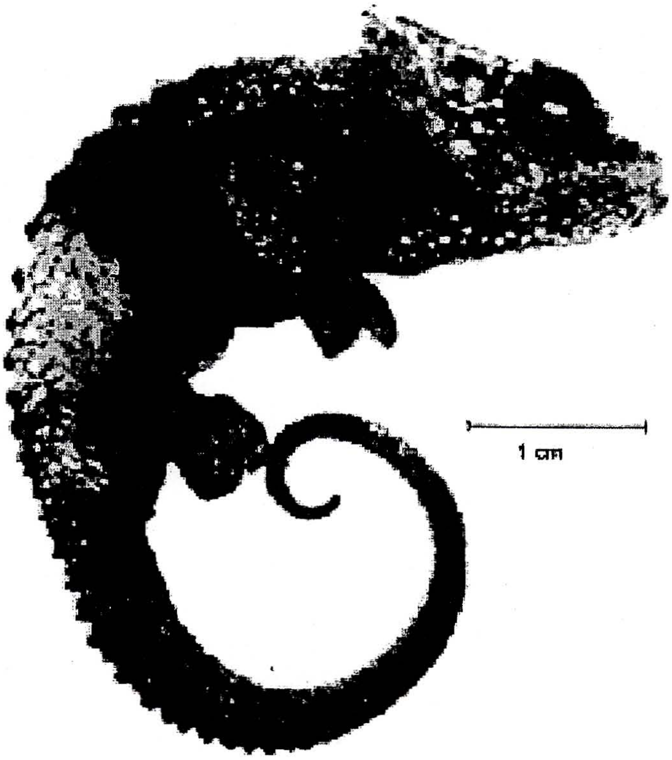


Figure 18: Neotype of *Chamaeleon caffer* Boettger, 1889
TM 15015 from Port St Johns (after FitzSimons, 1943).

Figure 19: *Bradypodion caffrum* from Second Beach, Port St Johns

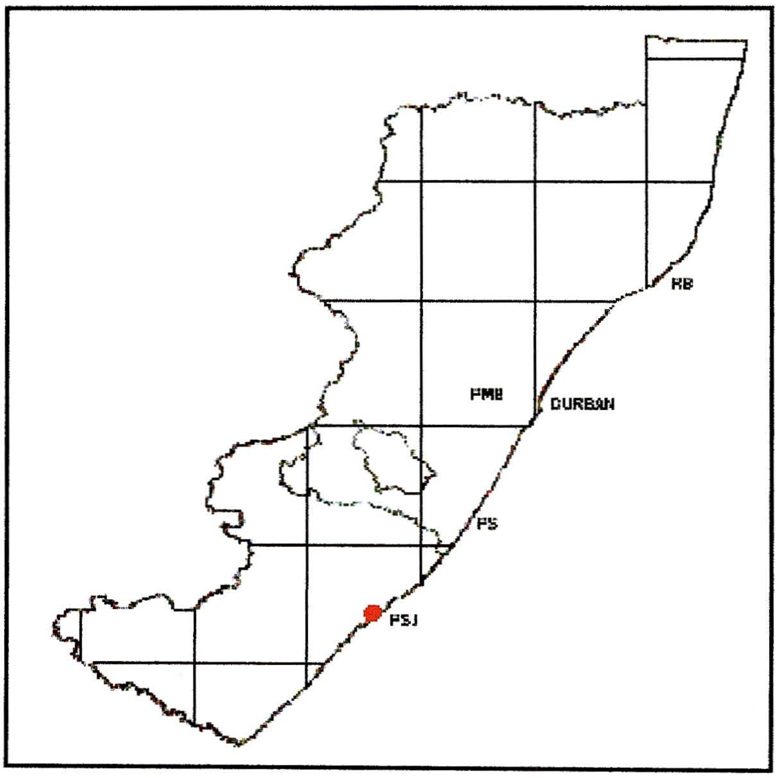


Figure 20: Distribution of *Bradypodion caffrum*

4.3.1.2 *Bradypodion mkambatiense* new species

Holotype:
Adult female, LR 2857, collected on 8 September 1991 from leafy forest canopy within river gorge by Wayne T. Vos, Trevor Edwards and Lynn R.G. Raw (figure 21).

Type locality:
Umtentu River Gorge, Mkambati Game Reserve, Transkei, Eastern Cape, South Africa (3129BD).

Diagnosis:
A small, slender dwarf chameleon distinguished by the dark blue-grey gular grooves and the lack of longitudinal grooves on the flanks.

Description:
Snout sharp, distance from tip to anterior edge of orbit less than diameter of orbit from. Casque is slightly raised; not strongly produced posteriorly and with median parietal crest straight. Posterior temporal (squamosal) crest continues parallel to lateral parietal crest at side of casque. Median parietal crest is raised to form an abrupt-edged keel and para-parietal tubercles are present anteriorly. There is a distinct parietal organ. Inter-orbital tubercles are present, but not pronounced. Lower temporal crest is distinctly developed but the posterior temporal crest tubercles are reduced. Subocular tubercle is not raised, slightly convex and borders mouth. Colour of interstitial skin of gular grooves is blue-grey. Gular lobes have first and second lobes larger than the remaining lobes. Gular lobes are mostly rounded, distal tip with denticulate edges. Flanks do not have longitudinal grooves or striations. Posterior dorsolateral scales form a distinct barred pattern of alternating larger and smaller scales. Flank tubercles slightly enlarged; forming an indistinct single row. Dorsal crest extends along tail; tubercles strongly differentiated to form a very distinct pattern. Tail length is less than head-and-body length; tail form slender without distinct tip region.

Counts:
The holotype has 14 gular lobes and 17 dorsal tubercles.

Measurements:
The holotype has a head-and-body length of 57mm and tail length 54mm.

Colour in life:
Gular groove colour dark blue-grey; body colour greenish with brown to grey mottling, sometimes showing two distinct hourglass-shaped dorso-lateral markings. Dorsal crest orange, centres of scales on upper dorsum and scattered lateral tubercles orange. No lines of

greatly enlarged lateral tubercles but a line of orange, slightly enlarged, tubercles on each flank. No irregular longitudinal grooves on flanks. There are several vertical rows of slightly enlarged, orange-centred, scales on upper flanks. These rows curve slightly forward ventrally. Tail with dorsal crest, enlarged scales orange. Enlarged scales on the limbs are yellowish as are some on the sides of the throat. Cranial crests are moderately distinct, not horn-yellow in colour and with dark prominences (figure 22).

Hemipenes:
Not observed.

Reproduction:
The holotype contained 10 yolky eggs.

Distribution:
Only known from the Mkambati Game Reserve (figure 23).

Recorded localities and specimens examined:
One specimen examined.
Mkambati Game Reserve, Umtentu River Gorge (3129BD) – LR 2857 (coll. W.T. Vos, T. Edwards and L.R.G. Raw, 8 September 1991).

Remarks:
The holotype was eviscerated to obtain tissue for mtDNA analysis. Unfortunately the extracted DNA material, together with all the other samples, was lost as the result of the accidental failure of the power supply to the refrigeration equipment in which it had been stored.

The species was reported to be common in coastal forest at Mkambati Game Reserve (M. M. Tugela, pers. com.).

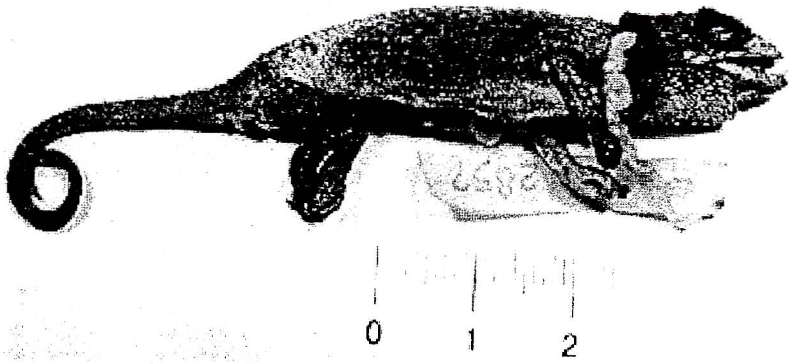


Figure 21: Holotype specimen of *Bradypodion mkambatiense* new species (scale in cm)

Figure 22: ***Bradypodion mkambatiense*** **from Mkambati (same animal while alive)**

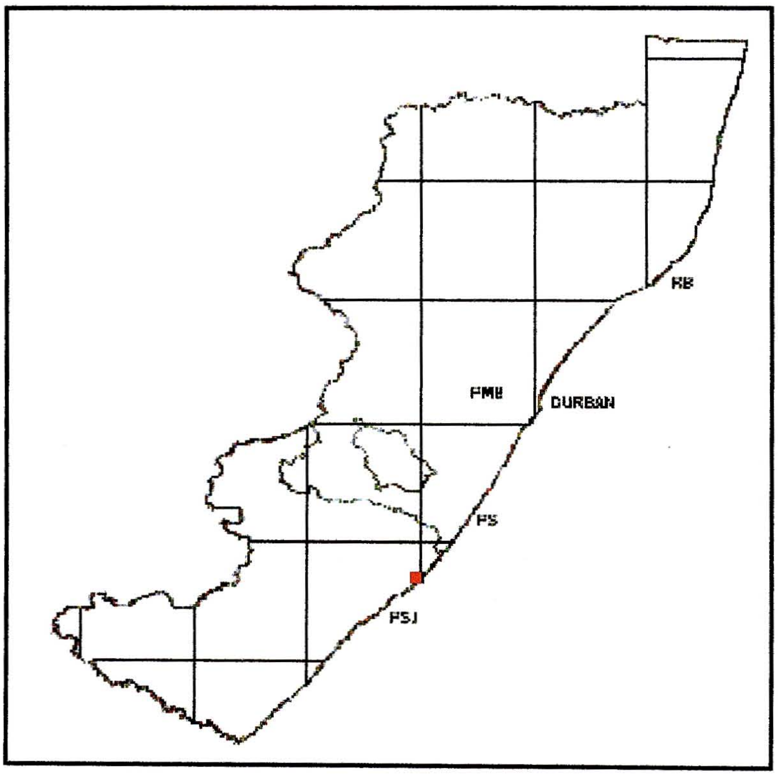


Figure 23. Distribution of *Bradypodion mkambatiense*

4.3.1.3 *Bradypodion angustiarum* new species

Holotype:
Adult female, L R G Raw Collection number LR 2232 collected in early 1984 by L R G Raw (figure 24).

Type locality:
Oribi Gorge near Paddock, Port Shepstone District, southern KwaZulu-Natal, South Africa (3030CB). Collected at night in roadside forest undergrowth on the north scarp of the Gorge.

Diagnosis:
This taxon is distinguished by possessing black lateral flank grooves and brownish gular grooves.

Description:
Snout sharp, shorter than diameter of orbit. Casque slightly raised and produced posteriorly; median parietal crest convex. Posterior temporal (squamosal) crest replaces lateral parietal crest at side of casque; median parietal crest raised to form an abrupt-edged keel; paraparietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests developed, posterior tubercle of lower temporal crest most pronounced. Subocular tubercle is not raised, borders mouth. Colour of interstitial skin of gular grooves is brown. Gular lobes all more or less equal in size. Gular lobes mostly triangular, distal tip sharply papillate, without denticulate edges. Flanks have black longitudinal grooves. Posterior dorsolateral scales form a distinct barred pattern. Flank tubercles distinctly enlarged, forming single row. Dorsal crest does not reach tail; tubercles strongly differentiated to form a very distinct pattern. Tail much less than head-and-body length; slender without a distinct tip region.

Counts:
There are 17 gular lobes and 24 dorsal tubercles.

Size:
LR 2232 has a head and body length of 61 mm and tail length of 49 mm.

Colouration in life:
Light brown with darker hourglass markings and black lateral grooves on sides; gular grooves pale brown. The specimen was photographed in life (see figure 25).

Hemipenes:
Not observed.

Reproduction:

Not observed.

Field notes:

LR 2232 was found at night while sleeping on forest undergrowth on the road verge on the north-bank ascent of the Oribi Gorge. Another specimen was recovered from the stomach of a vine snake, *Thelotornis c. capensis,* collected in the Oribi Gorge Nature Reserve (O. Bourquin, pers. com.). A number of attempts were made to obtain further specimens of this population during 1991. Although both night and daylight searches were employed no additional specimens were found.

Distribution:

Known only from the Oribi Gorge (figure 26).

Recorded localities and specimens examined:

One specimen examined.

Oribi Gorge (3030CB): LR 2232 (coll. L.R.G. Raw, 1984).

Etymology of specific name:

The name *angustiarum,* Latin genitive plural noun for defile or gorge, refers to the Oribi Gorge in which this taxon presumably occurs.

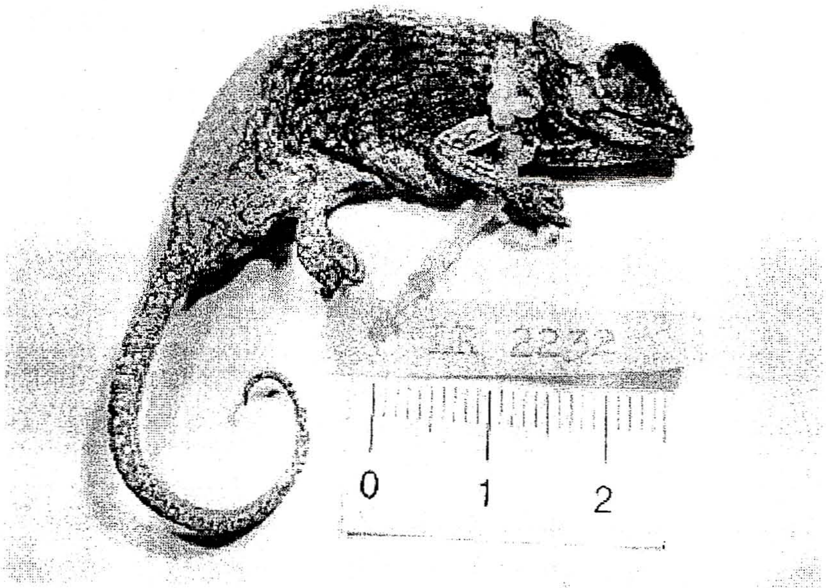


Figure 24: Holotype specimen of *Bradypodion angustiarum* new species (scale in cm)

Figure 25: *Bradypodion angustiarum* from Oribi Gorge
(Photograph by Johan Marais)

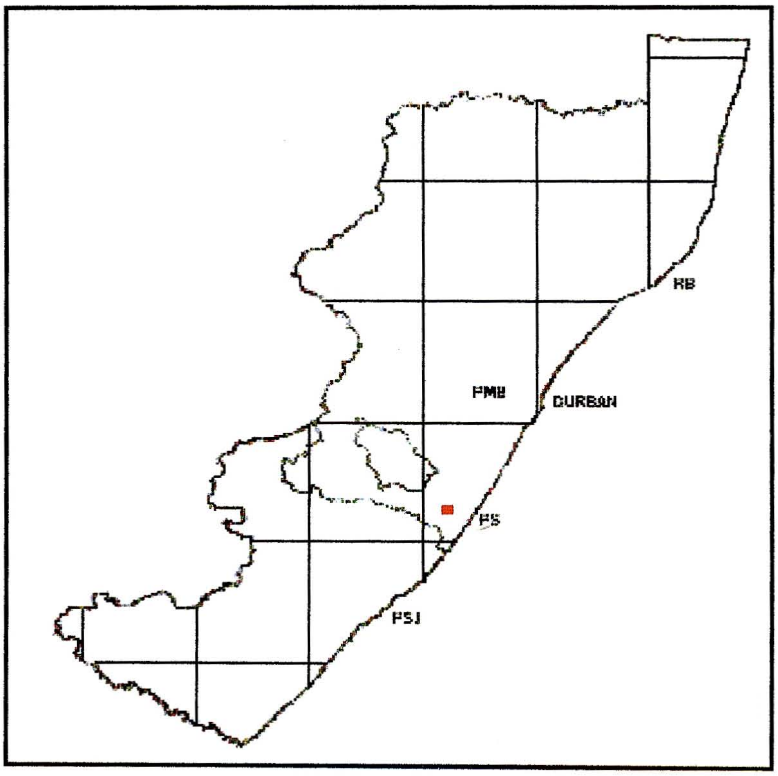


Figure 26: Distribution of *Bradypodion angustiarum*

4.3.1.4 *Bradypodion* species *incertae sedis* (related to *B. caffrum*)

4.3.1.4.1 Umtamvuna specimens

Locality:
Umtamvuna Nature Reserve.

Description:
Two subadult specimens were examined, both formalin preserved. Their gular grooves are pale with darker spotting and there are longitudinal grooves on their flanks. Apparently, one was collected from the bottom of the gorge while the other was collected on the upper edge of the gorge. The differences between the two specimens are sufficient to raise suspicions that two distinct taxa may be involved. The specimens both appear to be females, the first (figure 27) has 18 gular lobes and 14 raised dorsal tubercles on the dorsal crest, which does not extend on to the tail. The other has 11 gular lobes and 32 raised dorsal tubercles on the dorsal crest. There is an indistinct crest on the tail.

Field notes:
Found in forest in Umtamvuna River Gorge.

Distribution:
Umtamvuna River Gorge (figure 29).

Recorded localities and specimens examined:
Two specimens examined.
Umtamvuna Nature Reserve (3130AA): Two un-accessioned specimens, one collected by Stannard, the other (illustrated in figure 27) by 'E.R.?' on 13 August 1986.

4.3.1.4.2 Specimen from inland of Port St Johns

A single specimen (LR 2750) collected by D.R.J., L.A. & L.R.G. Raw in December 1991 from approximately 15-20 Km inland on the Lusikisiki road north of Port St Johns (figure 29) resembles *caffrum* except for white rather than yellow gular grooves (figure 28). In view of the similarity to *B. caffrum* it seems best to wait for additional material before making any taxonomic decision as to its status.

4.3.1.4.3 Sightings from Dwesa and Mbotyi

A specimen observed high in an *Erythrina* tree at Dwesa, southern Transkei coast (H. Thomas, 1994, pers. com.) seems likely to belong to this group. Apparently, two species may occur in the Dwesa reserve. This could mean that representatives of the *caffrum* and *melanocephalum* or *ventrale* species groups may occur there.

A reported sighting from Mbotyi (I Hertogs, pers. com.) may involve *B. caffrum* but no specimens are available for confirmation.

These observations are recorded here in the hope that it will encourage a search for chameleons in these areas.

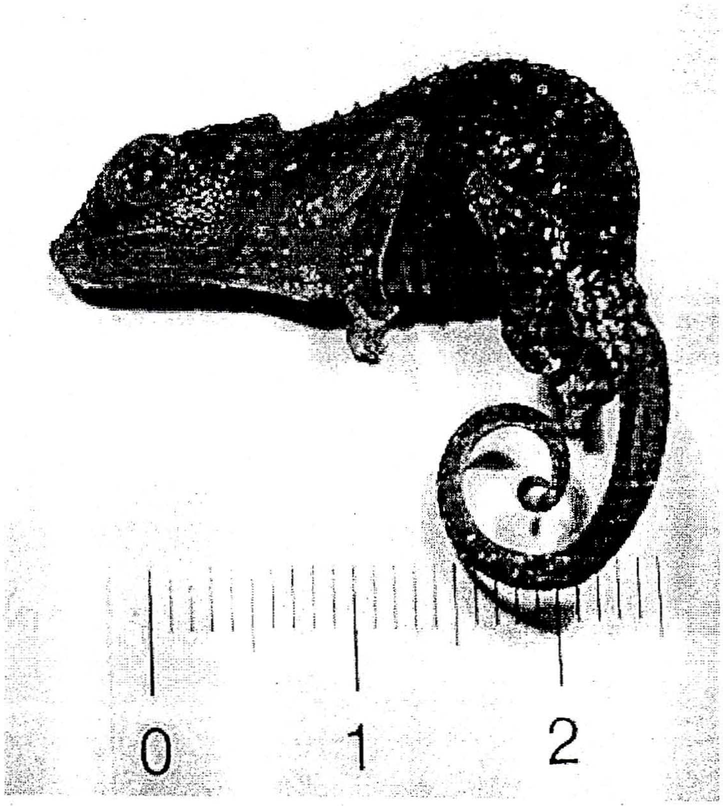


Figure 27: Specimen from Umtamvuna Nature Reserve (scale in cm)

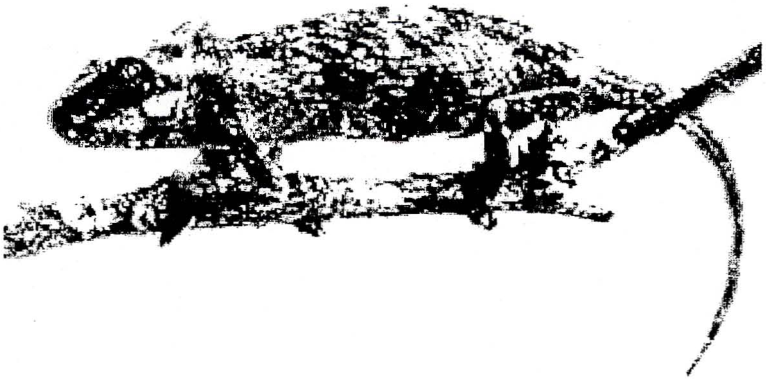


Figure 28: Specimen from road to Lusikisiki
(Approximately 20 km north of Port St Johns)

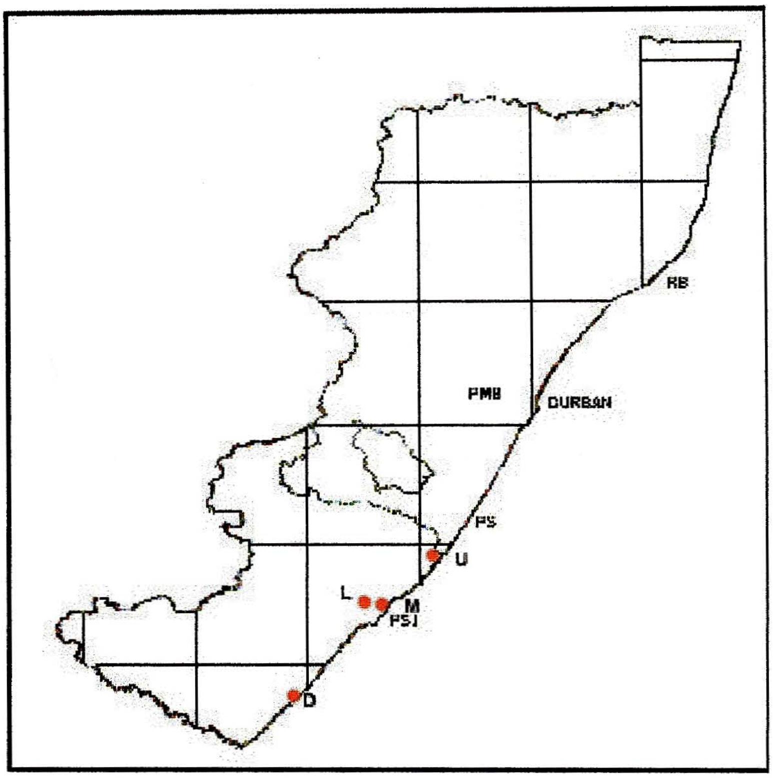


Figure 29: Distribution of undetermined specimens allied to *B. caffrum*
(U = Umtamvuna; M = Mbotyi, L = road to Lusikisiki; D = Dwesa)

4.3.2 *Bradypodion setaroi*

Along the coast, specimens of *B. setaroi* occur from Richards Bay northwards towards the Mozambique border.

4.3.2.1 *Bradypodion setaroi* Raw, 1976

?*Lophosaura melanocephala* (Gray); Power, 1932: 217, pl. III; fig. 1. (Part, Zululand: Makowe and Portuguese East Africa: Delagoa Bay specimens. See remarks below.)

?*Microsaura melanocephala* Gray; FitzSimons, 1943: 160–161.

Bradypodion setaroi Raw, 1976:152-154, fig. 4, plate 1.

Chamaeleo pumilus setaroi (Raw); Hofman, Maxson and Arntzen, 1991: 245-265.

Bradypodion setcersi Frank & Ramus, 1996: 136. (Incorrect subsequent spelling.)

Holotype:

LR 686, an adult male in the L.R.G. Raw Collection (figure 30). Collected in undergrowth in disturbed coastal dune forest by L.R.G. Raw and G. Setaro on 1 June 1974.

Type locality:

St Lucia Estuary, Zululand, KwaZulu-Natal, South Africa (2832AD).

Diagnosis:

A small species in which the dorsal crest does not reach the tail. There are blue lateral grooves on the flanks and the gular grooves are blue-white.

Description:

Snout sharp, distance from tip to anterior border of eye greater than diameter of eye. Casque raised and produced posteriorly; median parietal crest straight. Posterior temporal (squamosal) crest continues parallel to lateral parietal crest at side of casque; median parietal crest raised to form a less-distinct ridge; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests distinctly developed. Subocular tubercle slightly raised and not bordering mouth. Colour of interstitial skin of gular grooves is blue-white. Gular lobes have median lobes largest. Gular lobes mostly triangular, distal tip not sharply papillate, with denticulate edges. Flanks have blue longitudinal grooves. Posterior dorsolateral scales form a distinct barred pattern. Mid-flank tubercles distinctly enlarged to form a single row. Dorsal crest does not reach tail; tubercles strongly differentiated to form a very distinct pattern. Tail is usually less than head-and-body length in males and females, slender and without a distinct tip region.

Counts:

There are 13-25 gular lobes (mean 17,7 and median 17) and 10-20 dorsal tubercles (mean 13,5 and median 14).

Size:

Largest male has head and body length 67mm and tail length 63mm; largest female has head and body length 72mm and tail length 55mm.

Colouration in life:

The overall colour is light greyish brown with an irregular light orange lateral streak. Lateral streak with three darker orange blotches, the surfaces immediately above and below vermiculated with grey-green. There is grey-green barring on the tail and speckling on the head and limbs. Some enlarged scales on lower sides pale orange. Colours brighter when basking. Interstitial skin of gular region is bluish-white and lateral grooves are blue. A photograph is provided (figure 31).

Hemipenes:

Left hemipenis of LR 686: short, broadening towards apex. Four inward curving apical structures (rotulae), grouped two anteriorly, two posteriorly. Anterior pair larger. All with grooves radiating outwards, forming denticulate outer edge. Basal surface smoothly calyculate, calyces more distinct than in *B. melanocephalum*. Single deep, broad groove along anterior of surface of organ, inner border formed by longitudinal ridge terminating between inner anterior and posterior rotulae. Ridge at anterior edge of median surface not in centre as in B. *melanocephalum*, continuing into the inner posterior rotula. Sulcus spermaticus traverses base of organ posteriorly, passing outwards to lateral surface then turning sharply lengthwise along organ. Rotulae resemble those of *B. melanocephalum* but comparatively smaller. Right hemipenis mirror image of left, i.e., sulcus at outer posterior surface.

Reproduction:

Ovoviviparous, litters recorded in November (Haagner & Els, 1986), December (Haagner, 1989) and April (Bruton & Haacke, 1980). Litter sizes of 8–9 recorded with a neonate total length range of from 37.0 mm to 41.5 mm and a mean length of 39,74 mm (Haagner, 1989).

Field notes:

Found in undergrowth in disturbed dune forest at St Lucia. Observed high in tall tree at Monzi (G. Setaro, pers. com.). Found in roadside vegetation adjacent to swamp forest and reed-beds, as well as in a reed-bed at Richards Bay. Found on tall grass stems along a small stream at Arboretum, Richards Bay (Haagner, 1989). Haagner records that they could not be found in coastal thicket on the seaward side of the dunes nor were they found on evergreen shrubs adjacent to the Arboretum collection site.

Distribution:

Occurs from the vicinity of Richards Bay in the south to at least 10 kilometres north of Lake Sibayi in the north. Possibly extends northwards into southern Mozambique (figure 32).

Recorded localities and specimens examined:

Eighty seven specimens examined.

Cape Vidal (2832BA): TM 62827 (coll. O. Bourquin, 13 January 1985), 62832 (coll. O. Bourquin, 12 January 1985).

Dukuduku Forest, 3 km west of St Lucia bridge (2832AD): TM 64890 (coll. O. Bourquin, 26 May 1986).

Futululu Research Station (2832AD): TM 63534 (coll. G. Haagner, 17 May 1985).

Lake Sibayi, 10Km North (3027CA): UM 28446 (coll. M. Bruton ?, data not available).

Lake St Lucia (2832AD): TM 51698, 51708 (coll. S.L. Bourquin, December 1976, donated O. Bourquin, 8 August 1977).

Mapelane (2832AD): TM 52104, 52116, 52117, 52118 (coll.W.D. Haacke, 7 October 1978), 52171, 52535, 52551 (coll. W.D. Haacke, 16 October 1978), 55293 (coll. D. Densham, 9 July 1981), 58105, 58120, 62920, 62921 (coll. G. Haagner, 2 December 1984).

Mtubatuba (2832AC): TM 34477; 34478, 34479 (coll. D. Muller, June 1966).

Richards Bay (2832CC): LR 945, 946, 947, 948, 949 (coll. L.R.G. Raw, September 1977), 2660 (coll. D.R.J., L.R.G. & R.R.G. Raw, 4 October 1989), 2791, 2830 (data lost).

Richards Bay, Arboretum (2832CC): TM 67352, 67368, 67370, 67371, 67372, 67391, 67392, 67393 (coll. G. Haagner, 26 March 1988).

Sibayi Research Station, 4,3Km to south (3027CA): TM 48144 (coll. M. Bruton, 21 April 1976).

Sodwana Bay Nature Reserve (2732DA): TM 62839 (coll. O. Bourquin, 27 January 1985).

St Lucia Estuary (vicinity of village) (2832AD): LR 677, 678, 679 (coll. G. Setaro, December 1971), 686, 687, 688 (coll. L.R.G. Raw & G. Setaro, 1 June 1974), 689, 690, 691, 692, 693 (coll. L.R.G. Raw & G. Setaro, 31 August 1974), 702, 703 (coll. L.R.G. Raw & G. Setaro, 1 June 1974), 704 (coll. L.R.G. Raw & G. Setaro, 31 August 1974), 950, 951 (coll. L.R.G. Raw, September 1977), 1696 (coll. L.R.G. Raw, September 1982), 1776, 1777, 1780, 1812, 1813, 1864 (coll. M. Pickersgill, 21-26 November 1982), 2140, 2141, 2142 (coll. J. Marais, 26 May 1984), 2676, 2801, 2802, 2803, 2804, 2805, 2806, 2807, 2808, 2809, 2810, 2811, 2812, 2813 (data lost), TM 52225 (coll. R.H. Taylor, 2 October 1976), 55842 (coll. R. Taylor, 27 September 1978), UM 31496, 31497, 31512 (dune forest), 31639, 31662 (coll. D.G. Broadley, dates not available).

Sight Records:

Haagner (1989) records the following sightings – Perrier's Rocks, Tewate, Mission Rocks, 21 km north of Richards Bay, Monzi, Lake Bangasi North and Cape St Lucia.

Paratypes (Raw, 1976): LR 677-679, 687-693, 702-704, UM 28446, 31496-7, 31512, 31639, 31662, TM 34477-9 and 48144 (details listed above).

Remarks:

Reports of a dwarf chameleon from Delagoa Bay (= Maputo), Mozambique (SAM 9141) could possibly have referred to this species (FitzSimons, 1943; Power, 1932), as may their record of a specimen in the Durban Museum (DM 93, now lost), from Makowe. An attempt to find chameleons at Makowe resulted in only *Chamaeleo* being found. While the habitat appears suitable for dwarf chameleons it would seem that, if any population does occur, then it would most likely represent a different taxon from *B. setaroi,* which seems to prefer a strictly coastal habitat. Attempts to confirm the Delagoa Bay locality (see Raw, 1976) were not successful. It would seem that the specimen, SAM 9141, is apparently a *Chamaeleo dilepis* (G McLachlan, *in litt.)*

Etymology of specific name:

The specific name honours Mr Gordon Setaro, an enthusiastic field collector of southern African herpetofauna. The common name Setaro's Dwarf Chameleon proposed by Branch (1988) is therefore most suitable.

Figure 30: Holotype specimen of *Bradypodion setaroi* Raw, 1976 (scale in cm)

Figure 31: Male *Bradypodion setaroi* from St Lucia Estuary

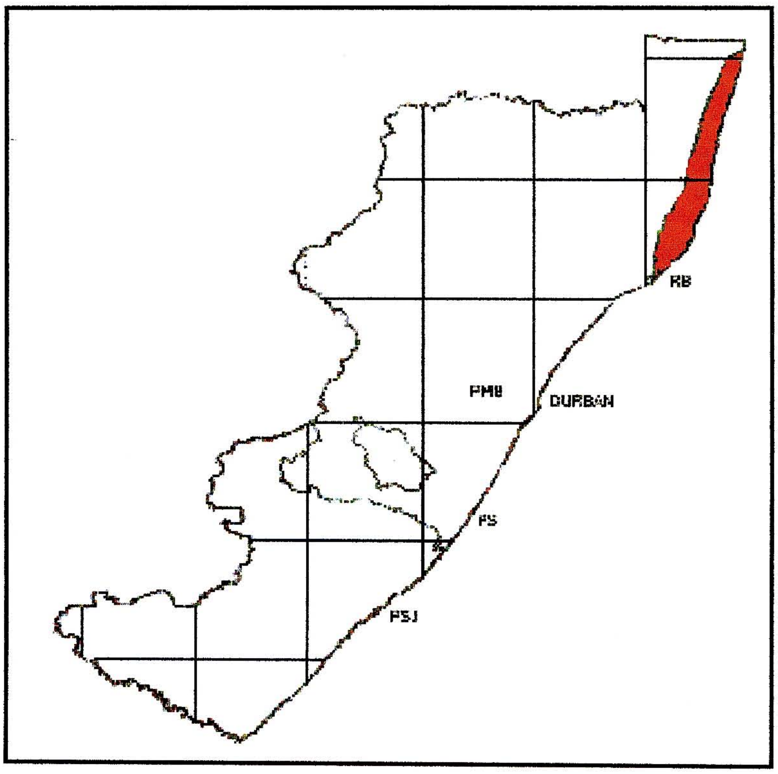


Figure 32: Distribution of *Bradypodion setaroi*

4.3.3 *Bradypodion nemorale s.l.*

These taxa occur north of the Tugela Valley in the indigenous forests of Nkandla and Qudeni, Entumeni and Dlinza, Eshowe as well as at Ongoye forest (*B. nemorale* and others). While these have all been regarded as a single species (Branch, 1988) it is clear that there are actually three distinct taxa in this area.

4.3.3.1 *Bradypodion nemorale* Raw, 1978

Bradypodion nemorale Raw, 1978: 265-269, figs. 1, 2.

Holotype:

NMP 1474, an adult female in the Natal Museum collection, Pietermaritzburg, collected by R F Lawrence, C S Holliday and T Schofield, 16-23 February, 1953 (figure 33).

Type locality:

Qudeni Forest, Zululand, KwaZulu-Natal, South Africa (2830DB).

Diagnosis:

A medium sized dwarf chameleon. The casque is strongly raised. Subocular tubercle is not or only slightly raised. Cranial crests are developed and distinct but not swollen or horn-coloured. Gular lobes are longer than broad. Throat region is pigmented with white gular grooves. The flanks do not have longitudinal grooves. The dorsal crest is distinct, continuing on tail.

Description:

Snout sharp, distance from tip to anterior edge of orbit is greater than diameter of orbit. Casque is distinctly raised; not produced posteriorly, median parietal crest convex. Posterior temporal (squamosal) crest continues parallel to lateral parietal crest at side of casque; median parietal crest raised to form a less-distinct ridge; paraparietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests distinctly developed. Subocular tubercle not raised and not bordering mouth. Colour of interstitial skin of gular grooves is white. Gular lobes all more or less equal in size. Gular lobes mostly rounded, distal tip papillate, without denticulate edges. Flanks are without longitudinal grooves or striations. Posterior dorsolateral scales do not form a discernable pattern of alternating larger and smaller scales. Flank tubercles slightly enlarged, forming single row. Dorsal crest extends along tail; tubercles equal or sub equal. Tail length is less than head-and-body length; tail slender without a distinct tip region.

Counts:

There are 9-15 gular lobes (mean 11,71 and median 12) and 14-29 dorsal tubercles (mean 21,6 and median 21).

Size:

Largest female (NMP1474 – Holotype) has head-and-body length 80 mm and tail length 65 mm.

Colouration:

Basic colour is shades of brown, more or less uniform with white gular grooves. A photograph is provided (figure 35).

Hemipenes:

Not known.

Reproduction:

Not known.

Field notes:

This rather elusive species has been collected on road verges in indigenous forest.

Distribution:

Known from the Qudeni Forests north of the Tugela River, Zululand (figure 36).

Recorded localities and specimens examined:

Twenty-one specimens examined.

Qudeni Forest (2830DB): LR 915, 916, 917, 918, 919, 920, 921, 922, 923, 924, 925 (coll. F.L. Farquharson, M.N. Harris & L.R.G. Raw, 23 April 1977); 2761, 2762, 2763, 2764, 2773, 2774, 2775, 2776, 2793 (coll. D.R.J., K.L., L.A., L.R.G. & P.E.V. Raw, January 1992); and NMP 1474 (coll. R.F. Lawrence, C.S. Holliday & T. Schofield, 16-23 February, 1953).

Paratypes:

LR 915-925, 873-884, 885-914 (Raw, 1978). Note: Paratype specimens LR 873-884 and 885-914 are now recognised as belonging to the new taxon *B. nkandlae*.

Etymology of specific name:

This is derived from the Latin, *nemoralis*, meaning living in or frequenting groves or woods, and refers to the preferred forest habitat of the species (Raw, 1978). While Zululand Dwarf Chameleon has been proposed as a common name (Branch, 1988), this is not the only dwarf Chameleon found in Zululand. In view of its localised distribution, the substitute name of Qudeni Dwarf Chameleon is suggested as being more appropriate.

Comment:

The type series of *Bradypodion nemorale* Raw 1978 has been shown to comprise two taxa, *nemorale* and *nkandlae*, while a third new taxon, *caeruleogula*, has been misidentified as *B. nemorale* (Branch, 1988). A paratype specimen LR 925 (figure 34) was previously erroneously illustrated as a specimen from Nkandla Forest (Raw, 1978).

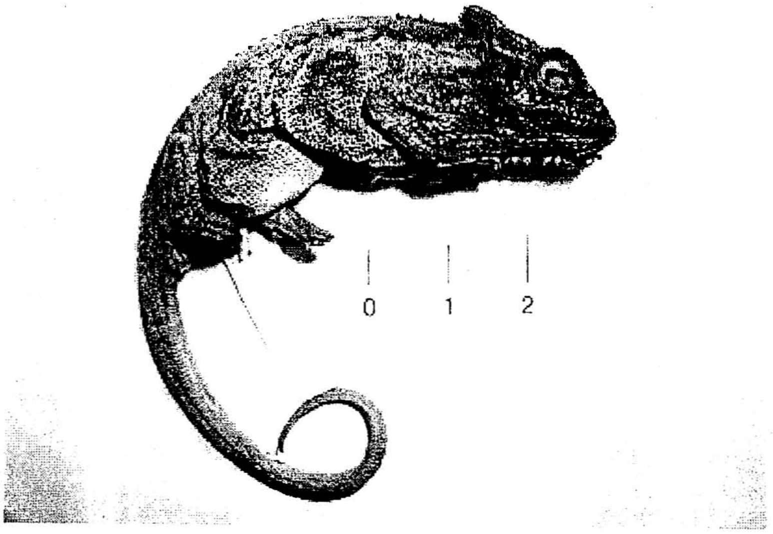


Figure 33: Holotype specimen of *Bradypodion nemorale* Raw, 1978 (scale in cm)

Figure 34: *Bradypodion nemorale* paratype LR 925 in life

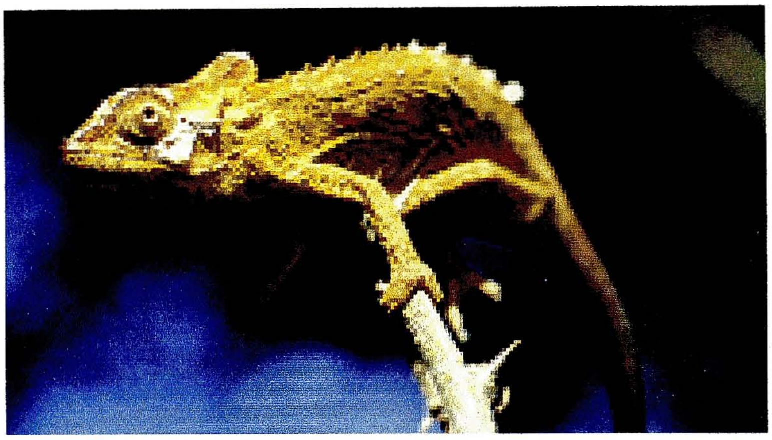


Figure 35: ***Bradypodion nemorale*** **from Qudeni Forest**

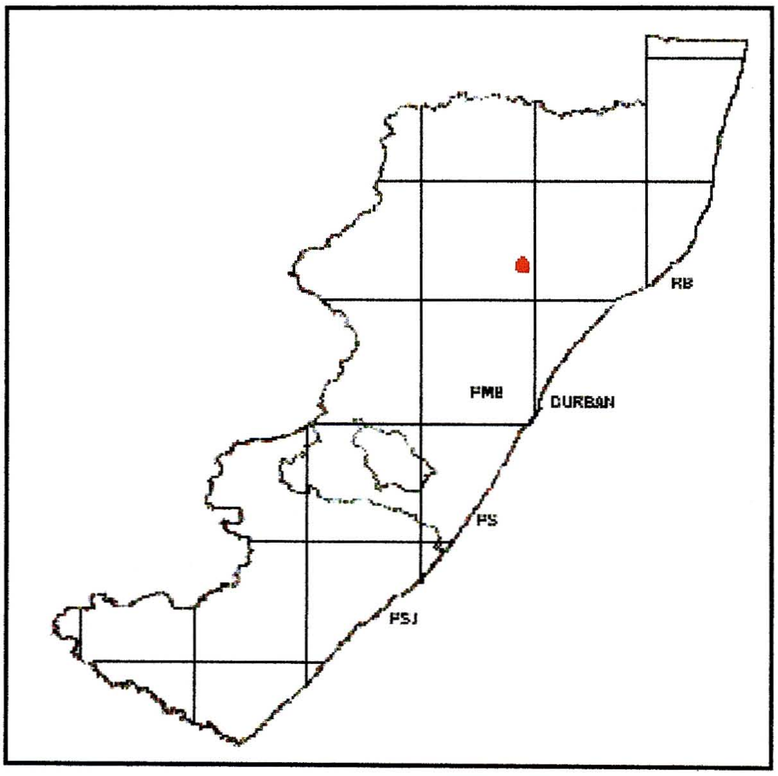


Figure 36: Distribution of *Bradypodion nemorale*

4.3.3.2 *Bradypodion nkandlae* new species

Syn. *Bradypodion nemorale* Raw, 1978 (part, Nkandla Forest specimens): 265-269,

Holotype:

L R G Raw Collection number LR900 collected by FL Farquharson, M N Harris and L.R.G. Raw on 23 April 1977 (figure 37). This is presumably an immature specimen but no obviously adult specimens of this taxon have yet been collected.

Type locality:

Nkandla Forest, Zululand, KwaZulu-Natal, South Africa (2831CA).

Diagnosis:

A smaller species with raised parietal region of casque. Throat region pigmented, with white gular grooves. Flanks have red longitudinal grooves.

Description:

Snout sharp, length from tip to anterior border of orbit is less than diameter of orbit. Casque raised, median parietal crest concave. Posterior temporal (squamosal) crest replaces lateral parietal crest at side of casque; median parietal crest raised to form an abrupt-edged keel; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests with lower temporal crest poorly developed except for posterior tubercle and posterior temporal crest tubercles reduced. Subocular tubercle not raised and not bordering mouth. Colour of interstitial skin of gular grooves is white. Gular lobes have median lobes largest. Gular lobes mostly triangular, distal tip papillate, without denticulate edges. Flanks have red longitudinal grooves or striations. Posterior dorsolateral scales form a slightly discernable pattern of alternating larger and smaller scales. Flank tubercles are slightly enlarged, forming a single row. Dorsal crest does not reach tail; tubercles not strongly differentiated forming a slight pattern. Tail length is less than head-and-body length; tail slender and without a distinct tip region.

Counts:

There are 8-20 gular lobes (mean 14,69 and median 15) and 11-28 dorsal tubercles (mean 18 and median 18).

Size:

LR 900: Head-and-body length 48 mm; tail length 45 mm.

Colouration in life:

A sub adult male was brown with irregular greenish blotches, mainly along upper flank but also forming irregular islands of colour on the lower flank. Slightly enlarged tubercles along middle of flank orange; tubercles of dorsal crest reddish brown. Skin on flanks arranged into longitudinal pattern with intervening grooves orange. Scattered enlarged tubercles on flanks, limbs and tail orange. Throat grooves greyish white and eyelids with thin greenish lines radiating outward from eye.

Hemipenes:

Everted left hemipenis of LR 880 (sub-adult) short, broadening towards apex. Four inward curving, denticulate rotulae on apex grouped in anterior and posterior pairs. The outermost of each pair is largest. Basal surfaces smoothly calyculate. Sulcus spermaticus passes along posterior base of organ before turning sharply length-wise between enlarged, fleshy lips to end on outer side of organ. Right hemipenis forms a mirror image of the left.

Reproduction:

Has not been observed.

Field notes:

This elusive species has been collected on road verges in the indigenous Nkandla Forest. When originally collected it was suspected that this may be a neotenic species since no obvious adults were found.

Distribution:

Known from the Nkandla Forest north of the Tugela River, Zululand (figure 39).

Recorded localities and specimens examined:

Forty-two specimens examined.

Nkandla Forest (2831CA): LR 873, 874, 875, 876, 877, 878, 879, 880, 881, 882, 883, 884 (coll. F.L. Farquharson, M.N. Harris & L.R.G. Raw, February 1977), 885, 886, 887, 888, 889, 890, 891, 892, 893, 894, 895, 896, 897, 898, 899, 900, 901, 902, 903, 904, 905, 906, 907, 908, 909, 910, 911, 912 and 913 (coll. F.L. Farquharson, M.N. Harris & L.R.G. Raw, 23 April 1977).

Paratypes:

The following specimens are designated as paratypes: LR 873, 874, 875, 876, 877, 878, 879, 880, 881, 882, 883, 884, 885, 886, 887, 888, 889, 890, 891, 892, 893, 894, 895, 896, 897, 898, 899, 901, 902, 903, 904, 905, 906, 907, 908, 909, 910, 911, 912 and 913. Note that all these specimens are also paratypes of *B. nemorale.*

Etymology of specific name:

The Latinised genitive "of Nkandla" refers to the origin from the Nkandla Forest. If a common name is required, it is suggested that Nkandla Dwarf Chameleon would be suitable.

Figure 37: Holotype specimen of *Bradypodion nkandlae* new species (scale in cm)

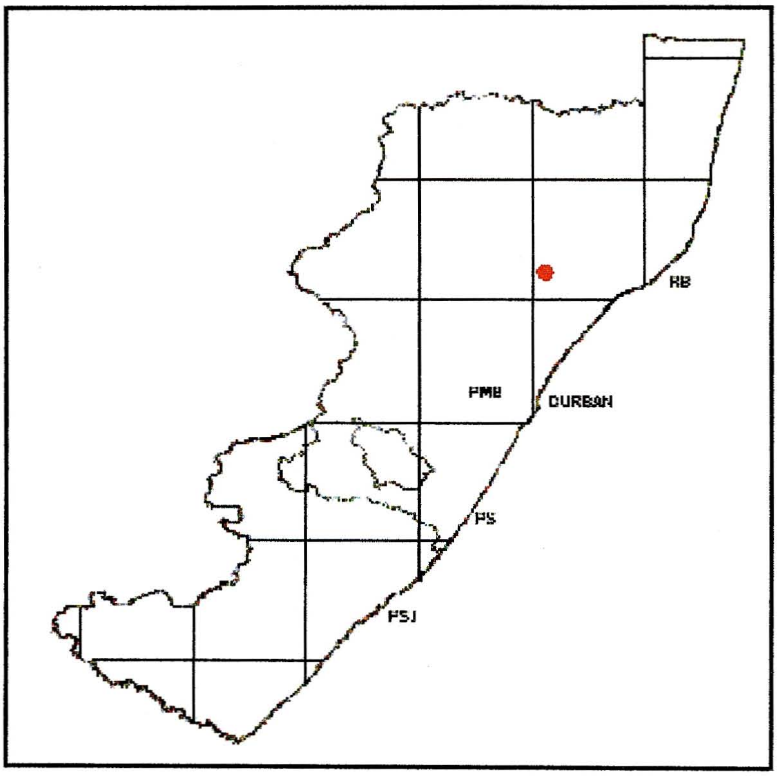


Figure 38: Distribution of *Bradypodion nkandlae*

4.3.3.3 *Bradypodion caeruleogula* new species

Syn. *Bradypodion nemorale* (non Raw, 1978) Branch, 1988.

Holotype:

L.R.G. Raw Collection number LR 2777. An adult female collected by D.R.J., K.L., L.A., L.R.G. & P.E.V. Raw in January 1992 (figure 40).

Type locality:

Eshowe, Zululand, KwaZulu-Natal, South Africa (2831CD).

Diagnosis:

Living animals can be distinguished from other *Bradypodion* by the dark blue-grey gular grooves and red lateral flank grooves.

Description:

Snout sharp, distance from tip to anterior edge of orbit is greater than diameter of orbit. Casque distinctly raised, not produced posteriorly; median parietal crest straight. Posterior temporal (squamosal) crest replaces lateral parietal crest at side of casque; median parietal crest raised to form a less-distinct ridge; paraparietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests with lower temporal crest not developed except for posterior tubercle and posterior temporal crest tubercles reduced. Subocular tubercle not raised and not bordering mouth. Colour of interstitial skin of gular grooves is blue-grey. Gular lobes all more or less equal in size. Gular lobes are mostly narrowly triangular and sharply pointed, not papillate or with denticulate edges. Flanks have red longitudinal grooves or striations. Posterior dorsolateral scales form a slightly discernable pattern of alternating larger and smaller scales. Flank tubercles slightly enlarged; forming single row. Dorsal crest does not reach tail; tubercles strongly differentiated to form a very distinct pattern. Tail length is less than head-and-body length in females, longer in males; tail slender without a distinct tip region.

Counts:

There are 14-20 gular lobes (mean 16,67 and median 17) and 11-22 dorsal tubercles (mean 15,3 and median 15).

Size:

LR 2777 Head and body length 62 mm, tail length 54 mm. Largest male (LR 2847) Head and body length 62 mm, tail length 54 mm. Largest female (LR 2833) Head and body length 67 mm, tail length 56 mm.

Colouration in life:
(Entumeni – LR 2790 and Eshowe – LR 2789) Overall colour greyish-green or yellow. Throat grooves dark grey-blue. Eyelids have dark greenish lines radiating outwards. Tubercles on dorsal crest and numerous tubercles on flanks, limbs and tail orange. Flanks have 9–12 reddish-orange irregular stripes in grooves on flanks. Gular crest is white. (See figure 41)

Hemipenes:
LR 2847 has right hemipenis with finely calyculate sides and four apical rotulae. The outer posterior rotula is distinctly larger than the inner posterior rotula. Both anterior rotulae are much smaller. The sulcus spermaticus passes posteriorly around the base then turns to form a channel up the posterior of the outer side as is usual with *Bradypodion* species. The left hemipenis is incompletely everted.

Reproduction:
Has not been observed.

Field notes:
This species has been collected while sleeping on leaves on trees in indigenous forest and on hedges in suburban gardens.

Distribution:
Known from the Entumeni, Dlinza and Ngoye Forests north of the Tugela River, Zululand (figure 42).

Recorded localities and specimens examined:
Sixteen specimens examined.
Entumeni Forest (2831CD): LR 2770, 2790; 2816, 2847 (coll. D.R.J., K.L., L.A., L.R.G. & P.E.V. Raw, January 1992).
Eshowe (vicinity Dlinza Forest) (2831CD): LR 2765, 2768, 2769, 2772, 2777, 2778, 2779, 2780, 2789, 2817, 2818, 2833 and 2834 (coll. D.R.J., K.L., L.A., L.R.G. & P.E.V. Raw, January 1992).

Other records:
Ngoye Forest (2831DC): Sight record only (Raw, January 1992) since specimens were not preserved (figure 41).

Paratypes:
The following specimens are designated as paratypes: LR 2765, 2768, 2769, 2770, 2772, 2778, 2779, 2780, 2789, 2790; 2816, 2817, 2818, 2833, 2834, 2847.

Etymology of specific name:

This is derived from *caeruleus* (Latin, dark blue) and gula (Latin, throat) and refers to the dark blue-grey of the gular grooves. It is used as a noun in apposition. Formerly included under the common name Zululand Dwarf Chameleon (Branch, 1988). If a common name is required then perhaps Eshowe Dwarf Chameleon would be appropriate. The alternative name of Blue-throated Dwarf Chameleon could possibly cause confusion with *B. mkambatiense* that also has blue gular grooves.

Figure 40: Holotype of *Bradypodion caeruleogula* new species (scale in cm)

Figure 41: *Bradypodion caeruleogula* from Entumeni Forest

Figure 42: Subadult *Bradypodion caeruleogula* from Ngoye Forest

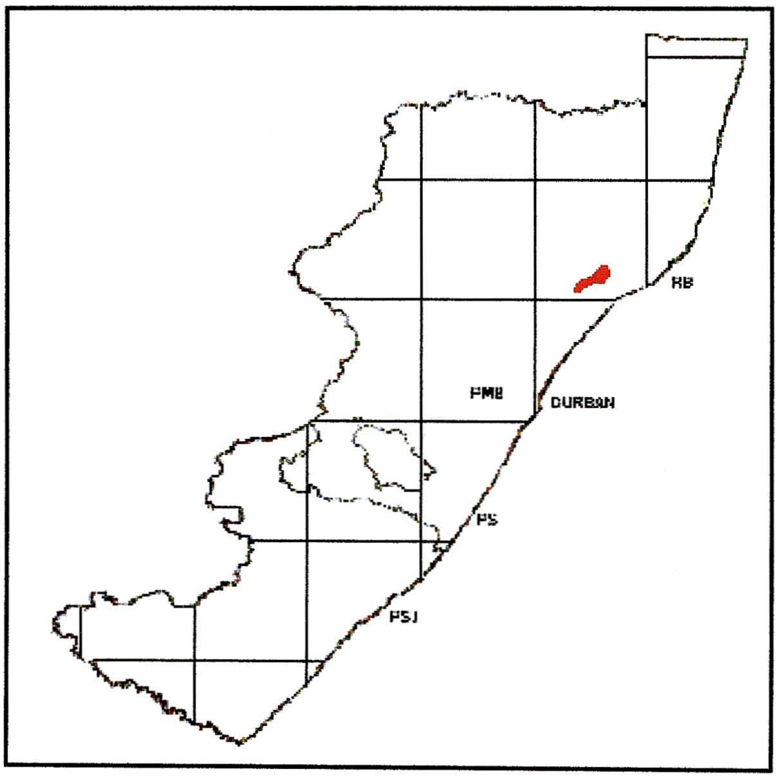


Figure 43: Distribution of *Bradypodion caeruleogula*

4.3.4 *Bradypodion nebula*

This population has not been recorded before and occurs on the forested slopes of the Karkloof Range between Howick and Rietvlei.

4.3.4.1 *Bradypodion nebula* new species

Holotype:

LR 2743, an adult male, collected early 1992, D.R.J., G.R.J., L.A., L.R.G. & R.R.G. Raw (figure 44).

Type locality:

Northern section of Karkloof Forest, KwaZulu-Natal Midlands.

Diagnosis:

A medium sized taxon with casque raised posteriorly. The subocular tubercle is distinctly raised. The gular grooves are yellow or white and there are no longitudinal flank grooves,

Description:

Snout sharp, distance from tip to anterior edge of orbit is less than diameter of orbit.

Casque distinctly raised and produced posteriorly; median parietal crest convex. Posterior temporal (squamosal) crest replaces lateral parietal crest at side of casque; median parietal crest raised to form an abrupt-edged keel; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests distinctly developed. Subocular tubercle distinctly raised and not bordering mouth. Colour of interstitial skin of gular grooves is white or yellow. Gular lobes more or less equal in size with anterior lobes slightly larger. Gular lobes mostly rounded, distal tip not sharply papillate, with denticulate edges. Flanks are without longitudinal grooves or striations. Posterior dorsolateral scales form a discernable pattern of alternating larger and smaller scales. Flank tubercles distinctly enlarged; forming a single row. Dorsal crest extends along tail; tubercles equal, sub-equal, or differentiated to form a pattern. Tail is longer than head-and-body length in males and shorter in females, slender without a distinct tip region.

Counts:

Gular lobes: 8-16 (mean 12,56, median 13).

Dorsal tubercles: 25-44 (mean 31,7, median 32).

Size:

Largest female (LR 2835): head and body length 78 mm, tail length 65 mm.

Largest male (LR 2702): head and body length 65 mm, tail length 70 mm.

Colouration in life:

(LR 2702) had the head greenish with two short, broad white streaks, one above temporal crest, one above corner of mouth on each side. The throat tubercles were white and there was yellow gular interstitial skin in the throat grooves. The dorsal crest, upper dorsum and median flanks were orange with olive-green streaks on the mid-upper flanks from nape to groin. White streaks, continuous with those above the temporal crests, extended to just above the axillae. There were scattered patches of olive-green on flanks. The ventral region was greenish to white. Smaller granules on the limbs and tail were greenish, but larger tubercles were orange. There were scattered orange tubercles on the eyelids. Photographs of a male (figure 45) and a female (figure 46) are provided.

Hemipenes:

LR 2702 has short and stout hemipenes with calyculate sides, apex with only two rotulae opposite a soft, fleshy, terminal papilla. LR 2696 is similar but has 4 large apical rotulae in 2 pairs separated by a papillate structure resembling a group of 4 small fleshy rotulae.

Reproduction:

LR 2766 contained 12 embryos. LR 2751 had black testes and a live mass of 4,1g.

Field notes:

Found on road verge adjacent to indigenous forest. Weather conditions during collection were mist and light rain.

Distribution:

Found in forests in the northern Karkloof range (figure 47).

Recorded localities and specimens examined:

Seventeen specimens examined.

Karkloof District (2930AD): LR 2684, 2685; 2686, 2687, 2688, 2691, 2692, 2694, 2695, 2696, 2702, 2719, 2722, 2731, 2751, 2766, 2835 (coll. D.R.J., G.R.J., L.A., L.R.G. & R.R.G. Raw, ca. 1992).

Paratypes:

The following specimens are designated as paratypes: LR 2684, 2685, 2686, 2687, 2688, 2691, 2692, 2694, 2695, 2696, 2702, 2719, 2722, 2731, 2743, 2751, 2766, 2835.

Etymology of specific name:

Nebula means mist in Latin. Used as a noun in apposition, it refers to the misty conditions prevalent in their habitat during the summer months when they are active. If a common name is required then Karkloof Dwarf Chameleon seems appropriate.

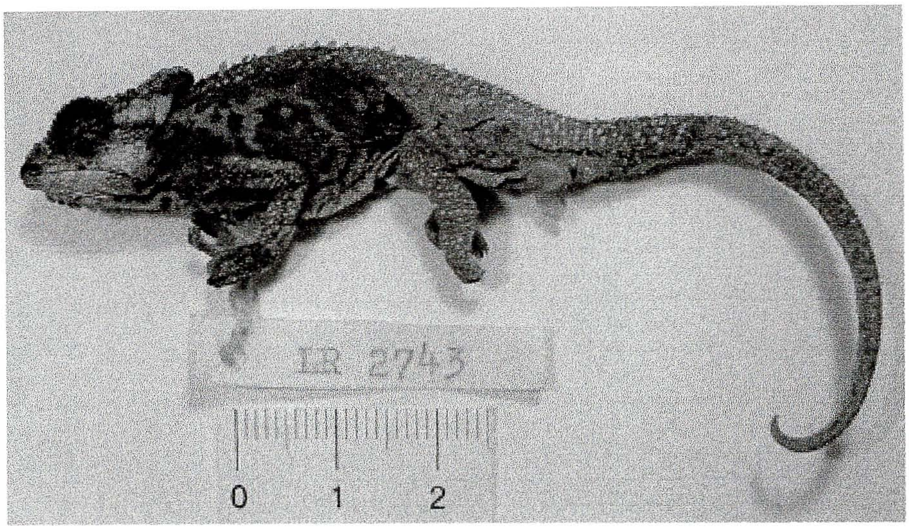


Figure 44: Holotype of ***Bradypodion nebula*** new species (scale in cm)

Figure 45: ***Bradypodion nebula*** male from Karkloof Forest

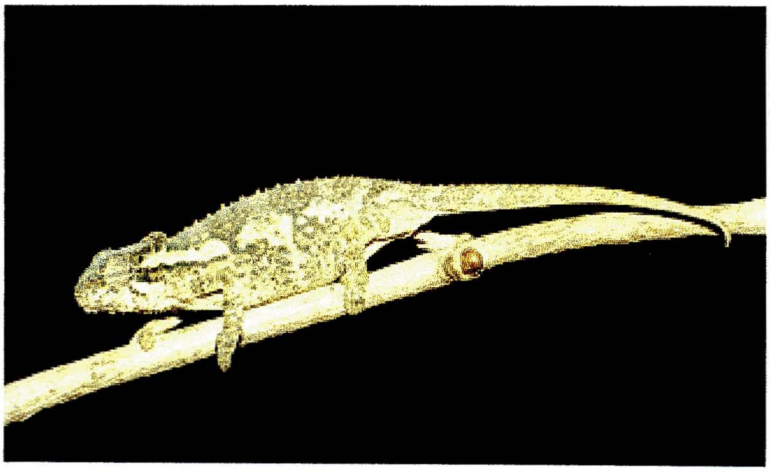


Figure 46: ***Bradypodion nebula*** female from Karkloof Forest

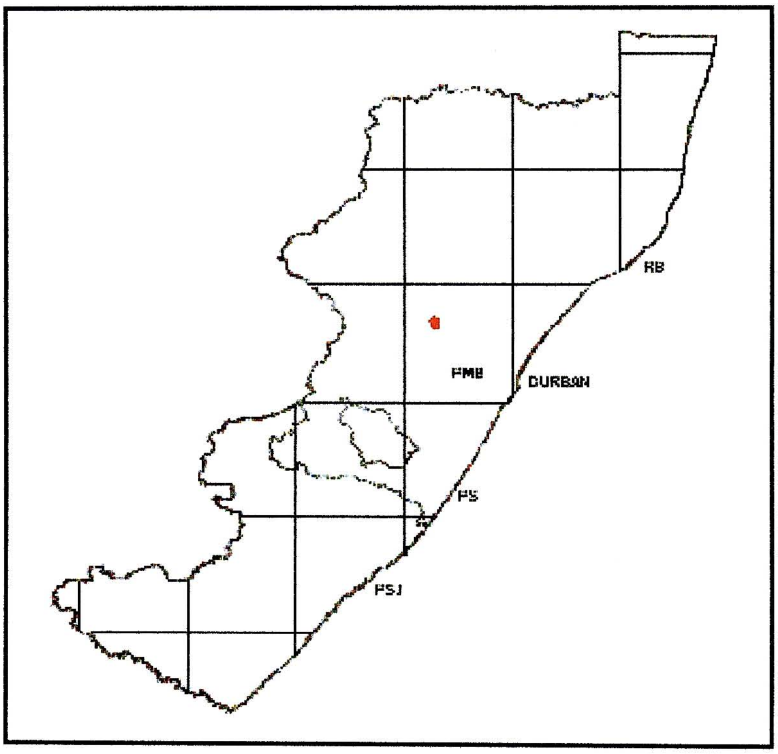


Figure 47: Distribution of ***Bradypodion nebula***

4.3.5 *Bradypodion melanocephalum* group

The following taxa include *Bradypodion melanocephalum* and several others that show some resemblance to *Bradypodion melanocephalum.*

4.3.5.1 *Bradypodion melanocephalum* (Gray, 1865)

Microsaura melanocephala Gray, 1865: 474, & text figure; FitzSimons, 1943: 160–161.

Chamaeleon melanocephalus (Gray); Boulenger, 1887: 457; Boulenger, 1910: 492; Werner, 1911: 22.

Lophosaura melanocephala (Gray); Power, 1932: 217.

Microsaura melanocephala Gray;

Chamaeleo pumilus melanocephalus (Gray); Hillenius, 1959: 56-64; Mertens, 1966: 24.

Bradypodion melanocephalum (Gray); Raw, 1976: 157-158.

Holotype:

Described from a single specimen housed in the Natural History Museum, London, specimen number BM 1946.8.21.7 (coll. 1862) (figures 48, 49).

Type locality:

South Africa, Port Natal (i.e., Durban, KwaZulu-Natal).

Diagnosis:

Small brownish chameleons with the casque feebly elevated and temporal crests well developed. The posterior temporal crest meets the lateral parietal crest at the side of the casque. There are usually two irregular rows of moderately enlarged flattened tubercles along flanks. The interstitial skin of the gular region is white. The dorsal crest continues on to tail.

Description:

Snout sharp, distance from tip to anterior border of orbit less than diameter of orbit. Casque not or only slightly raised, barely produced posteriorly with median parietal crest more or less straight. Posterior temporal (squamosal) crest meets lateral parietal crest at side of casque; median parietal crest forms a raised ridge; para-parietal tubercles present anteriorly; inter-orbital tubercles present; temporal crests distinctly developed, sometimes with tubercles of posterior crest reduced. Subocular tubercle not raised or bordering mouth. Colour of interstitial skin of gular grooves is white. Gular lobes all more or less equal in size; mostly triangular with distal tip not papillate. Flanks without longitudinal grooves or striations. Posterior dorsolateral scales equal or subequal not forming a discernable pattern. Mid-flank tubercles slightly to distinctly enlarged forming one or two rows. Dorsal crest extends along tail, tubercles equal or sub-equal. Tail slender; slightly longer to shorter than head-and-body length in males and much less than head-and-body length in females.

Counts:

Gulars 13-24 (mean 18,18 and median 18), dorsals 29–55 (mean 41,75 and median 41).

Size:

Largest female (LR 830) has head and body length 76 mm, tail length 62 mm.

Largest male (LR 929) has head and body length 62 mm, tail length 66 mm.

Mass:

LR 2756, a gravid female, had a live mass of 5,7g.

Colouration in life:

Colouration variable in shades of brown, usually with an irregular darker pattern of varying intensity. Sleeping individuals uniform, pale brownish grey. Excited individuals usually have pattern much intensified or even becoming virtually black. General appearance resembles a dead leaf. Interstitial skin of gular region is white. A photograph is provided (figure 50).

Hemipenes:

Everted left hemipenis of LR840 short, broadening towards apex. Four inward curving apical structures (rotulae), grouped two anteriorly, two posteriorly, these latter larger. All with grooves radiating outward forming denticulate outer edge. Some specimens with a fifth smaller apical structure between inner two. Basal section smoothly calyculate. Longitudinal ridge rises along median surface, continuing into inner rear rotula. Sulcus spermaticus traverses base posteriorly, outwards and forwards, then turns sharply to follow hemipenis lengthwise. Two enlarged, fleshy lips border sulcus. Sulcus terminates approximately midway along organ, opening into smooth area on outer surface. Apical structures with free outer ends recurving rearwards in anterior pair and forwards in posterior pair. Right hemipenis not everted but LR 834 has right hemipenis structure a mirror image of left, i.e., sulcus traversing posteriorly to outer edge before turning to follow shaft (after Raw, 1976).

Reproduction:

This species is ovoviviparous, usually with less than 12 young in a litter (LR 2756 contained 13 embryos while LR 839 contained 10 yolky oviducal eggs). Young are usually born in the summer months (Raw, 1976).

Field notes:

Under ideal circumstances this species is relatively common where found with high population densities. Often found in reed beds in coastal swamps and along rivers and streams, but also found on higher areas in tall grasses and other vegetation, shrubs and bushes, and even high in trees. Rather secretive during the day but usually easily found on calm, warm, evenings when, like most of these chameleons, they can be found sleeping in exposed situations at the end of branches or on the stems of vegetation. Males tend to sleep with the tail extended along the stem while females tend to coil the tail next to the stem. Windy conditions force them to find more sheltered and therefore less easily located sleeping sites.

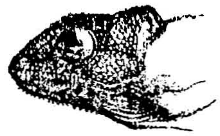
Distribution:
Recorded from the central KwaZulu-Natal coast from the vicinity of Warner Beach in the south north to Mt Edgecombe in the north. Similar specimens were also found on the south bank of the Sinkwazi River near Darnall (Johnson, 1984 & 1987; Johnson & Raw, 1989) but the lack of records from the intervening areas suggests that the extensive cultivation of sugar cane may have lead to its extirpation from these areas. If reports of chameleons from Umzinto can be confirmed it is possible that the former range could be extended to the coastal belt between Umzinto and the Tugela rivers and inland up to an altitude of ca. 100-150 m (figure 51).

Recorded localities and specimens examined:
Sixty-six specimens examined.
Durban (2930DD): LR 830, 831, 832, 833, 834, 835, 836, 837, 838, 839 (coll. L.R.G. Raw, 1975), 840 (coll. L.R.G. Raw, 1976), TM 47298, 47299, 47300, 47301, 47302 and 47303 (coll. L.R.G. Raw, October 1975).
Durban, Bellair (2930DD): LR 669 (coll. L.R.G. Raw, January 1974) and 1125 (coll. L.R.G. Raw, 9 December 1981).
Durban, Coedmore (2930DD): LR 2061, 2062, 2063, 2064 and 2065 (coll. J. Marais, 6 June 1983).
Durban, Hillary (2930DD): LR 406 (coll. L.R.G. Raw, 12 April 1972), 670, 671 (coll. L.R.G. Raw, no date), 672, 673, 674, 675, 676 (coll. L.R.G. Raw, January 1974), 694 (coll. L.R.G. Raw, July 1974), 695, 696, 697 (coll. L.R.G. Raw, August 1974), 698, 699 (coll. L.R.G. Raw, September 1974), 700 (coll. L.R.G. Raw, 1973), 701 (coll. L.R.G. Raw, August 1974), 717, 718 (coll. L.R.G. Raw, December 1974), 719 (coll. L.R.G. Raw, no date), 829 (coll. L.R.G. Raw, July1974), 856 (coll. L.R.G. Raw, October 1976), 1629, 1690, 1691, 1692, 1695, 1805, 1842, 1866, 1867 and 2337.
Durban, Overport (2930DD): LR 842 (coll. G. Setaro, May 1976).
Durban, Rossburgh (2930DD): LR 935 (coll. M. Pickersgill & L.R.G. Raw, October 1977).
Mt Edgecombe (2931CA): LR 929, 930 (coll. M. Pickersgill, September 1977) and 938 (coll. M. Pickersgill, October 1977).
Natal (Port Natal, i.e. Durban) (2930DD): BMNH 1946.8.21.7 (coll. 1862).
South bank of the Sinkwazi River, near Darnall (2931AD): LR 2855 (coll. P.A. Johnson & L.R.G. Raw, data lost).
Umbogintwini (3030BB): TM 33756 (no data available).
Warner Beach (3030BB): LR 926, 927 and 928 (coll. M. Pickersgill & L.R.G. Raw, October 1976).

Sight records from herpetofaunal survey of Municipal Durban (Alexander, 1987, 1990):
Airport, Athlone, Austerville, Avoca, Bay Head, Bellair, Blackhurst, Bonela, Brighton Beach, Havenside, Hillary, Kharwastan, Longcroft, Melkhoute, Merewent, Mobeni Heights, Mount Vernon, Montclair, Palmiet, Red Hill, Ridgeview, Umkumbaan, Wentworth, Westbridge and Woodlands. These sightings were made during the period February 1985 to October 1986.

Etymology of specific name:
The specific name *melanocephalum* (meaning black-headed) resulted from what was obviously an artefact of preservation in the type specimen. Gray's (1865) type description states " White (in spirits), head and shoulders black, fore legs blackish". It is likely that Gray's specimen was injured during preservation since injuries can cause the blackening of parts of the body in this species. These marks are likely to be fixed in preservation. Personal examination of the type (February 2000) confirmed that the markings described by Gray (see figure 49) are an artefact of preservation rather than a natural colour pattern.

The suggested common name of "Black-headed Dwarf Chameleon" (Branch, 1988) is inappropriate since no living black-headed individuals have been observed. It seems inadvisable to continue the misleading use of the English translation as a common name and it is recommended that a more appropriate name such as "Durban Dwarf Chameleon" or "KwaZulu-Natal Coast Dwarf Chameleon" be adopted. This species is called "uNwabu" in Zulu, the same name as applied to all chameleons. Bantu languages do not appear to recognise different species of chameleons.



Head of *Microsaura melanocephala.*

Figure 48: Drawing from original description of *Microsaura melanocephala* Gray, 1865

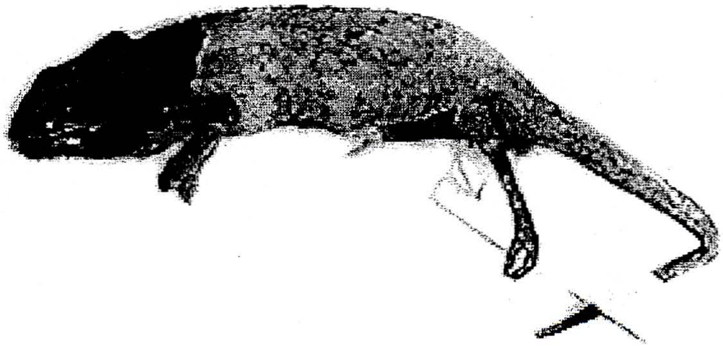


Figure 49: Type specimen of *Microsaura melanocephala* BM 1946.8.21.7

Figure 50: *Bradypodion melanocephalum* from Avoca, north of Durban

Typical colouration showing that this species does not have a black head.

Figure 51: Distribution of *Bradypodion melanocephalum*

4.3.5.2 *Bradypodion bourquini* new species

Chamaeleon melanocephalus (non Gray, 1865); Werner, 1902: 362. (part, Pietermaritzburg specimen)

Chamaeleon taeniobronchus (*sic*) (non Smith, 1831); Boulenger, 1908. (Town Hill, Pietermaritzburg)

Bradypodion melanocephalum (non Gray, 1865); Raw, 1976: 157-158. (part, Pietermaritzburg, Town Bush and Hilton specimens).

Holotype:

LR 2784, an adult female, collected ca. 1992 by D.R.J. & L.R.G. Raw (figure 52).

Type locality:

Collected in roadside vegetation on hills between Merrivale and Boston, KwaZulu-Natal.

Diagnosis:

A smaller species with casque feebly raised and with posterior temporal crest tubercles reduced or absent. Posterior temporal crest continues parallel to the lateral parietal crest at the side of the casque. Gular grooves are white, rarely yellow. Previously confused with *B. melanocephalum* but shows tinges of green and orange colouration, which that species never displays.

Description:

Snout moderate, length from tip to anterior border of orbit is equal to the diameter of orbit. Casque slightly raised and produced posteriorly; median parietal crest slightly convex.

Posterior temporal (squamosal) crest continues parallel to lateral parietal crest at side of casque; median parietal crest raised to form an abrupt-edged keel; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; lower temporal crests distinctly developed with posterior temporal crest tubercles reduced or absent. Subocular tubercle raised and bordering mouth. Colour of interstitial skin of gular grooves is usually white, rarely yellow. Gular lobes have median lobes largest. Gular lobes mostly triangular, distal tip not sharply papillate, without denticulate edges. Flanks are without longitudinal grooves. Posterior dorsolateral scales form a slightly discernable pattern of alternating larger and smaller scales. Mid-flank tubercles distinctly enlarged; forming a single row. Dorsal crest extends along tail; tubercles not strongly differentiated forming a slight pattern. Tail is longer than or less than head-and-body length in males; much less in females, slender without a distinct tip region.

Counts:

There are 10-25 gular lobes (mean 16,44 and median 16) and 15-57 dorsal tubercles (mean 38,9 and median 38).

Size:
Largest female (LR 2757) has head and body length 78 mm and tail length 72 mm.
Largest male (LR 2720) has head and body length 72 mm and tail length 74 mm.

Mass:
LR 2757 had a live mass of 8,6g.

Colouration in life:
Colour usually an overall brown, patterned with darker markings; often with tinges of green or red on the dorsum; the dorsal crest sometimes tinged with red; some specimens may have an overall greenish colouration. A photograph is provided (figure 53).

Hemipenes:
LR 2787 has both hemipenes everted. The sulcus spermaticus is postero-laterally located. There are four rotulae with the posterior pair more or less equal in size and larger than the anterior pair. The lateral surfaces are calyculate. The hemipenes are more or less mirror images of each other.

Reproduction:
Ovoviviparous with young born in summer, LR 2757 contained 12 embryos.

Mass:
LR 2757, a gravid female, had a live mass of 8.6g.

Field notes:
An ecotonal species frequently found in disturbed habitat, e.g., gardens and road verges, as well as forest edges.

Distribution:
Found in suitable areas between the Umkomaas and Umgeni River valleys from Pietermaritzburg southward to near Richmond and westward to Deepdale (figure 54).

Recorded localities and specimens examined:
Sixty nine specimens examined.
Between Boston and Deepdale: LR 2741, 2786 and 2787 (coll. D.R.J. & L.R.G. Raw, ca. 1992).
Between Merrivale and Boston: LR 2697, 2698, 2699, 2708, 2718, 2727, 2736, 2737, 2738, 2739, 2748, 2784, and 2785 (coll. D.R.J. & L.R.G. Raw, ca. 1992).
Boston: LR 2728, 2729 and 2747. (coll. D.R.J. & L.R.G. Raw, ca. 1992)

Deepdale, Lundy's Hill (2930BA): LR 1782, 1802 (coll. L.R.G. Raw, 29 November 1982), 2667, 2700, 2701, 2717, 2726, 2730, 2734, 2735, 2742, 2782, and 2783 (coll. D.R.J. & L.R.G. Raw, ca. 1992).

Hilton (2930CA): LR 1051, 1052, 1053, 1054, 1055, 1056, 1057, 1058 (coll. L.R.G. Raw, 8 April 1978), 1122, 1126 (coll. L.R.G. Raw, 9 December 1981), 1693, 1697, 1698, 1699, 1700, 1701, 1702 (coll. L.R.G. Raw, September 1982), 1861 (coll. L.R.G. Raw, 5 December 1982), 2716, 2720 (coll. L.R.G. Raw, ca 1992) and TM 51691 (coll. O. Bourquin, 10 April 1976).

Pietermaritzburg, Sweetwaters Rd, Blackridge (2938CA): LR 2659, 2661 and 2662 (coll. D.R.J., L.R.G. & R.R.G. Raw, 4 October 1989);

Pietermaritzburg, Ketelfontein (2930CA): LR 2293 (coll. L.R.G. Raw, 30 January 1985).

Pietermaritzburg, Link Rd, Town Hill (2930CA): LR 2757 (coll. L.R.G. Raw, ca. 1992).

Pietermaritzburg, Old Howick Rd (2930CA): TM 51693 and 51694 (coll. O. Bourquin, 22 April 1976).

Pietermaritzburg, Queen Elizabeth Park (2930CA): TM 51692 (coll. O. Bourquin, 14 April 1976) and 51702 (coll. O. Bourquin, 18 April 1976).

Pietermaritzburg, Town Bush (2930CB): LR 709, 710, 711 and 712 (coll. R. Auerbach & L.R.G. Raw, 14 December 1974).

Pietermaritzburg, Town Hill (2930CB): NMP 1381.

Pietermaritzburg, Town Hill Rd (2930CB): TM 51690 (coll. O. Bourquin, 5 April 1976).

Pietermaritzburg, Prestbury (2930CB): LR 2087 (coll. M.N. Smit, April 1983).

Pietermaritzburg, University of Natal, Scottsville (2930CB): DM 190 (coll. O. Bourquin)

Other records:

Richmond, in disturbed grassland between plantations some 5 km outside village towards Hella-Hella: sight record only (L.R.G. Raw, ca. 1982).

Paratypes:

The following specimens are designated as paratypes: LR 709, 710, 711, 712, 1051, 1052, 1053, 1054, 1055, 1056, 1057, 1058, 1122, 1126, 1693, 1697, 1698, 1699, 1700, 1701, 1702, 1782, 1802, 1861, 2087, 2293, 2659, 2661, 2662, 2667, 2697, 2698, 2699, 2700, 2701, 2708, 2716, 2717, 2718, 2720, 2726, 2727, 2728, 2729, 2730, 2734, 2735, 2736, 2737, 2738, 2739, 2741, 2742, 2747, 2748, 2757, 2782, 2783, 2785, 2786, 2787, TM 51690, 51691, 51692, 51693, 51694, 51702.

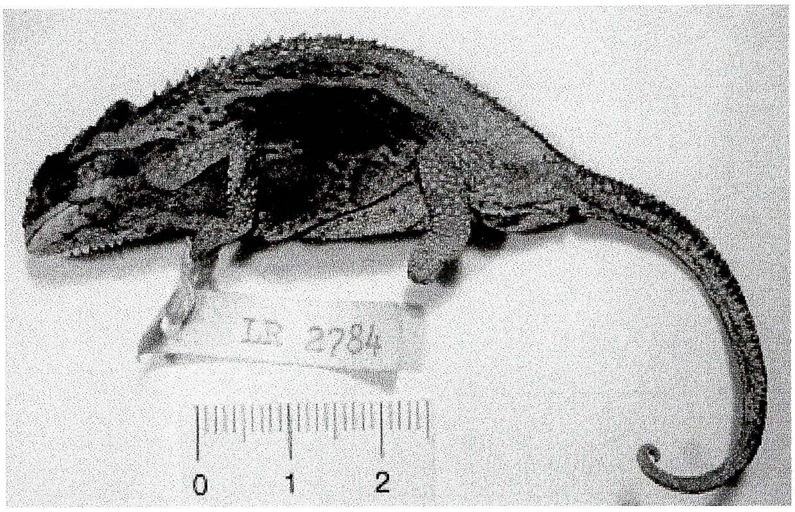


Figure 52: Holotype of *Bradypodion bourquini* new species (scale in cm)

Figure 53: Male *Bradypodion bourquini* from Hilton

(Photograph by Achim Breuer)

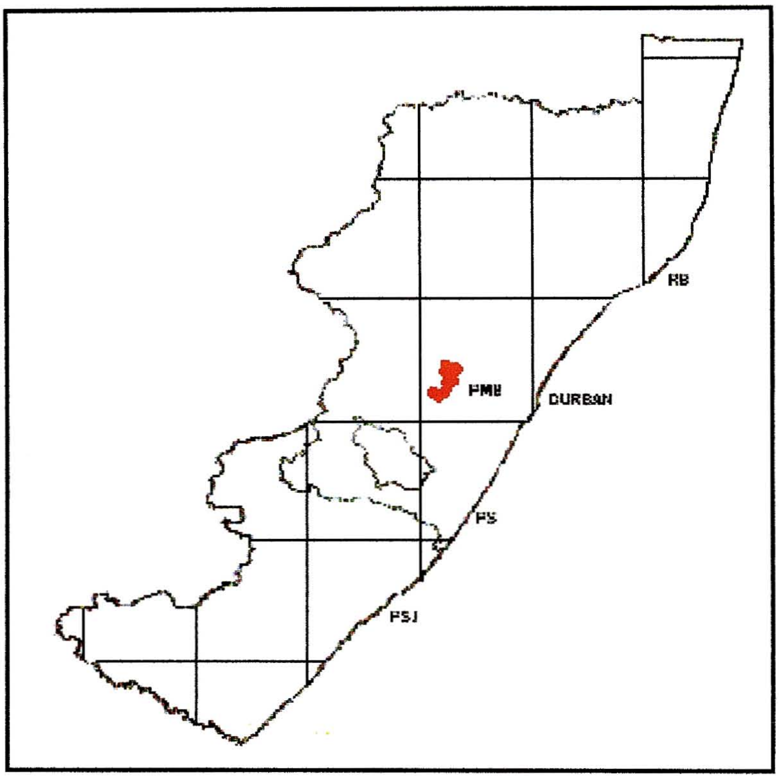


Figure 54: Distribution of *Bradypodion bourquini*

4.3.5.3 *Bradypodion tilburyi* new species

Holotype:

LR 2723, an adult female, coll. D.R.J., L.A. & L.R.G. Raw, 1992 (figure 55).

Type locality:

Entrance to Methley Dam, near Greytown, KwaZulu-Natal.

Diagnosis:

A smaller species that has a grey-brown colouration, white gular grooves and a feebly raised casque. The posterior temporal crest replaces the lateral parietal crest at the side of the casque. There are no lateral flank grooves.

Description:

Snout moderate, distance from tip to anterior border of orbit is less than diameter of orbit. Casque slightly raised and produced posteriorly; median parietal crest slightly convex.

Posterior temporal (squamosal) crest replaces lateral parietal crest at side of casque; median parietal crest raised to form an abrupt-edged keel; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests distinctly developed. Subocular tubercle slightly raised and not bordering mouth. Colour of interstitial skin of gular grooves is white. Gular lobes all more or less equal in size tapering slightly posteriorly. Gular lobes mostly triangular, distal tip not sharply papillate, without denticulate edges. Flanks do not have longitudinal grooves. Posterior dorsolateral scales equal or sub equal not forming a discernable pattern. Flank tubercles enlarged to form a single row, sometimes not enlarged. Dorsal crest extends along tail with tubercles equal or sub-equal. Tail longer than, or less than head-and-body length in males, much less in females. Tail slender without a distinct tip region.

Counts:

There are 10-25 gular lobes (mean 17,56 and median 19) and 30-49 dorsal tubercles (mean 37,3 and median 37).

Size:

Largest male (LR 1519) has head and body length 71 mm and tail length 55 mm.

Largest female (LR 2723) has head and body length 77 mm and tail length 70 mm.

Colouration:

Basically brown with irregular patterns of darker brown or with a lighter streak (figure 56).

Hemipenes:

LR 2703 has both hemipenes everted. The sulcus spermaticus is postero-laterally located. There are four apical rotulae with the outer rotulae larger than the inner and with the posterior largest. The lateral surfaces are calyculate with the calyces extending on to the apical surface between the rotulae. The hemipenes are more or less mirror images.

Reproduction:

LR 2767 contained 8 embryos.

Field notes:

Found on roadside weedy vegetation.

Distribution:

Only known from the Greytown area (figure 57).

Recorded localities and specimens examined:

Eighteen specimens examined.

Greytown (2930BA): LR 1516, 1517, 1519, and 1518 (coll. C.R. Tilbury, December 1979).

Methley Dam, Greytown (2930BA): LR 2693, 2703, 2704, 2705, 2706, 2707, 2714, 2715, 2723, 2724, 2725, 2746, 2749, and 2767 (coll. D.R.J., L.A. & L.R.G. Raw, 1992).

Paratypes:

The following specimens are designated as paratypes: LR 1516, 1517, 1519, 1518, 2693, 2703, 2704, 2705, 2706, 2707, 2714, 2715, 2724, 2725, 2746, 2749, 2767.

Etymology of specific name:

Named for Dr Colin Tilbury who donated the first collected specimens to me and alerted me to the presence of this population in the Greytown area..

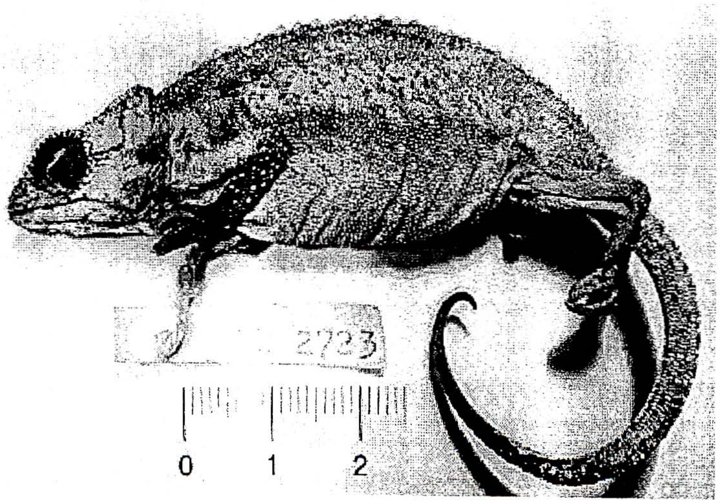


Figure 55: Holotype of *Bradypodion tilburyi* new species (scale in cm)

Figure 56: *Bradypodion tilburyi* from Methley Dam entrance

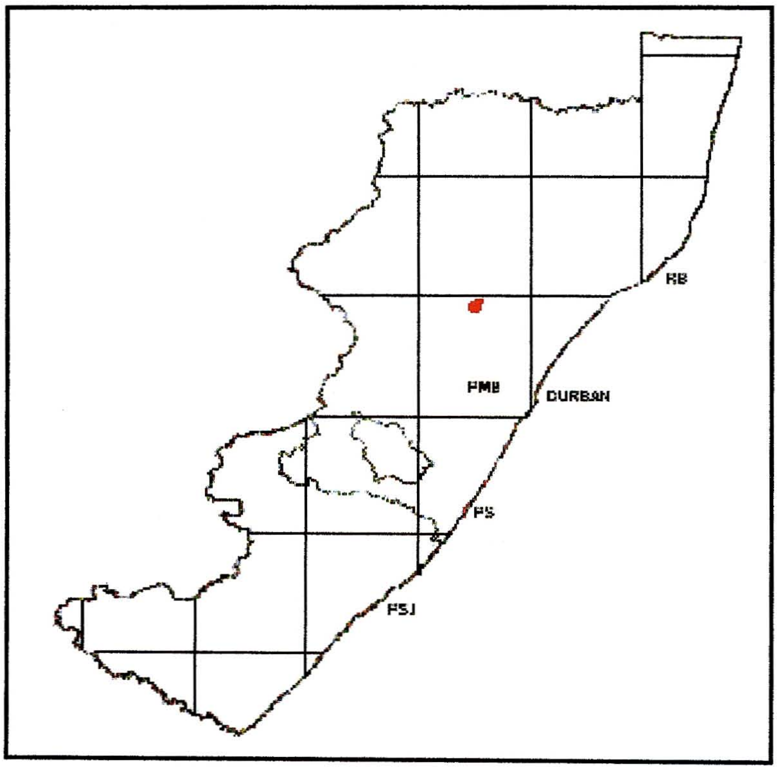


Figure 57: Distribution of *Bradypodion tilburyi*

4.3.5.4 *Bradypodion kentanicum* (Hewitt, 1935)

Lophosaura pumila taeniabroncha (Smith, 1831); Power, 1932: 215-216. (Part, Kentani specimens)
Lophosaura melanocephala kentanica Hewitt, 1935: 303-304, pl. XXVIII, fig. 3.
Microsaura melanocephala Gray, 1865; FitzSimons, 1943: 160–161. (Kentani specimens.)
Chamaeleo pumilus melanocephalus (Gray, 1865); Hillenius, 1959: 56-64; Mertens, 1966: 24. (Pondoland specimens.)
Bradypodion kentanicum (Hewitt, 1935); Raw, 1976: 149.
Bradypodion pumilum melanocephalum (Gray, 1865); Klaver & Böhme, 1997: 26.

Syntypes:
AMG 4538 (2 specimens) coll. Miss O. Abernethy, Kentani, Cape Province, 7 March 1922 (figure 58).

Type locality:
Kentani, southern Transkei, Eastern Cape, South Africa.

Diagnosis:
A small, slender species with casque feebly raised. Both temporal crests are well developed with the posterior crest continuing parallel to the lateral parietal crest. The gular grooves are white and there are no longitudinal flank grooves.

Description:
Snout not sharp, shorter than diameter of orbit. Casque very slightly raised; not produced posteriorly; median parietal crest convex. Posterior temporal (squamosal) crest continues parallel to lateral parietal crest at side of casque; median parietal crest raised to form an abrupt-edged keel; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; temporal crests developed with posterior tubercle of lower temporal crest prominent. Subocular tubercle raised and bordering mouth. Colour of interstitial skin of gular grooves is white. Gular lobes all more or less equal in size with median lobes largest. Gular lobes mostly triangular, distal tip not sharply papillate, without denticulate edges. Flanks are without longitudinal grooves. Posterior dorsolateral scales equal or sub equal. Flank tubercles slightly enlarged; forming a single row. Dorsal crest extends along tail; tubercles equal or sub-equal. Tail longer than head-and-body length, slender without distinct tip region.

Counts:
There are 17-32 gular lobes (mean 24 and median 25) and 40-57 dorsal tubercles (mean 48,4 and median 49).

Size:
Largest male (AMG 5438/1) has head and body length 54mm and tail length 60mm.
Largest female (LR 1814) has head and body length 64mm and tail length 53mm.
Coloration: The basic colour is pale greyish brown with irregular longitudinal markings that may or may not be apparent. Gular grooves are greyish white. No tinges of other colours observed.

Reproduction:
Has not been observed.

Field notes:
Specimens were collected in a valley near Kentani in the early evening. They were sleeping on grasses and small trees and shrubs on and near the banks of a small stream.

Distribution:
Known from the Kentani area of southern Transkei (figure 59).

Recorded localities and specimens examined:
Fifteen specimens examined.
Kentani (3228CB): AMG 4538 (2 co-types now in PEM) (coll. O. Abernethy, 7 March 1922), AMG n/n (now in PEM, coll. O. Abernethy), LR 1771, 1793, 1798, 1799, 1800, 1814, 1816, 1820, 1836, 1837, 1838 and 1846 (coll. L.R.G. Raw & M. Pickersgill, 3 December 1982).

Etymology of specific name:
The specific name '*kentanicum*' refers to the village of Kentani of the extreme south of the Transkei.

Remarks:
Although Hewitt (1935) states that the type specimens were presented by Miss Alice Pegler, a note enclosed with the specimens was inscribed " *Lophosaura melanocephala kentanica* Hewitt, 2 co-types, coll. Miss O. Abernethy, Kentani, Cape Province, 7/3/22". Presumably both statements are correct, with the specimens collected by Miss Abernethy and presented to the Albany Museum by Miss Pegler, a well-known botanical collector of the period.

Figure 58: Syntype of *Lophosaura melanocephala kentanica* Hewitt, 1935 (scale in cm)

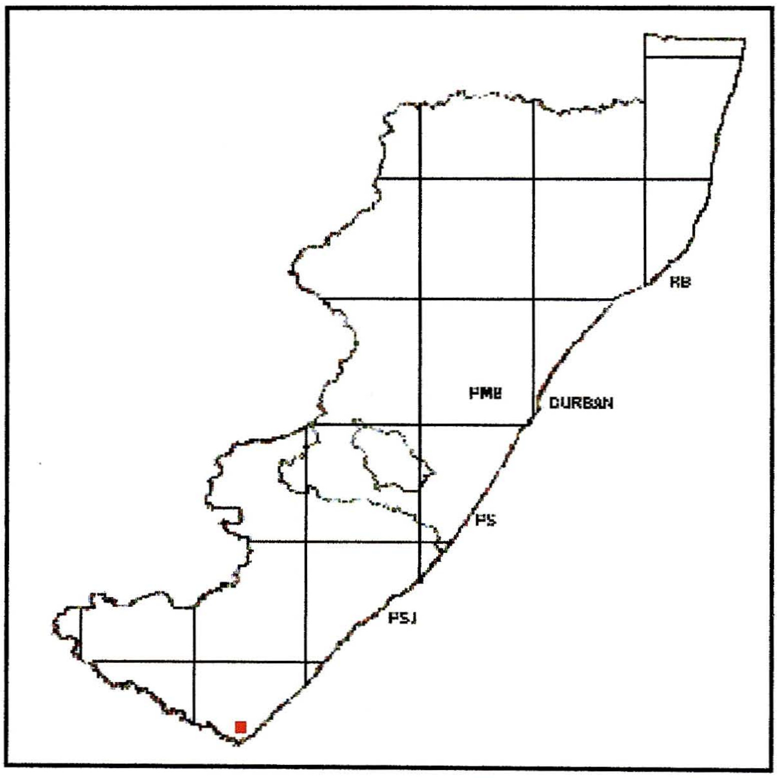


Figure 59: Distribution of *Bradypodion kentanicum*

4.3.5.5 *Bradypodion wezae* new species

Holotype:
LR 1120, an adult female, coll. 16-17 September 1981 by L.R.G. Raw (figure 60).

Type locality:
Weza, collected about 1 km from village on north side of road to Harding.

Diagnosis:
This small, almost neotenic, species has a feebly raised casque, and no longitudinal flank grooves. It is distinguishable from all other *Bradypodion* by the red colour of the gular grooves.

Description:
Snout moderate, distance from tip to anterior border of orbit is less than diameter of orbit. Casque not or only slightly raised; hardly produced posteriorly; median parietal crest convex. Posterior temporal (squamosal) crest meets lateral parietal crest at side of casque; median parietal crest raised to form a less-distinct ridge; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; lower temporal crest distinctly developed with posterior temporal crest tubercles reduced. Subocular tubercle raised and not bordering mouth. Colour of interstitial skin of gular grooves is red. Gular lobes all more or less equal in size. Gular lobes mostly triangular, distal tip not sharply papillate, without denticulate edges. Flanks do not have longitudinal grooves or striations. Posterior dorsolateral scales equal or sub equal. Flank tubercles slightly enlarged; forming a single row. Dorsal crest extends along tail; tubercles equal or sub-equal in a continuous series. Tail length is less than head-and-body length in both sexes, much shorter in females. Tail is slender without a distinct tip region.

Counts:
There are 15-23 gular lobes (mean 20 and median 21) and 46-60 dorsal tubercles (mean 53,2 and median 53).

Size:
Largest male (LR 1775): head and body length 58 mm; tail length 53 mm.
Largest female (LR 1120): head and body length 62 mm; tail length 50 mm.

Mass:
LR 2754 had a live mass of 2,4g.

Coloration in life:
Overall colour pale brownish, lighter longitudinal markings and some darker patterning may be indicated. Gular grooves a bright red. A photograph is provided (figure 61).

Hemipenes:

LR 1775 has both hemipenes everted. Sulci postero-laterally located. Three large apical rotulae are present, outer posterior being largest. Outer anterior rotula replaced by a series of three closely approximate much smaller rotulae. Surface smoothly calyculate with sulcus spermaticus terminating on outer lateral surface. Hemipenes more or less mirror-imaged. LR 1625 has both hemipenes everted and differs in that there are four apical rotulae with the outer posterior rotula largest. LR 1791 is similar but the anterior outer rotulae are not fully everted.

Reproduction:

Number of young: LR 1121 contains 10 developing eggs, 5 in each oviduct.. Neonates were found in late December. LR 2754 had black testes. There is a black visceral lining.

Field notes:

Found in tall grass and shrubs on road verges on the fringes of indigenous forest or in disturbed land. Not observed in the interior of either indigenous forests or exotic plantations.

Distribution:

Found associated with indigenous forests at Weza and Ingeli, possibly more widespread in the area between the Umzimkulu and Mtamvuna rivers (figure 62). A specimen collected on the road verge near Port Edward may have been transported from the interior by human agency.

Recorded localities and specimens examined:

Fifteen specimens examined.

Weza (3029DA): LR 1120, 1121 (coll. L.R.G. Raw, 16-17 September 1981), 1123, 1124 (coll. L.R.G. Raw, 1-3 December 1981), and 1625 (coll. L.R.G. Raw, 16 September 1982).

Ingeli Forest (3029DA): LR 1775, 1791 (coll. L.R.G. Raw & M. Pickersgill, 4 December 1982), 2680 (coll. J. Marais & L.R.G. Raw, 13 April 1991), 2754 (data not recorded), 2858, 2859, 2860, 2861, 2862 and 2863 (coll. D.R.J., L.A. & L.R.G. Raw, December 1991).

Sight Record:

Port Edward (3130AA): single specimen seen (collected by a Mr Stannard on road verge outside village, probable translocation from Weza area).

Paratypes:

The following specimens are designated as paratypes: LR 1121, 1123, 1124, 1625 1775, 1791, 2680, 2754, 2858, 2859, 2860, 2861, 2862 and 2863.

Etymology of specific name:

Latinised genitive of Weza.

Figure 60: Holotype of *Bradypodion wezae* new species (scale in cm)

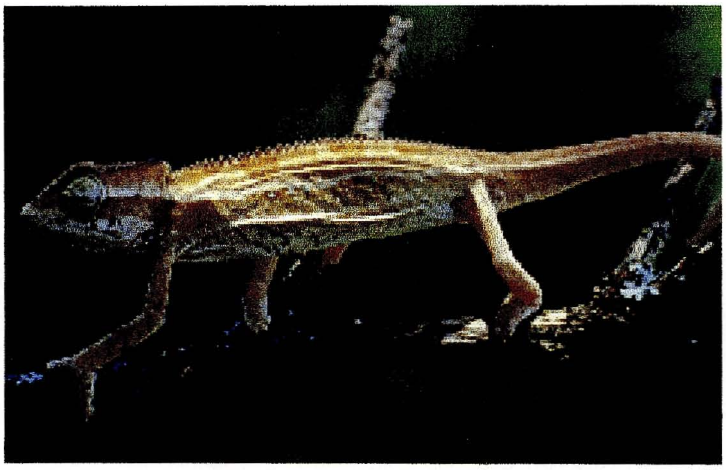


Figure 61: *Bradypodion wezae* from Weza, Harding District

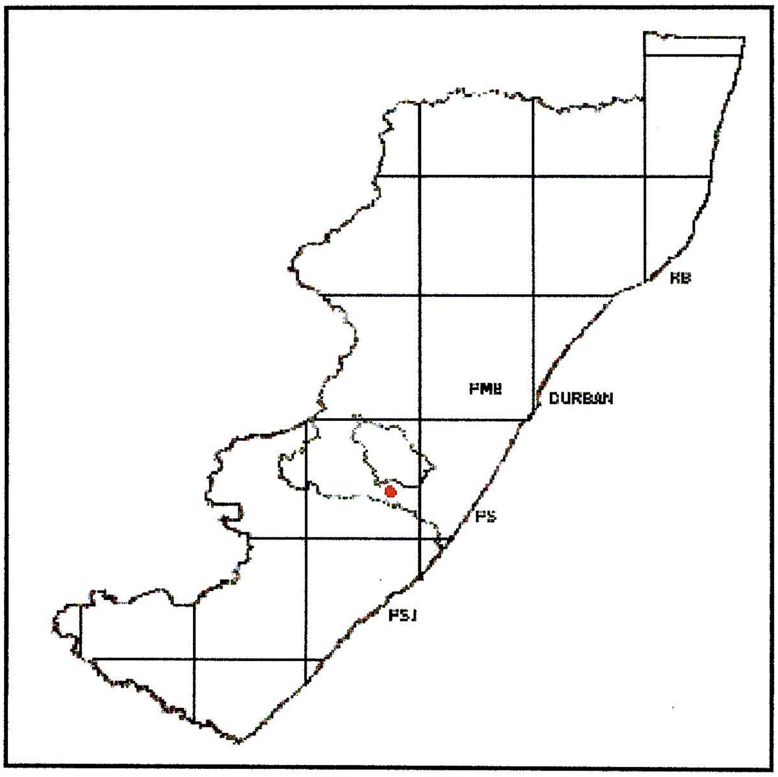


Figure 62: Distribution of *Bradypodion wezae*

4.3.5.6 *Bradypodion melix* new species

Bradypodion dracomontanum Raw, 1976: 157-158. (part, Donnybrook specimen only).

Holotype:

LR 1127, an adult male, coll. L.R.G. Raw, 18 September 1981 (figure 63).

Type locality:

Ixopo, on high-lying ridge 5-10 km south towards Umzimkulu.

Diagnosis:

This small species has a feebly developed casque. The posterior temporal crest joins the lateral parietal crest at the side of the casque. The posterior temporal crest tubercles are reduced or absent. The throat has white gular grooves.

Description:

Snout moderate, distance from tip to anterior border of orbit is slightly less than diameter of orbit. Casque not or only slightly raised; not produced posteriorly; median parietal crest slightly convex. Posterior temporal (squamosal) crest meets lateral parietal crest at side of casque; median parietal crest raised to form a less-distinct ridge; para-parietal tubercles present anteriorly; Inter-orbital tubercles present; lower temporal crests distinctly developed with posterior temporal crest tubercles reduced or absent. Subocular tubercle not raised and not bordering mouth. Colour of interstitial skin of gular grooves is white. Gular lobes all more or less equal in size with median lobes slightly larger. Gular lobes mostly triangular, distal tip not sharply papillate, without denticulate edges. Flanks do not have longitudinal grooves or striations. Posterior dorsolateral scales are equal or sub equal, not forming a discernable pattern of alternating larger and smaller scales. Flank tubercles slightly enlarged and forming a single row. Dorsal crest extends along the tail; tubercles equal or sub-equal. Tail longer than to less than head-and-body length in males, much less in females; slender without a distinct tip region.

Counts:

There are 16-21 gular lobes (mean 18,56 and median 18) and 43-55 dorsal tubercles (mean 48,6 and median 48).

Size:

Largest male has head and body length 64 mm and tail length 62 mm.

Largest female has head and body length 67 mm and tail length 47 mm.

Mass:

LR 2754 had a live mass of 2,4g.

Coloration in life:
Light brown with a lighter lateral streak (figure 64). A reddish brown lateral streak often present on the sides of the head. Gular grooves pale brownish white.

Hemipenes:
LR1127 – Ixopo – Both hemipenes everted. Sulci postero-laterally located. Four rotulae are present, inner larger than outer, with posterior being largest. A toothed ridge resembling the apical edge of a rotula lies along inner edge of apex between anterior and posterior rotulae. Inner anterior surface smoothly calyculate Hemipenes mirror-imaged.

LR 843 (described in Raw (1976) as *B. dracomontanum*) has everted left hemipenes short, broadening towards apex. There are four inward curving, denticulate, apical structures or rotulae with one pair positioned anteriorly and two posteriorly. Posterior pair projects far beyond anterior pair with their bases level with the tips of the anterior pair. The sides are irregularly calyculate. The sulcus spermaticus passes posteriorly around the base to the lateral surface, turning along length of organ between two fleshy lobes, terminating on distal lateral surface. Posterior lobe to sulcus continues as a high ridge posteriorly and on to apical structure. The right hemipenis is a mirror image of the left with the sulcus terminating on the outer lateral surface.

Reproduction:
LR 2798 contains 8 eggs, 5 in the right oviduct and 3 in the left. Testes of LR 2755 were white, but viscera of LR 2798 and 1127 are black pigmented. Females collected in September had no oviducal eggs.

Field notes:
Collected from tall grasses and other roadside vegetation amongst indigenous forests and plantations on the heights between Ixopo and Umzimkulu.

Distribution:
Known only from near Ixopo and Donnybrook (figure 65). Possibly fairly widespread in association with indigenous forest patches on the higher lying areas between the Umzimkulu and Umkomaas river valleys. Replaced by *B. thamnobates* at Bulwer. Reports of chameleons near Centacow mentioned by Hewitt (1937) were thought to involve this species. A survey on 27 October 1991 that found chameleons in forests near Riverside and between Centacow and Bulwer showed that these resemble *B. thamnobates* and are not the present taxon. A specimen (LR 843) from Donnybrook, regurgitated by a freshly caught snake, *Psammophis crucifer* (G. Setaro, pers. com.), was originally referred to *B. dracomontanum* (Raw, 1976).

Recorded localities and specimens examined:

Nine specimens examined.

Donnybrook (2929DD): LR 843 (coll. G. Setaro, August 1976) (damaged).

Ixopo, 5-10 km south on road to Umzimkulu (3030AA): LR 1127, 1128 (coll. L.R.G. Raw, 18 September 1981), 1630 (coll. L.R.G. Raw, 14 September 1982), 1688 (coll. L.R.G. Raw, September 1982), 1707, 1708, 1709 and 1710 (coll. L.R.G. Raw, 18 September 1981), LR 2755, LR 2759, LR 2760 (coll. D.R.J., L.A. & L.R.G. Raw, December 1991), LR 2792, LR 2798 and LR 2827 (coll. L.R.G. Raw, 1992-1998).

Paratypes:

The following specimens are designated as paratypes: LR 1128, 1630, 1688, 1707, 1708, 1709 and 1710, LR 2755, LR 2759, LR 2760, LR 2792, LR 2798, LR 2827.

Etymology of specific name:

A coined name derived from the first syllables of *melanocephalum* (mel) and Ixopo (ix), hence "melix", a noun in apposition.

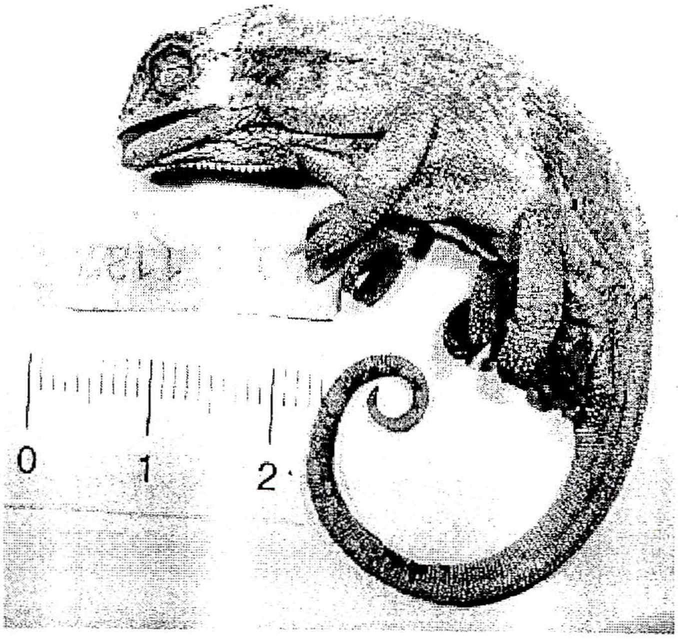


Figure 63: Holotype of *Bradypodion melix* new species (scale in cm)

Figure 64: ***Bradypodion melix*** **from near Ixopo**

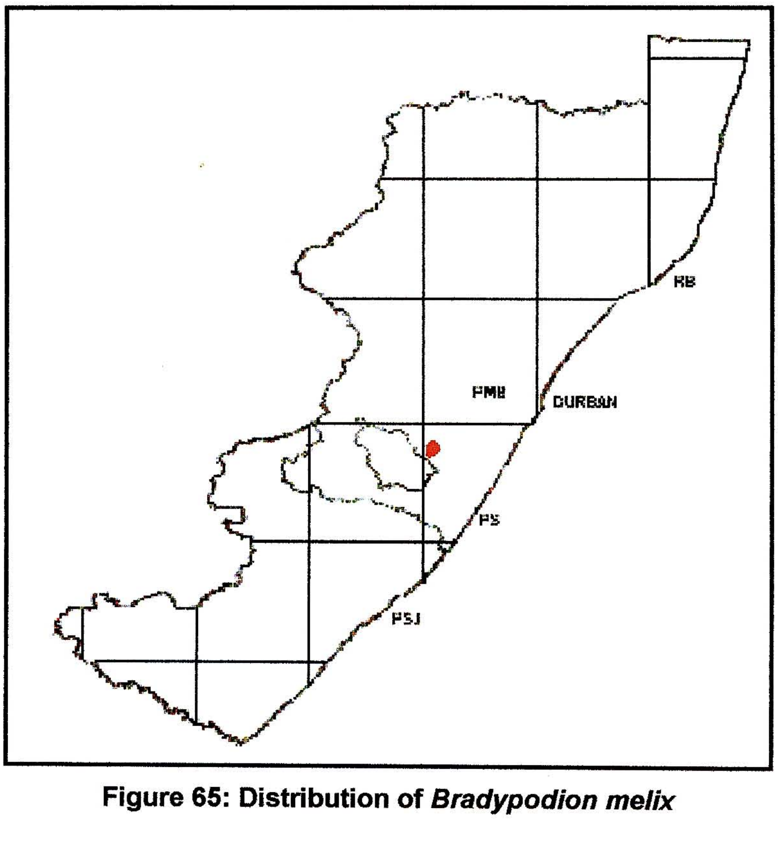


Figure 65: Distribution of ***Bradypodion melix***

4.3.5.7 *Bradypodion* species *incertae sedis* (related to *B. melanocephalum*)

At least three other populations are present in the study area that cannot be assigned to the above species with any certainty (figure 68). They are discussed below.

4.3.5.7.1 Waterfall specimen

One specimen, AJL 1907, collected by A.J.L. Lambiris at Waterfall, Hillcrest District, KwaZulu-Natal on 10 October 1983. Lambiris (pers. com.) states that the living specimen was green in colour, slightly paler ventrally, with yellow-orange gular grooves. This description excludes it from typical *B. melanocephalum*.

4.3.5.7.2 Southport specimens

LR 2721 collected near Southport (3029DA) (early 1978, G A Setaro); TM82886 next to the Mahlangamkulu River near Southport, below 100m a.s.l. (3030CB) (9 February 1999, W.R. Schmidt).

Remarks:

These two specimens have lower dorsal counts (28 & 29 respectively) than all other *B. melanocephalum* examined (32-55, mean 42). TM 82886 (figure 66) was collected at 21h35. It was found sleeping exposed on the top of a reed stem. Two juveniles were found in similar positions.

Habitat: Inundated grassland and waterlogged reed bed, surrounded by coastal forest and sugar cane. LR 2721 was found basking on a termite mound in grassland during the day. A report of dwarf chameleons from Umzinto (M. Hlengwa, pers. com.) requires confirmation in the form of specimens and could indicate a link between the Warner Beach and Southport populations.

Reproduction:

W. D. Haacke (Head Curator, Transvaal Museum) provided information on TM 82886 which produced 8 young (1 stillborn) on 21st March 1999.

4.3.5.7.3 Ngqeleni specimen

Lophosaura melanocephala (Gray, 1865); Power, 1932: 217, pl. III; fig.1. (part, Ngqeleni).

Lophosaura caffer (Boettger, 1888); subspecies, Hewitt, 1935: 302, pl. XXVIII, figs. 2 and 5. (Ngqeleni, Transkei).

Microsaura melanocephala Gray, 1865; FitzSimons, 1943: 160–161. (part., Ngqeleni).

Bradypodion kentanicum (Hewitt, 1935); Raw, 1995, app. 1: 14 (part., Ngqeleni).

Ngqeleni (3129CA): AMG 2431 (figure 67). (Note: an attempt to collect further material from this locality in December 1991 was unsuccessful.)

Possible record: Mqanduli (3128DD): AMG 6980 (8 specimens). These newborn specimens were not examined due to their small size. It is quite possible that they may be representatives of the *B. ventrale* group that has been collected at both Butterworth and Umtata. Further collecting is needed to confirm this record.

Remarks: This specimen originated from an isolated area of Eastern Province Thornveld and is separated from the Kentani population by unsuitable habitat that is thought to form a barrier between the two populations. Hewitt (1935), when describing *Lophosaura melanocephala kentanica* referred to this specimen as an un-named subspecies of *B. caffrum*.

4.3.5.7.4 Other Transkei localities

Although there have been reports of chameleons in the north of Transkei near Centacow (Hewitt, 1937), no specimens had been collected until 1992 when specimens were found near Riverside and between Centacow and Bulwer. These appear to be related to *B. thamnobates*. Apparently, dwarf chameleons also occur at Mount Frere (M. M. Tukela, 1991, pers. com.) but an attempt to obtain specimens was unsuccessful.

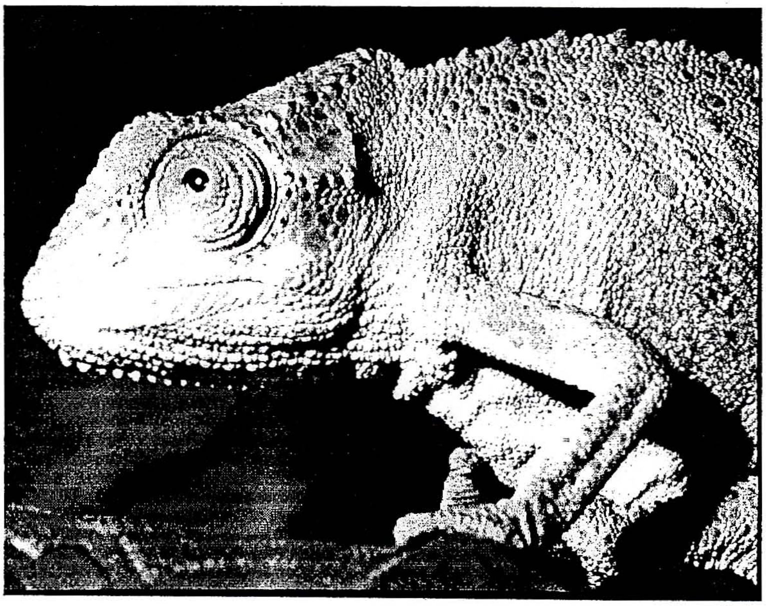


Figure 66: Specimen from Southport
(Photograph by W. Schmidt, courtesy of W.D. Haacke)

Figure 67: Albany Museum specimen from Ngqeleni

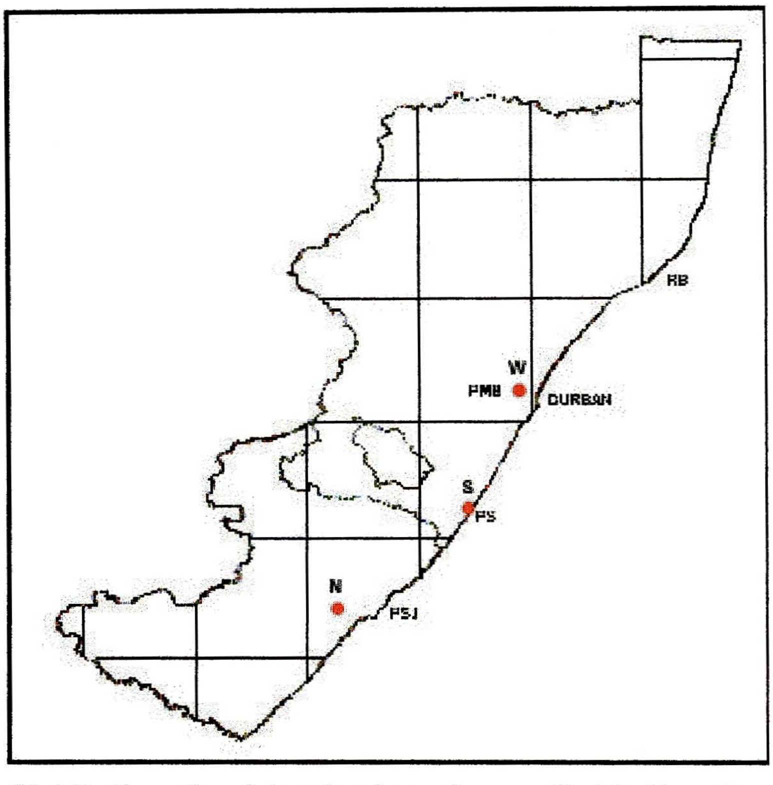


Figure 68: Distribution of undetermined specimens allied to *B. melanocephalum*

(W = Waterfall; S = Southport; N = Ngqeleni)

5 BIOGEOGRAPHY

5.1 The aspects of biogeography

Biogeography may be defined as the study of the distributions of organisms both past and present. Essentially there are two components. One, concerned more with the causes and effects of present ecological constraints, is known as ecological biogeography (Myers & Giller, 1988) or distribution ecology (Hengeveld, 1990). The other, concerned more with reconstructing the sequences of origin, dispersal and extinction of taxa, is known as historical biogeography (Myers & Giller, 1988) or dynamic biogeography (Hengeveld, 1990). Hengeveld (1990) defines dynamic biogeography as 'the analysis and understanding of spatial biological phenomena in terms of past and present factors and processes'. He contrasts this with what he calls 'synoptic ecology' or 'distribution ecology', stating that the two disciplines differ in both the scale and direction of their approaches. Synoptic ecology looks from local through to broader, global scales while dynamic biogeography focuses in from broad to narrower perspectives in order to examine and explain broad-scale phenomena. Hengeveld also makes the important point that the boundaries of the disciplines overlap and cannot be clearly defined. A further important point that he makes is that while 'the immediate aim of dynamic biogeography is to describe and explain spatial patterns and processes of taxa, its ultimate goal is to aid our understanding of evolutionary processes'.

5.2 Description of study area

The study area is in the southeast of the continent of Africa, between the great escarpment of the Drakensberg range on the west and the coastal littoral fringing the Indian Ocean on the east. The land rises rapidly from sea level to over 3000 metres a.s.l. in a series of scarps deeply incised by the courses of numerous relatively short, fast-flowing rivers. The geology consists of a succession of more or less horizontal strata of sandstones, tillite and shales of the Cape / Natal and Karoo sequences of deposits underlain by granites of the basement. Overlying this are the shales and sandstones of the Beaufort series and above this the basalts of the Stormberg series. This last deposit was accompanied by the formation of numerous dolerite dykes and sills within the underlying strata. It is these, along with the harder strata of the Cape / Natal series sandstones that have resisted erosion and remain as the upland areas now inhabited by a number of the *Bradypodion* taxa discussed in this review. The major geomorphic feature of this region has been the development of the Natal Monocline (King, 1982), a seaward tilting of the rock strata along an axis from the Ciskei to Swaziland (Partridge & Maud, 1987). This tilting has been accompanied by the formation of numerous faults in the rock strata.

5.2.1 Historical geomorphology

Partridge and Maud (1987) examined the geomorphic history of the areas now known as KwaZulu-Natal and the northeastern part of the Eastern Cape (Transkei) in an investigation of the evolution of land surfaces of southern Africa since the Mesozoic. They observed that important Gondwana surface features have affected subsequent geomorphic evolution in southern Africa. These are the initial high elevation of the African continent, the existence of the Cape Fold Mountains that had formed by the end of the Lower Triassic (Truswell, 1970; Kent, 1980), the overall westward trend of the drainage and the presence of tabular, Karoo-sequence rocks beneath most of the land surface.

The rifting and break-up of Gondwana began some 200 Ma (million years before present). This cycle continued until some 120 Ma. The initial phases of disruption, during the Jurassic to early Cretaceous, laid out the future continental fragments through faulting, flexure of the basement and the development of narrow marine troughs. Both basic and alkaline igneous activity was widespread (Read and Watson, 1975). South African examples of each type are the Drakensberg and Lebombo volcanics respectively which have been radiometrically dated at early Jurassic for the former and early Cretaceous for the latter (Kent, 1980).

Partridge and Maud (1987) estimate that the pre-rifting surface had an elevation of 1800m at Kimberley, in the northern Cape, and 2350m at Letseng Le Terai in Lesotho. This would be an appropriate elevation for the ancestors of *Bradypodion* to have evolved since all its members show an ovoviviparous mode of reproduction that is more likely to evolve in areas of low temperatures such as found at high altitudes (Shine & Bull, 1979). Partridge and Maud's concept differs from that of King (1962) who thought that considerably lower elevations of around 600m were likely. In any event, the separation of eastern Gondwana (Antarctica) resulted in a steep scarp face on the eastern seaboard. This was subjected to intense erosion and the scarp face has now receded some 200 km inland and has been dissected by numerous river valleys. The principle geomorphic events since the Mesozoic as recognised by Partridge and Maud (1987) are listed in table 5 below.

5.2.2 Climatic factors

The study area falls within the summer rainfall region. The subtropical coast climatic zone generally has humid, wet summers and warm, but drier winters and the plateau slopes zone has warm, wet summers and warm, dry winters (Reader's Digest, 1984). Most of the 500-1000 mm per annum of rain falls between November and April. This summer rain results from the effects of the Inter Tropical Convergence Zone and often falls in the form of thunderstorms. Some 125-375 mm of rain also falls in winter as cold fronts move in from the southwest. The variation in rainfall shows a deviation of some 15-25% over the years. Humidity is high with ranges from 50% to over 70%. Average temperatures vary from 10-20°C in July to 17,5-27,5°C in January but temperatures of below 0°C and above 40°C may occur, particularly further inland. This area has less sunshine than most of southern Africa with less than 60% for most of the area but up to 70% in parts. Hail is possible in summer while occasional snow may fall over the higher areas in winter. Frosts occur at higher altitudes during winter. The tendency of rain-bearing winds to blow from the south-west while the topography is dissected by deep river valleys running south-east to the sea causes local variation in rainfall with the south-facing slopes of the valleys experiencing cooler, wetter conditions than the north-facing slopes which receive more direct insolation and are drier through being in the rain shadow.

Table 5: Geomorphic events since the Mesozoic (after Partridge & Maud, 1987)

Break up of Gondwanaland through rift faulting and initiation of the Great Escarpment in the late Jurassic to early Cretaceous (ca. 100 - 150 million years ago (Ma)).
African cycle of erosion leading to advanced planation throughout the subcontinent up until the end of the early Miocene (ca. 18 Ma).
Moderate uplift of 150 - 300m with slight westward tilting of the African surface and limited coastal monoclinal warping at the end of the early Miocene (ca. 18 Ma).
Post-African I cycle of erosion forms imperfectly planed Post-African 1 surface from early mid-Miocene to late Pliocene (ca. 2,5 - 18 Ma).
Major asymmetrical uplift of up to 900m in eastern marginal areas and tilting to westward of interior land-surfaces with monoclinal warping along eastern and southern coastal margins during late Pliocene (ca. 2,5 Ma).
Post-African II cycle of major valley incision, especially in the southeastern coastal hinterland from late Pliocene onwards (ca. 5 Ma).
Climatic oscillations and glacio-eustatic sea-level changes, during the late Pleistocene (ca. 1,2 Ma) to Holocene, result in low-level marine benches, coastal dunes deposits and river terraces.

5.2.3 Vegetation patterns

The study area lies within the Tongaland-Pondoland Regional Mosaic (Moll, 1978; White & Moll, 1978) which itself extends from the mouth of the Limpopo River south to near Port Elizabeth. Reference to Acocks' map of the Veld Types of South Africa shows that the following veld types fall within the study area. The descriptions that follow have been based on those provided in the accompanying publication (Acocks, 1988).

Coastal Forest and Thornveld - This is a more or less open thornveld with numerous and extensive patches of forest. The grassveld constituent is scrubby, full of tall herbs, shrubs and tall coarse grasses, showing a strong successional movement towards forest. The forest is mostly short (5-10 m high), very dense and tangled, but taller (ca. 20 m high) and less tangled further inland. The upper boundary ranges from about the 450 m contour in the north, down to

the 300 m contour in the south. Acocks (1988) divides the veld type into 5 subtypes. The relevant subtypes are as follows: -
Typical Coast-belt Forest (Acocks' veld type 1a) - very species-diverse forests occurring in small patches within scrubby thornveld on a steeply rolling topography consisting of a maze of ridges between numerous rivers. Both *B. melanocephalum* and *B. setaroi* occur within this subtype and appear to be restricted to altitudes below 150 m above sea level. Much of this veld type has been eliminated by agriculture (particularly sugar cane plantations), forestry and urban development.

Zululand Palm Veld (Acocks' veld type 1b) - this mainly occurs on sandy, poorly drained soils in the area to the north of the Tugela River. This distribution coincides with a gap between the ranges of *B. setaroi* and *B. melanocephalum* along the coast. The reason for this apparent barrier and unsuitability for these chameleons is not immediately obvious.

Dune Forest (Acocks' veld type 1d) - this occurs in a narrow belt along the row of high dunes that follow the east coast. The forest is stunted on the seaward side and taller on the landward side. Where the forest has been removed, it is replaced by a scrubby thornveld of generally subtropical affinities although some Fynbos species occur, especially to the south and in loose, disturbed, sand. Chameleons are not known to occur in this subtype. The wind-driven salt spray may inhibit the occupation of this subtype by chameleons.

Mangrove Forest (Acocks' veld type 1e) - this specialised forest type occurs in limited patches on mudflats at the mouths of some rivers. The largest occurrence, in Durban Bay, has almost been eliminated by harbour expansion. While *B. setaroi* has been found in reed beds and non-forest wetland areas adjacent to Mangrove forest, it is not known whether chameleons actually occupy this habitat.

Pondoland Coastal Plateau Sourveld (Acocks' veld type 3) - this is found on an elevated plateau some 300 to 450 m above sea level. The plateau rises steeply from the coast and is deeply broken and indented by forest-filled gorges. The escarpment is forest covered, tropical at the coast and sub-tropical on its upper slopes. It shows an affinity to the Knysna Forest and differs from the coastal forest mainly by the significant presence of the Yellowwood trees, *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb. *Bradypodion caffrum* and its allies inhabit the coastal and gorge forests. The plateau itself has a substrate of sandstone covered by a very dense and vigorous grassveld, very sour in areas of high rainfall. Outliers occur on The Heads at Port St Johns with conspicuous fynbos elements. This veld type has interesting links to the Knysna Forest and Fynbos in the south and the high altitude sour grassveld types of the former Transvaal. These may have significance in evaluating the historical biogeography of the associated chameleon species. *B. caffrum* shows a resemblance to *B. damaranum* of the Knysna Forests and the *B. transvaalense* group from upper KwaZulu-Natal and the

Mpumalanga and Northern Province escarpment in having a higher casque than all the other species considered here, only *B. nemorale* coming close.

'Ngongoni Veld (Acocks' veld type 5) - This is found in a narrow and irregular belt of rolling country just above the Coastal Forest belt. It lies on the slopes of the lowest of the series of escarpments that rise from the eastern seaboard, between 450 - 900m a.s.l. and is cooler and less humid than the coast. The natural vegetation is forest and scrub-forest with tropical affinities, but this has been replaced for the most part by sour grassveld dominated by 'Ngongoni grass (*Aristida junciformis* L.). Major forests, which still survive, are the Weza, Qudeni and Nkandla forests that are important habitats for dwarf chameleons. Away from the forests, the veld type consisted of open thornveld with a well-mixed redgrass (*Themeda* Forsk.) dominated sourveld. As happened with the forest, this has mostly been replaced by 'Ngongoni grassland. The veld type occurs on ridges separated by lower lying riverine valley bushveld on the seaward and lower boundaries. In the western and upland boundaries it occurs in valleys between ridges which are covered with Highland or Döhne Sourveld or KwaZulu-Natal Mist Belt 'Ngongoni Veld. The veld type supports both *B. nemorale* and *B. wezae*.

Zululand Thornveld (Acocks' veld type 6) - this veld type forms a link between the 'Ngongoni Veld and the Lowveld Sour Bushveld and the Lowveld. It has a strong Bushveld affinity and has probable forest and scrub-forest origins. It lies in a similar position to the 'Ngongoni Veld on the first escarpment from 150 to 1050 m above the sea and replaces that veld type from just north of Melmoth. The rainfall ranges from 650 to 1000 mm per year. Two forms are recognised by Acocks, (a) the Low Altitude Form with forests of tropical affinity persisting in narrow fringes along streams and on the hills at the upper limits. Otherwise, the vegetation consists of bushveld, which thins at higher altitudes and in parts thins to become *Acacia* Mill. thornveld. (b) The High Altitude Form with more open veld containing patches of persistent short forest and scrub occurs on the higher ridges such as the Lebombo range on which it is well established. For the most part, it is not suitable for dwarf chameleons and the drier parts are more likely to operate as a barrier to their dispersal. This seems to be confirmed by the fact that no specimens were collected at the Hlatikulu Forest at Gwaliweni even though searched for by researchers working on another project in the forest (D. Muir, pers. com.).

Eastern Province Thornveld (Acocks' veld type 7) - only the northern form of this veld type occurs in the study area. The damper areas of this veld type appear to form the typical preferred habitat of *B. kentanicum*. This veld type replaces the 'Ngongoni Veld in the south much as the Zululand Thornveld does in the north. It is found south of the Mzimvubu River in central Transkei where it is initially found inland of the 'Ngongoni Veld. From the vicinity of Ngqeleni and southwards it replaces the 'Ngongoni Veld completely. The topography is steeply rolling. The vegetation is essentially thornveld, often very open, almost grassveld, but the climax vegetation would be short forest and scrub-forest. These forest relicts are rare and mainly occur along streams. The rainfall ranges from ca. 500 to 900 mm with 600 to 750 mm more usual.

KwaZulu-Natal Mist Belt 'Ngongoni Veld (Acocks' veld type 45) - this is transitional between the 'Ngongoni Veld and the Highland Sourveld between 900 to 1350 m a.s.l. The rainfall is higher with 900 - 1150 mm per year and frequent mists. This is an important habitat type for *Bradypodion* species with the species *melix*, *bourquini*, *nebula* and *tilburyi* occurring within its forests. There has been a reduction of the forest component except for the upper margin, in which *Podocarpus* L'Hérit. Ex Pers. spp. dominates. The lower-lying forest has more affinity with coastal forests. The grassveld component was originally *Themeda* dominated sourveld but *Aristida junciformis* has largely replaced it. Exotic timber species now cover much of this veld type with large areas invaded by American Bramble.

Moll (1978) and White & Moll (1978) include veld types 1, 2, 6, 10, 23 and 24 within the Tongaland-Pondoland Regional Mosaic and point out that types 3 and 5 are transitional between Afromontane and Tongaland-Pondoland vegetation. Veld types 7 and 45 are omitted from their account, presumably because veld type 7 only occurs south of their Tongaland-Pondoland region and veld type 45 has Afromontane affinities. The Tongaland-Pondoland Regional Mosaic shows overwhelming tropical affinities due to the warming effects of the Mozambique Current. The climate can vary rapidly over short distances often resulting in great contrasts between xerocline and mesocline vegetation and between the deeply incised river valleys and slopes and the plains. The valleys are profoundly influenced by dry 'berg' winds while the vegetation, generally, is greatly influenced by the underlying geology and soils which differ in their nutrient status and water relations. The valley vegetation shows affinities with the Zambesian flora while vegetation of Cape affinities may occur in nutrient deficient sandy soils. Endemism is fairly well pronounced in the flora of this region with one, almost completely endemic plant family and 23 endemic plant genera. Endemic species include more than 200 of the larger woody plants. White and Moll (1978) believe that there is evidence to suggest that this region has served as a refuge for floral genera, which formerly had a more widespread distribution on the African continent. They also believe that the area has also been a region of recent diversification. This is in accord with the situation as seen in chameleons and *Streptocarpus*.

5.3 Dispersal pathways and barriers

The identification of paths for the dispersal of organisms provides a geographical basis for the understanding of the evolutionary history of these organisms. Insurmountable barriers will prevent dispersal into the areas beyond the barriers while barriers that are only occasionally overcome will cause very restricted gene flow and a founder effect more likely to cause speciation in the vicariant population. Barriers that arise after initial dispersal will result in the separation of palaeo-endemic taxa while those barriers that are overcome by small numbers of pioneer individuals may eventually result in the addition of neo-endemic taxa.

5.3.1 Pathways to dispersal

The present distribution of dwarf chameleons is presumably the result of past dispersals and therefore the pathways for dispersal are of interest in attempting to understand the evolution and origins of the present taxa. There appear to have been at least four major avenues for dispersal running more or less parallel in a southwest to northeast direction. These are firstly, the coastal plain which becomes increasingly narrow towards the south and disappears south of the Umtamvuna River; secondly, a first escarpment linking the high interior north of the Tugela with the dissected ridge that follows the Transkei coast before deviating from the coast near Port Edward and continuing as an inland feature through the KwaZulu-Natal coastal hinterland and across the Tugela River into Zululand; thirdly, a second parallel but higher escarpment crossing the Midlands further inland; and fourth, a pathway along the seaward slopes of the Drakensberg Mountains. It would appear that successive uplifting has occurred in the geological past (see table 2) and this may have resulted in the formation of pathways of suitable moist forest habitat encouraging chameleon dispersal. These paths for dispersal would eventually be interrupted as rivers eroded deep valleys and as the rainshadow effect of the prevalent southwest to northeast weather patterns created unsuitable hot and arid areas. The continued presence of dwarf chameleons is dependent on the presence of suitable habitat. The present vegetation of the study area is detailed in section 5.2.3 above. Of the veld types listed, only 1a, 3, 5, 7 and 45 appear to be able to sustain dwarf chameleon populations in the long term as they have higher rainfall, often with mist, and can support forests unlike the drier thorn bush areas.

5.3.2 Barriers to dispersal

The main barriers to the dispersal of these dwarf chameleons appear to be areas where hot and dry conditions (such as found on the north-facing aspects of the numerous river valleys of the study area) prevent their survival for even a short time. This results from their dependence on virtually constant daily supplies of water in the form of droplets on the leaves or stems of plants (personal observation of captives and in the field). This means that they are unable to cross any area where arid conditions are found. Veld types 6, 10, 11 and 23 form areas of much drier and more open habitat (less than 600 mm annual rainfall) where these smaller species of *Bradypodion* would soon succumb to desiccation.

In the coastal areas the presence of large rivers may also act as barriers that restrict the dispersal of *Bradypodion* species. The major riverine barrier along the coast appears to be the wide and relatively fast-flowing Tugela River separating the species *B. melanocephalum* and *B. setaroi*.

Further inland the erosion of river valleys has formed insurmountable barriers of unsuitable habitat. This has fragmented what was presumably an originally continuous population into the present series of isolated populations on relicts of the former land surface roughly parallel to the coast. For example, the Umzimkulu River Valley separates *B. melix* and *B. wezae* and the Umkomaas River Valley separates *B. melix* and *B. bourquini*. In these cases it is likely that it is the arid environment of the valleys that forms an insurmountable barrier rather than the physical presence of flowing water preventing the passage of poor swimmers such as these lizards. The marked north-east to south-west contrast in rainfall and vegetation restricts the suitable dwarf chameleon habitat to the wetter south-west facing slopes and summit areas of the ridges while the intervening river valleys contain hostile xerophytic Valley Bushveld that form barriers to prevent the dispersal of the moisture-dependent *Bradypodion* populations.

5.4 Biogeography of *Bradypodion*

5.4.1 Historical biogeography

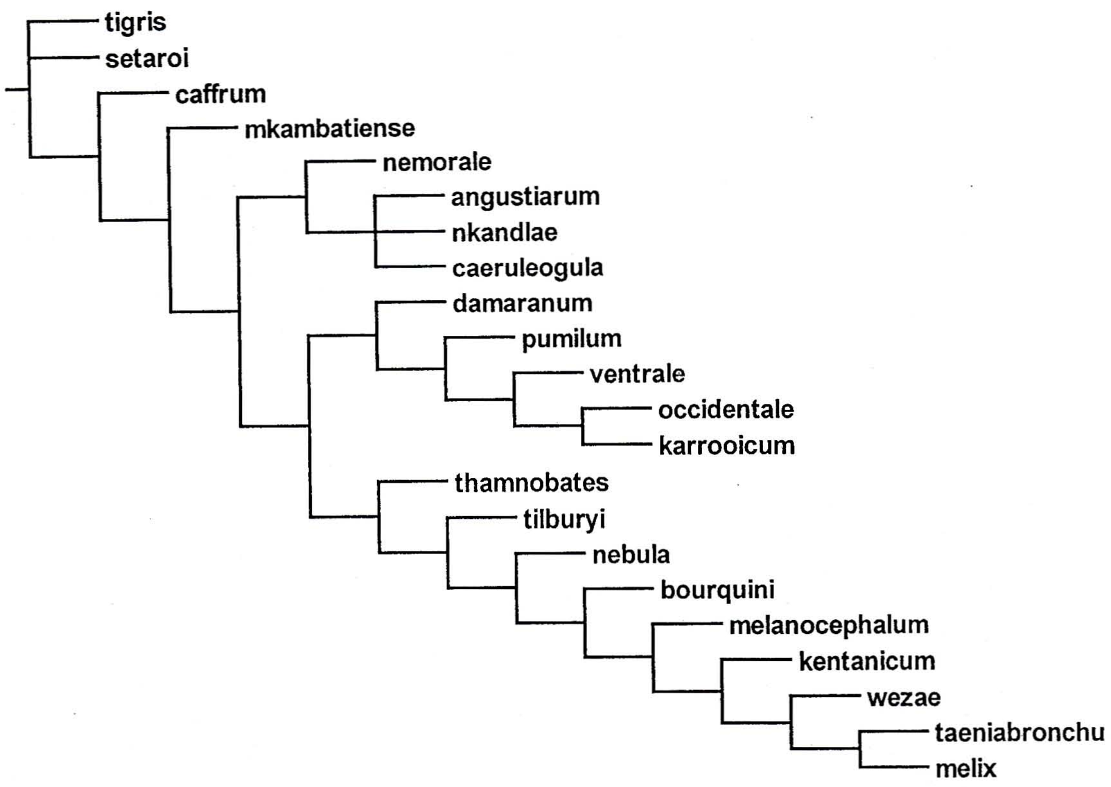
The historical biogeography of chameleons is essentially post-Gondwanan. In a cladistic analysis of the relationships of the chameleons Rieppel (1987) proposed that *Brookesia* is the sister group to all other chameleons while *Bradypodion* is the sister group to *Rhampholeon* and *Chamaeleo*. An alternative proposed by Klaver & Böhme (1986) included *Rhampholeon* with *Brookesia* as a sister group of *Bradypodion* which in turn was a sister group of all other chameleons. More recently, Rieppel & Crumly (1997) have suggested that chameleon relationships may be defined by three basic clades, *Brookesia*, *Rhampholeon* and *Bradypodion-Chamaeleo*. Whichever arrangement is considered, it seems reasonable to hypothesise that the taxa ancestral to *Brookesia*, *Rhampholeon*, *Bradypodion* and *Chamaeleo* occurred along the area of the east coast of Africa and Madagascar that were still part of a single landmass before being divided by the separation of the Mozambique channel during the Cretaceous period (Rabinowitz *et* al, 1983). Hofman *et* al (1991) obtained an estimate of the timing of the divergence of *C. quilensis* and *C. pardalis* that fits well with this separation. Interestingly they also found a similar divergence time between *C. tigris* and *C. pardalis*. Subsequent isolation of a southern population led to the evolution of the ancestor of *Bradypodion*. This isolation probably had its origins in climatic and geomorphic changes. It was later maintained by the incision of the hot and dry Limpopo River valley until, geologically more recently, when more derived, savannah-adapted chameleons were able to cross this barrier.

The biogeography of the genus *Bradypodion* seems to indicate a history of dispersal and vicariance, much as the biogeography of most species groups. While palaeontological evidence of the historical biogeography of *Bradypodion* is lacking, there is some biochemical evidence. Hofman, *et al* (1991) compared three *Bradypodion* taxa during a study of immunological distances within the chameleons. These were *B. thamnobates*, *B. melanocephalum* and *B. setaroi*. They state, 'They are geographically reproductively isolated from each other and in the case of *setaroi* this coincides with the fixation of some unique alleles. For the moment these taxa are best considered rather recently diverged species with their origins in the late Pleistocene, when a former continuous distribution was broken into discontinuous patches due to climatic changes (Hamilton, 1976; Brain, 1981)'. From this it would seem that they concur with Raw (1976), 'it seems preferable to maintain the various known forms at the species level at this stage until their relationships are better understood'.

Kingdon (1990) wrote: 'Many puzzling anomalies in biogeography are partly explained by the progressive restriction of older forms to more difficult and outlying zones where they may become more or less specialised. It is a pattern that suggests itself for many plants and animals. This is also not inconsistent with a more limited regional theatre in which ancestral populations first evolved and flourished in the southern half of the continent only to become progressively more and more restricted. This may have happened to a genus of chameleons, *Bradypodium* (sic) which has fourteen species confined to South Africa. Their original range may well have contracted under pressure of competition from the dominant tropical genus *Chamaeleo*.' On the contrary, it seems that the species of *Bradypodion* have been restricted by their specialisation for habitat types that are dwindling due to climate changes and the effects of human modification of the environment rather than being affected by competing *Chamaeleo*.

5.4.2 Indications for historical biogeography from cladistic analysis

The species shown on tree 3 below are discussed as they appear from top to bottom of the tree. The tree should be regarded as preliminary and as more character and taxa are added it is likely to become a more accurate portrayal of the evolution of these taxa. Nevertheless it can be used 'as is' as a basis for formulating a hypothetical explanation of the historical biogeography of *Bradypodion*.



Tree 3: Tree diagram of selected species of Bradypodion (based on Tree 2).

The outgroup species, *Calumma* (or *Chamaeleo*, depending on opinion) *tigris*, occurs on the Seychelles, a granitic island group of continental origin, and is considered to have arisen through vicariance. It has been isolated from the other species for some considerable time (Hofman *et* al, 1991) probably as least as long as the separation of the *Bradypodion* lineage from other chameleons.

The historical biogeography suggested by the tree indicates an early dispersal in coastal forest (phase 1) with the species, *B. setaroi*, *B. caffrum* and *B. mkambatiense* perhaps representing relict populations after subsequent vicariance events, perhaps sea-level changes or riverine barriers. This seems to have been followed by two more or less simultaneous radiations (phase 2), one leading to a secondary inland forest dispersal now represented by the following species, *B. nemorale*, *B. angustiarum*, *B. nkandlae* and *B. caeruleogula* which have probably split off from an original continuous range of a single taxon after the division of that range by the erosion of deep river valleys. The second radiation also indicates a division into two (phase 3), the first part apparently spreading initially southwards then radiating into the more arid environments of the interior and western coastal areas. This initial dispersal is now represented by the species *B. damaranum* and *B. pumilum*, presumably formed by the separation of an initial single taxon by tongues of arid habitat extending to the coast. The second dispersal into the more arid interior has led to the evolution of *B. ventrale*, *B. occidentale* and *B. karrooicum* and their relative *B. gutturale*, presumably as the result of habitat fragmentation due to climatic change or because of the mountain ranges causing bottle-necks to gene exchange as these populations spread.

The second apparent dispersal (phase 4) seems to have entered the area along the escarpment that runs from the Transkei coast inland through the KwaZulu-Natal Midlands. This initially appears to have formed a radiation in the central Midlands where subsequent division of the initial taxon by the erosion of deep river valleys has left the isolated populations now represented by *B. thamnobates* (and its relatives *B. dracomontanum* and *B. transvaalense* that have themselves since radiated into the Drakensberg escarpment) as well as *B. tilburyi*, *B. nebula* and *B. bourquini*. This seems to have been followed by a further coastal dispersal southwards that resulted in *B. melanocephalum* and *B. kentanicum*. This seems, in turn, to have led to a further dispersal into the southern areas of the same escarpment that produced the representatives *B. wezae* and *B. melix*. Once again this escarpment radiation has probably become divided into vicariant species as a result of river valley erosion. A synchronous or possibly subsequent southern dispersal seems to have produced *B. taeniabronchum* in the south of the Eastern Cape. This species appears to have been split off from the other species by the tongue of arid habitat that reaches the coast between East London and Port Elizabeth.

Without the support of palaeontological or molecular evidence this interpretation must remain purely speculative even though the explanation does not seem infeasible as it stands. The more recent phase 4 radiation (and perhaps the phase 3 radiation as well, but this is outside the scope of this study) seems likely to have taken place during the late Quaternary and would be likely to have been affected by the same vicariance events and environmental factors as the plants, butterflies and monkeys discussed below.

5.5 Biogeographic comparison with other taxa in the study area

One method of testing hypotheses in historical biogeography is to compare the distributions of different organisms with similar ecological requirements in order to establish whether they have responded to the same causative factors. In this case we are able to compare the distributions of some rather different organisms in order to find out if similarities are present. These are the genus *Streptocarpus* (Hilliard & Burtt, 1971), the samango monkey (Lawes, 1990) and the Satyrid butterfly species *Paralethe indosa* and *P. dendrophilus* (Quickelberge, 1993).

5.5.1 Distribution of *Streptocarpus* species

The genus *Streptocarpus* Lindl. of the plant family Gesneriaceae has a wide range over Africa and Madagascar that, in many ways, coincides with that of chameleons. The genus has been thoroughly reviewed, both taxonomically and biogeographically, by Hilliard & Burtt (1971).

Comparison of the KwaZulu-Natal and Transkei species of *Streptocarpus* may indicate a shared evolutionary history for some of the endemic taxa of both genera.

Hilliard & Burtt (1971), in their assessment of evolution in the genus *Streptocarpus*, assert that KwaZulu-Natal is a centre of recent evolution and speciation rather than the primary centre of evolution. This opinion concurs with the conclusions of Hofman *et al* (1991) for *Bradypodion*. Hilliard & Burtt also speculate on an East African centre of evolution and dispersal for these plants, much as has been suggested for chameleons by Hillenius (1959).

In many aspects, these two groups, the plant genus *Streptocarpus* and the chameleons, appear to have followed similar historical and geographic paths in their evolution. The subgenus *Streptocarpella* shows congruence with the combined ranges of the leaf chameleons *Rhampholeon* and *Brookesia*, while the subgenus *Streptocarpus* is more similar to the range of *Chamaeleo* (*sensu* Hillenius, 1959). There are some differences in that the leaf chameleons do not extend to Southeast Asia and that *Streptocarpus* does not extend into West Africa, or into the Mediterranean littoral, Arabian Peninsula and Indian subcontinent.

Some species such as *Streptocarpus porphyrostachys* Hilliard, 1966, *Streptocarpus wendlandii* Sprenger, 1890 and *S. kentaniensis* Britten & Story, 1954, have ranges that closely approximate to those of localised *Bradypodion* species. These correllated local endemics probably indicate an extended period of isolation resulting from either topographic or climatic effects.

Others have a wider distribution overlapping those of several *Bradypodion* species and possibly indicate dispersal paths that previously existed in eastern South Africa. While dwarf chameleons occur in suitable habitat along each of these paths, none have been found along the second path between the Umzimkulu and the Tugela Rivers except for a single specimen from Waterfall, near Hillcrest. This may mean either that their present populations are very difficult to locate or that they perhaps did occur there at some time in the past but have been unable to survive. This could be due to habitat modification by man or perhaps due to the small size of the remaining habitat following the erosion of wide river valleys nearer the coast. Reduction in habitat could have dropped numbers below the minimum required for survival and hence led to their extinction.

The distributions of *Streptocarpus* and *Bradypodion* species are compared in figures 69 and 70. Figure 69 shows a limited path but figure 70 shows a more extensive southwest to northeast distributional pattern resulting from the complementary ranges of these two closely related *Streptocarpus* species. This presumably indicates an earlier avenue for dispersal that has now been interrupted by the cutting of the physical and ecological barriers of the major river valleys.

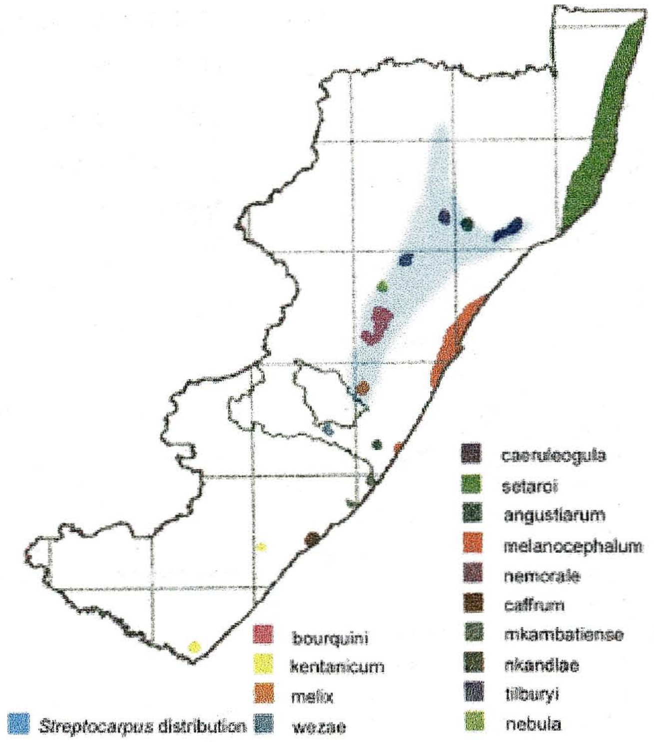


Figure 69: Distribution of ***Streptocarpus grandis*** **subsp.** ***grandis***

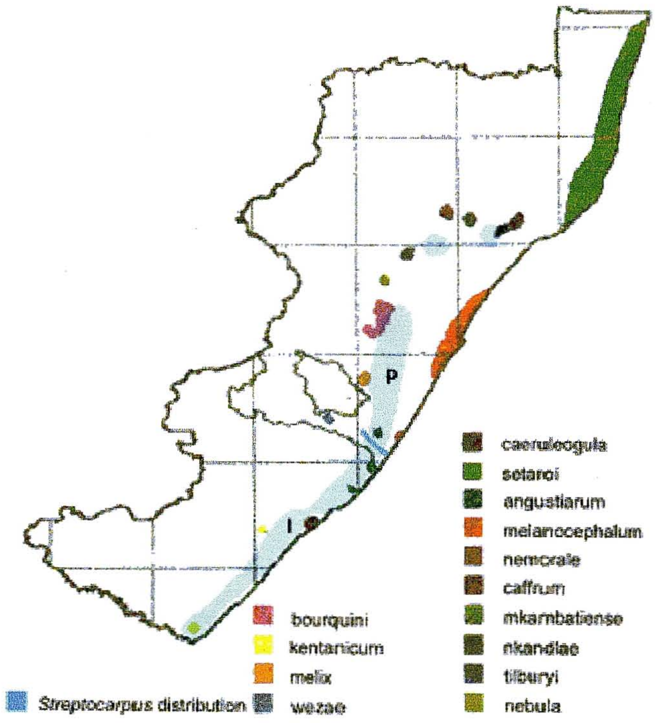


Figure 70: Distribution of *Streptocarpus insignis* (I) and *S. primulifolius* (P)

5.5.2 Distribution of the samango monkey

The historical basis for the distribution of the samango monkey put forward by Lawes (1990) resulted from his examination of events during the Quaternary and the radiation of these monkeys in a the temporal context of changes in the extent of the forested areas in response to some twenty glacial and interglacial events. It seems likely that there are significant differences between the effects these would have had on the monkeys and the dwarf chameleons. For instance the monkeys probably need much more extensive areas to maintain viable populations than the chameleons. They are also relatively vagile in comparison with the chameleons and would be able to disperse across local barriers far more readily. While both are associated with Afromontane forests in eastern South Africa, it seems that the chameleons have been evolving in this region for much longer than the samango monkeys. It seems likely that the major dispersal events in their history are most likely to have occurred during the periods of uplift at ca. 18 Ma and ca. 2,5 Ma followed by subsequent vicariance as a result of the cutting of the major river valleys. The Quaternary glacial events have probably had some consequences for their evolution, perhaps even leading to the separation of pairs of taxa such as *Bradypodion wezae* and *B. melix* and *B. nkandlae* and *B. caeruleogula*. This concept of an old group that has survived since the break up of Gondwanaland on the south-eastern slopes of the continent has much in common with that proposed by Stuckenberg (1962) for invertebrates such as onychophorans and other taxa that show an overall Gondwanan distribution pattern. The differences between the distribution of chameleons and that of other more widespread Gondwanan taxa could be due to a rather limited original distribution in the area that was split by the separating continental fragments that now comprise Africa and Madagascar. Chameleons may have already separated into at least two lineages by this time, one leading to the present *Brookesia*, the other to *Bradypodion* in the south and *Chamaeleo* in the north and on Madagascar and the Seychelles. There appears to be a possibility that some of the resemblences between Rhampholeon and Brookesia may be due to convergence resulting from the adoption of semi-terrestrial habitat and consequent reduction in size rather than actual shared immediate ancestry.

5.5.3 Distribution of *Paralethe* butterflies

The butterfly species *Paralethe indosa* and *P. dendrophilus* occur in many forest localities in the study area that are also inhabited by *Bradypodion* species. These have been treated as two species with *Paralethe dendrophilus* (Trimen) 1862 being regarded as monotypic and *Paralethe indosa* divided into the three subspecies *P. i. indosa* (Trimen) 1979, *P. i. albina* van Son 1955 and *P. i. junodi* (van Son) 1935 (Quickelberge, 1993). Temperature appears to have some correlation with the differentiation of subtaxa in these insects although it is possible that this is purely a coincidental relationship. The larvae of these species feed on grasses and the restriction of the species to forest areas appears to be caused by the reluctance of the imagoes to leave their forest habitat. Quickelberge (1993) considers these species to have one of the lowest degrees of vagility of forest butterfly species.

5.5.4 Overview of distribution patterns

Obviously, vagility or the ability to disperse must be an important factor in explaining the present distribution of these forest species. Dwarf chameleons probably exhibit the lowest degree of vagility of all the organisms considered here and the exchange of genes between geographically isolated populations must be non-existent. *Streptocarpus* species have small seeds but these are unlikely to be wind dispersed and are more likely to germinate close to the parent plant. While they were not certain about the mode of pollination, Hilliard and Burtt (1971) speculated that some species are pollinated by hawk moths, some by other insects and others by birds. While these processes still need to be investigated, it does raise the possibility that these species may well be able to exchange genes over long distances but it is probably likely that such exchanges are not sufficient to prevent the evolution of distinctive populations. *Paralethe* butterflies are far more mobile than either of these. While able to cross short distances under normal circumstances they may also be carried for long distances by high winds and this may explain why they show less differentiation than the previous two organisms. Samango monkeys live in troops, are able to move considerable distances fairly easily although they are limited by the need for corridors of suitable habitat. Their present distributional situation is well explained by the evidence presented by Lawes (1990) in relation to the historical geographic background of two dispersals into the study area. This evidence also applies to the historical biogeography of the other groups within the Quaternary. However it seems likely that at least for the dwarf chameleons, *Streptocarpus* and also the onychophorans, this evidence merely records the final stages of a much longer and more complex evolutionary history dating back to the end of the Jurassic or Early Cretaceous.

Overall, the similarities in the distributions of these unrelated groups of organisms offer much scope for further biogeographic study. This would be especially true if this could be combined with cladistic and biochemical studies to indicate the sequence and perhaps even the time periods of the various events of expansion and vicariance which eventually brought about the complex relict distributions which we find today. Not only will this allow for greater understanding of the evolution of these taxa and their associated fauna and flora but, also, perhaps give us the conceptual tools to create suitable conservation management plans to ensure their continued existence as climatic change begins to affect their present habitats.

6 CONSERVATION STATUS OF DWARF CHAMELEONS IN STUDY AREA

The dwarf chameleons of the study area, like all species of *Bradypodion*, are regarded with some concern by conservation bodies. All are listed under schedule II of CITES (an acronym for the agreement that is generally known as the Convention on the International Trade in Endangered Species) and therefore require permits for shipments between signatory countries. Permits are also required for the collection of dwarf chameleon specimens in the two provinces concerned. Two of the species considered here are listed in the South African Red Data Book – Reptiles and Amphibians (Branch, 1988b), namely *Bradypodion setaroi* and *Bradypodion nemorale*. It seems certain that all the species dealt with here will be added to this list in due course, especially in view of the more restricted distributions that this study has revealed.

The study area has been occupied by hominids, at least during favourable periods, during the past 300 000 years. While the earlier hunter-gatherer occupants probably had little effect on the habitat this has not been true of later human occupants. Unfortunately much of the vegetation of the region has been obliterated or drastically altered since the arrival of human agriculturists, initially Bantu slash and burn farmers (since about 1400 AD according to Brooks & Webb (1974) but since at least 200 AD or even 4000 BP according to Maggs's (1977) estimates) then later by European settlers from the early nineteenth century. Invasive plants such as *Lantana camara* L. and *Eupatorium odoratum* L. (*Chromalaena odorata*) also cause major changes to the vegetation of this area. We will probably never know whether this human activity has resulted in the extinction of any chameleon populations or taxa.

Some evidence exists which details the extent of the destruction of natural habitat in KwaZulu-Natal (Bourquin et al, 1996). Figures given in terms of the whole province are that urbanisation, settlements, mines and industrial developments have destroyed 36,35%, cultivation 13,97%, silviculture 5,65% and State dams 0,07% of the total natural habitat respectively. These figures do not include habitat loss resulting from roads or railway lines. More pertinent to dwarf chameleon conservation is the fact that of the prime dwarf chameleon habitats, only 35,86% of veld type 1 remains, 51,3% of veld type 3, 24,96% of veld type 5 and 31% of veld type 45. There is small consolation that some areas are under formal conservation as follows: veld type 1 with 11,44%, veld type 3 with 31%, veld type 5 with only 1,25% and veld type 45 with only 0,34% conserved. The Transkei area is likely to be slightly better although the already heavy pressure on these habitats from over-extensive burning, over-grazing, high demand for trees for fuel wood, construction timber and other uses is likely to increase considerably in the future.

6.1 Field observations

Fieldwork in Durban and Amanzimtoti in the 1990s has shown that *B. melanocephalum* has virtually disappeared from many localities where it was formerly abundant. In one locality, where more than 50 individuals were counted one evening along about 50 metres of pathway during the 1960s, not a single animal was found after an intensive search. Searches of a number of localities previously known to have large populations were also unsuccessful. Two specimens were eventually found near the Umbilo River at Bellair. Similarly, in Amanzimtoti, areas where chameleons were numerous before were also found to have no chameleons. A lengthy and wide-ranging search eventually turned up 2 specimens, widely separated from each other spatially, but both near open bushy areas. It would seem that urban development has resulted in the destruction of the large areas of undisturbed natural vegetation necessary for the survival of this species. The only changes obvious in the affected areas are the greatly increased number of dwellings in the areas mentioned as well as the development of large areas of previously vacant land. Other possible factors affecting these chameleons could be the widespread popularity of concrete fences, mechanical mowing of road verges which were formerly cut by hand and the pollution of dew and rain by industrial chemical emissions as well as the use of herbicides for the control of roadside weeds. It was interesting to note that several chameleons (mainly *Chamaeleo quilensis*) found were resting on *Chromolaena* (*Eupatorium*) plants. It is possible that the widespread invasion of this weed could also be having a negative effect on the abundance of these chameleons. (See also Raw, 1992). *Chromolaena* plants tend to invade and dominate extensive areas where they smother most other plant species with a consequent reduction of both plant and insect diversity. Few, if any, South African insect species feed on *Chromolaena* so the actual biomass of insects falls along with the diversity of species in these invaded areas.

6.2 Threats to *Bradypodion* habitat

As with most organisms with geographically restricted distributions *Bradypodion* species are very vulnerable to habitat destruction. Unfortunately, this situation does not seem to have been taken into account in conservation planning in South Africa. The importance of habitat protection was highlighted in a report submitted to World Wide Fund for Nature, South Africa (Raw, 1995) and distributed to all relevant conservation bodies in South Africa. The following section considers some threats produced by human activities.

6.2.1 Human activities

The proposed planting of extensive areas of KwaZulu-Natal and Transkei (Eastern Cape) to commercial forestry (chiefly pines and eucalypts) is likely to have a major effect on the existing biota. Observations in late 1991 show that new plantings of exotic timber species in grassland in southern KwaZulu-Natal were made right up to the edges of indigenous forest patches. The detrimental effects on ecotonal or forest edge species are likely to be severe and could result in their elimination. The threats to *Bradypodion* species are severe, and this practice could lead to the extinction of some of the more restricted species.

Indigenous forests are also under threat. Cooper (1985) reports on the problems facing indigenous forests because of a serious lack of understanding of their importance. He cites planting up the ecotones with exotic timber trees, grazing cattle in forests, burning the margins severely, allowing bark to be stripped and trees to be cut down as some of the major threats. Agriculture (mostly sugar cane), urbanisation and industry have already cleared some 90% of the KwaZulu-Natal coastal forests. During fieldwork for this study, we frequently heard the sound of woodcutters cutting trees in the forests visited, especially in the Transkei forests.

Another threat has resulted from squatters moving into forests to escape political attacks and violence. The destruction of forests through settlement could have serious repercussions on the chameleon populations within them. It is not known how likely it is that these areas would be permanently settled. In many instances, the forests are short-term refuges and settlement that is more permanent could reduce their value for this purpose. There have been a number of reports in the press of unauthorised, settlement and forest destruction in the Dukuduku forest near St Lucia. This settlement of supposedly conserved indigenous coastal forest poses a threat to the forest flora and fauna of the area.

The mining of coastal dune sands for minerals such as ilmenite may also offer a possible threat despite subsequent rehabilitation work. Studies on the lizard fauna in a similarly affected area in Australia have shown that the first lizards only returned to plots at least 5.9 years old. The time required before lizard faunas recovered after strip mining was likely to be well in excess of 20 years (Twigg & Fox, 1991). Provided that lizard species are able to maintain adequate populations outside the affected areas during the period of disturbance and rehabilitation, and provided that the rehabilitation restores the minimum requirements of the species concerned, then the effects of such mining are not likely to have long term consequences. Certainly the exploiters of these areas are attempting to mitigate the effects of their operations by active rehabilitation of the worked areas. How effective these rehabilitation efforts will be for dwarf chameleon species remains to be seen but it seems that the rehabilitation process has every chance of success.

Other threatened habitats used by *Bradypodion* are coastal plain swamps, wetlands and riverine vegetation. With the expansion of agriculture and urbanisation, many of these areas are being "reclaimed" for planting of crops, used as landfill sites for waste disposal, converted to canals and recreational areas, e.g., sports fields, or made uninhabitable as a result of industrial pollution which disrupts local ecosystems.

The effects of the above threats to their habitat could result in local extinctions of a number of species, possibly also including species of *Bradypodion*. It is essential that any future plans for development must be co-ordinated at a level where these concerns are taken into account and appropriate measures are applied to ensure that adequate areas of natural habitat are retained to maintain the biodiversity of the region.

6.3 Inter-specific competition

Competition from other species of chameleons could be another possible cause of decline in *Bradypodion* numbers. Observations in the field in and near Durban, where species of both *Bradypodion* and *Chamaeleo* occur in sympatry, showed that individuals of *Bradypodion* were much more numerous than individuals of *Chamaeleo* in areas of overlap. The discrepancy in size between the two species, the probable utilisation of different size classes of insect food resources and differences in preferred micro- and macro-habitats by the two species concerned seems to rule out any serious competition between them although it is likely that *Chamaeleo* will feed on smaller individuals of *Bradypodion* in direct predation and may also compete for food and habitat niches in some cases. *Bradypodion* is ovoviviparous in contrast with the oviparous *Chamaeleo quilensis*. While Burrage (1973) has reported multiple clutches per year in *Bradypodion pumilum*, it seems unlikely that KwaZulu-Natal and Transkei species produce more than a single litter per year. The larger egg-laying species, *Chamaeleo quilensis,* has only a single, more numerous, clutch, which takes approximately 270 days to hatch (Raw, 1993).

As an indication of relative abundance, some 54 *Bradypodion melanocephalum* and 5 *Chamaeleo quilensis* were collected (and subsequently released) within a short period on a single evening in the early 1960's. These were found on a hedge, wire strand fence, and the grass verges of a path of approximately 50 metres in length adjacent to the Hillary railway station in Durban. Several of the *Bradypodion* were newborn young while all of the *Chamaeleo* were adults. The distribution of *Bradypodion* seems to be restricted by its physiological habitat requirements resulting, in the case of *Bradypodion melanocephalum,* in an upper altitudinal limit in the Durban area of approximately 150 metres a.s.l. The physiological basis behind this restriction is unknown but is possibly associated with water availability.

These chameleons usually only drink water that is available in droplet form that they can lick up from the twigs and stalks of vegetation. In this relatively warm, coastal area, the localised low-lying mists and heavy dew may provide this moisture while slightly higher and dryer areas may prove too inhospitable for their survival. *Chamaeleo quilensis* has a much greater tolerance of dryer conditions and is able to utilise the hot and relatively dry Valley Bushveld areas as well as the coastal plain of KwaZulu-Natal. Its distribution appears to be limited by temperature, or perhaps insolation, in KwaZulu-Natal. Historical factors cannot be ruled out since *C. quilensis* is also found on the Highveld where winter temperatures are much lower. It seems likely that *C. quilensis,* a savannah species, is a recent immigrant that has invaded *Bradypodion* habitat.

6.4 Endemic areas and conservation

Most of the *Bradypodion* species of South Africa have small, biogeographically restricted ranges. Observations of the correlations with other organisms indicate that these areas are not merely associated with the chameleons but are also likely to indicate the presence of endemic forms of other elements of the South African fauna and flora.

Although not investigated here, it seems likely that similar patterns of endemicity will be found in a number of other taxonomic groups. To use of the distributions of dwarf Chameleon taxa to identify these endemic areas and to subsequently conserve vital parts of these areas will enable an essential step to be taken in the conservation of South Africa's unique endemic biota.

6.5 Priorities for conservation

The recording of the distributional ranges of the individual taxa provides the basis on which priority areas of habitat can be identified. Once these are established it is possible to derive a strategy to provide for effective conservation of sufficient habitat to provide for the long-term maintenance of viable populations of these chameleons and their associated fauna and flora.

This means that the priority action will be the conservation of the habitat. If necessary, this may mean land acquisition by conservation bodies or the establishment or augmentation of privately owned conservancies. Recommendations and an example of a conservation plan have been put forward for *Bradypodion* species (Raw, 1995).

Merely proclaiming legislative restrictions on killing or collecting, whether or not able to be implemented, can have little benefit to the taxa concerned if the habitat is being modified detrimentally by the expansion of pre-existing or new forms of land-use. These activities are often given a high profile and incur high expenditure of time and financial resources for very little conservation benefit relative to the actual protection of the essential habitat of the species concerned. Whether any appropriate action will be taken to implement the effective conservation of critical *Bradypodion* habitat by conservation bodies in South Africa remains to be seen.

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8 PERSONAL COMMUNICATIONS

Bourquin, Dr Ortwin – formerly of Pietermaritzburg, S. Africa.

Breuer, Mr Achim – Germany.

Broadley, Dr Donald G. – Bulawayo, Zimbabwe.

de Queiroz, Dr Kevin – U. S. National Museum, Washington, D.C., U.S.A.

Edwards, Mr Euan John – Madagascar.

Edwards, Dr Trevor J. – Pietermaritzburg, S. Africa.

Hertogs, Mr Irving – Howick, S. Africa.

Hlengwa, Mr Mthunzi – Highflats, S. Africa.

James, Ms Susan – California, U.S.A..

Lambiris, Dr Angelo J.L. – Hillcrest, S. Africa.

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Mgeyene, Mr Zola – Spaqeni, Flagstaff, S. Africa.

Muir, Mr Dirk – formerly of Pietermaritzburg

Setaro, Mr Gordon – Everton, S. Africa.

Thomas, Mr Hywel – Port Elizabeth, S. Africa.

Tilbury, Dr Colin – Cape Town, S. Africa.

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