Phylogenetic Relationships of the Subfamily Petropedetinae Noble, 1931 (Anura: Ranidae): A Simultaneous Analysis of Morphological and Molecular Data

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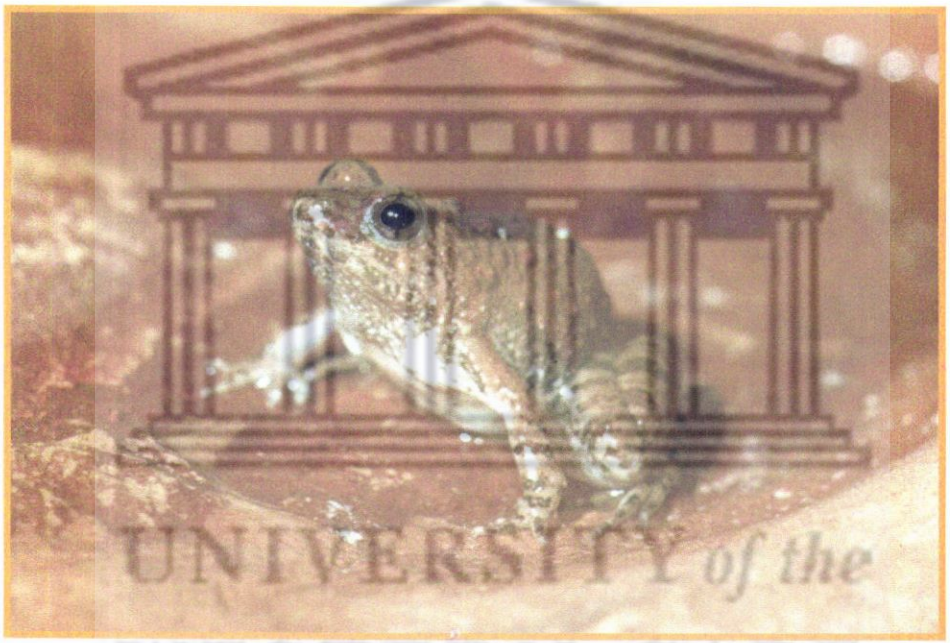

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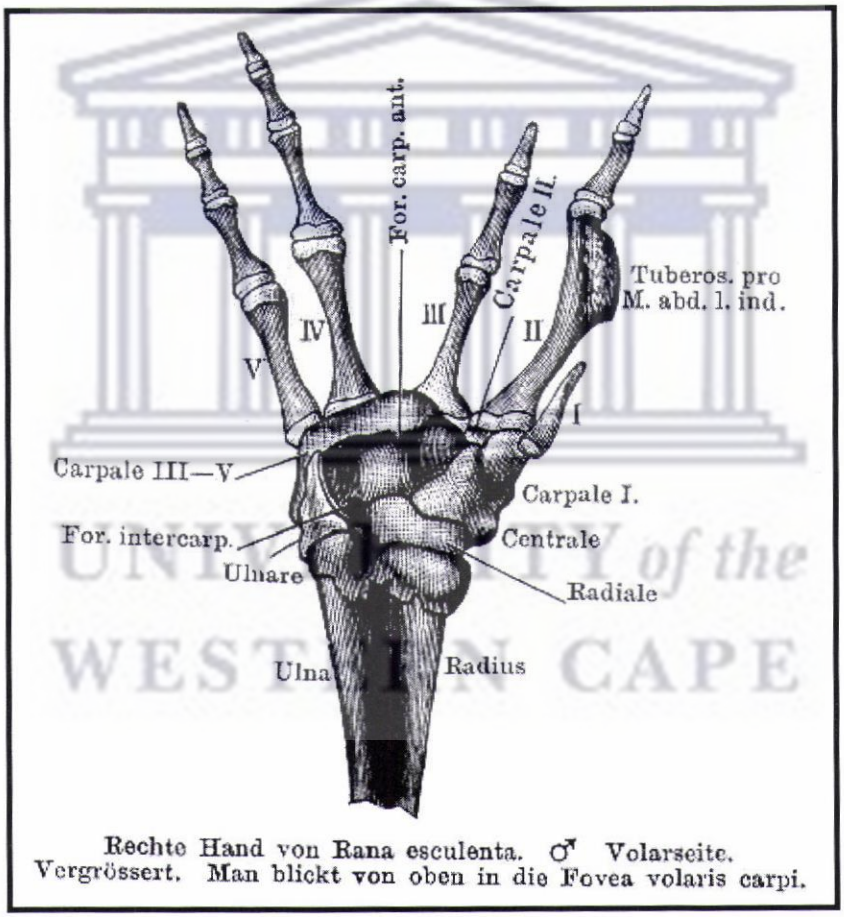
DECLARATION

I declare that this thesis is my own unaided work, both in concept and execution, and that apart from the normal guidance from my supervisors, I have received no assistance, except as acknowledged in the Acknowledgements section, and that it has not been submitted to any other university.

Elizabeth Scott

'*Nous nous sommes efforcés de poser un nouveau jalon dans la voie suivie par* Hewitt, Noble, de Villiers *et* Deckert. *Nous croyons, en effet, que, pour la systématique des Batraciens, l'étude du squelette doit avoir la priorité sur toute autre considération….. l'examen du squelette est indispensable pour ces derniers.*'

Laurent (1940:76)



Gaupp (1896) Fig. 44

CONTENTS

Keywords

Amphibia, Anura, Ranoidea, Ranidae, Petropedetinae, Microhylidae, Hemisotidae, Hyperoliidae, Arthroleptidae, Sooglossidae, Dendrobatidae, Rhacophoridae, Mantellidae, Evolution, Systematics, Phylogeny, Cladistics, Comparative Morphology, Osteology, Africa, Old World Biogeography.

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ABSTRACT

The Ranidae is one of the largest families of the Neobatrachia, but its taxonomy is in a state of flux. Major taxonomic rearrangements have recently been instituted for this family, but these have been mostly phenetic in nature and no comprehensive attempt has been made to reconstruct its phylogeny. Within both the older and the contemporary classification systems of the Ranidae, the subfamily Petropedetinae has always been recognized. This small subfamily is endemic to Africa and comprises thirteen genera, eight of which are monotypic. The current distribution of most genera appears to be relictual, and is concentrated primarily along the Afromontane Forest regions, with a centre of generic endemism in the Western Cape Province of South Africa. Despite the lack of known synapomorphies for the Petropedetinae, the group was recently raised to familial level by Dubois (1992), and its taxonomic status is in need of re-appraisal.

The major aim of the present study was to test the monophyly of the Petropedetinae. The generation of a phylogenetic hypothesis was also required to test the validity of the monotypic genera in this putative lineage, and to facilitate future evolutionary analyses of some of the more interesting behaviours and ecologies of species within this group, such as male-male combat, terrestrial breeding and various parental care strategies. Since affinities of the Petropedetinae are poorly understood, testing the monophyly required the inclusion of exemplars of most other major ranoid clades, particularly of those taxa that have previously been hypothesized to be related to any of the petropedetine genera. With the inclusion of exemplars of only a few additional groups, this was expanded to be a minimal exemplar analysis of the major clades of the Ranoidea, although that is not the primary focus of this work.

Seventy-eight exemplar species were examined from seven Neobatrachian families, all subfamilies of the Ranidae proposed in the new classification scheme of Dubois (1986, 1992) and two clades of uncertain rank, in addition to all thirteen genera of the subfamily Petropedetinae. The study utilised approximately 600 base pairs of sequence data from the mitochondrial 12S rDNA and 16S rDNA gene regions, which was combined with 192 characters from osteology, external morphology, breeding biology and behaviour in a simultaneous parsimony analysis. To avoid problems associated with multiple sequence alignment, direct optimization analysis of the sequence data was performed under 20 combinations of the insertion: deletion cost ratio (gap cost), and the transition: transversion cost ratio (change cost) for two sets of analyses, one with the morphology weighted to the change cost and one with the morphology weighted to the gap cost. The equally-weighted hypothesis is presented as the preferred estimate of the phylogeny, but the other analyses serve as a measure of the sensitivity of the result to analysis parameters. This procedure is used to identify robustly supported arrangements (those that are appear under a wide range of analysis parameter values),

from weakly supported arrangements (those that only appear under particular analysis parameter values).

The equally-weighted topology is consistent with the placement of the dendrobatids in the superfamily Bufonoidea, although the sensitivity analyses occasionally placed these as one of the basal lineages in the superfamily Ranoidea. The family Sooglossidae was found to be closely related to the Dendrobatidae, suggesting that both families may be 'transitional' or intermediate between the two superfamilies, as has been suggested for the sooglossids. A relationship between the Dendrobatidae and Arthroleptidae was not retrieved under any analysis parameter sets. The Microhylidae were also found to be basal in the ranoid lineage. The genus *Hemisus*, currently placed in its own family, was shown to be embedded in the microhylids. The Arthroleptidae and Hyperoliidae were found to be sister lineages, with the hyperoliid genus *Leptopelis* showing a tendency to group in the Astylosterninae, thus rendering both groups paraphyletic. More detailed studies in future may suggest incorporating the hyperoliids into the older family Arthroleptidae, which has nomenclatural priority.

The broadly defined family Ranidae (including the rhacophorids and mantellids) was found to be monophyletic in almost all sensitivity analyses, with two synapomorphies identified for this family: the presence of the musculus cutaneous pectoralis and an ossified metasternum. However, only the presence of a musculus cutaneous pectoralis is uniquely synapomorphic for the Ranidae. Monophyly of the ranid subfamilies (*sensu* Dubois 1992) Tomopterninae and Ranixalinae was not tested by this analysis. Only two of the remaining five subfamilies of the Ranidae (*sensu* Dubois 1992) were consistently retrieved by the sensitivity analyses as monophyletic, *viz.* the Ptychadeninae (*Hildebrandtia* + *Ptychadena*) and the Pyxicephalinae (*Pyxicephalus* + *Aubria*), although they were both embedded in the other 'subfamilies'. The Dicroglossinae (and its tribes the Dicroglossini and Limnonectini), the Petropedetinae, and the Raninae were never retrieved as monophyletic. Many genera in the Ranidae need to be reallocated amongst the subfamilies in order to alter the classification of the Ranidae to one reflective of their evolutionary history, and some subfamilies need to be abandoned altogether.

The equally-weighted topology and all sensitivity analyses indicated that the subfamily 'Petropedetinae' is paraphyletic, being composed of three clades. These are subsequently referred to as the cacosternids, phrynobatrachids and petropedetids. While the petropedetids are only distantly related to the cacosternids and phrynobatrachids, the latter two groups may be sister taxa. *Tomopterna* appears to be closely related to the cacosternids, with strong affinities apparent on the basis of the molecular data. The recently described enigmatic Ethiopian genus *Ericabatrachus* is demonstrated to belong to the cacosternine lineage, although its morphology is extremely aberrant, displaying novel character combinations intermediate between the basal ranoid clades and the Ranidae. Within the petropedetids and phrynobatrachids, the recognition of three monotypic genera renders other genera paraphyletic. *Arthroleptides* is more correctly

considered as a member of the genus *Petropedetes*. The large genus *Phrynobatrachus* is morphologically coherent, but is rendered paraphyletic by the recognition of the genera *Dimorphognathus* and *Phrynodon*, which will be synynomised with *Phrynobatrachus*. *Natalobatrachus* is the basal member of the phrynobatrachids and its recognition does not render *Phrynobatrachus* paraphyletic. Within the cacosternids, the recognition of *Anhydrophryne* renders *Arthroleptella* paraphyletic. Transferral of the species *hewitti* to the genus *Anhydrophryne* is advocated to rectify this situation, as the two genera are highly disparate morphologically.

The results indicate that the evolution of the Ranidae mirrors that of the Ranoidea in that it probably originated on the Gondwanan supercontinent, and challenges recent proposals of an Indian or Asian origin of the (non-monophyletic) subfamilies Dicroglossinae and Raninae. A close relationship between the fanged ranids of Asia (*sensu* Emerson & Ward 1998) and the large odontid-bearing ranids of Africa is suggested. However, further work is required to elucidate the internal relationships in the Raninae, which varied substantially in many of the sensitivity analyses. Much remains to be studied, but some blatently paraphyletic groups should be abandoned in the light of the present study. This analysis demonstrates the value of taking a large-scale approach to the problem of ranid frog phylogeny and biogeography. Our current knowledge of phylogenetic relationships in the Ranidae is exceedingly poor, and to work on taxa from single geographical regions or presumed groups in isolation may exclude pivotal taxa from other regions or groups, resulting in erroneous phylogenetic and biogeographic conclusions.

INTRODUCTION

The superfamily Ranoidea (*sensu* Ford & Cannatella 1993) comprises a large group of predominantly Old World Neobatrachian clades. Its distribution pattern suggests an origin of the lineage in Gondwanaland. Earlier this century, most ranoids were classified into the poorly defined family Ranidae[1], but many groups have subsequently been split into new families. While familial rank for the Hyperoliidae and Microhylidae are widely accepted, an equivalent rank for some of the other splinter ranid families (notably the Arthroleptidae, the Hemisotidae, the Rhacophoridae, the Mantellidae and the Petropedetidae), remains controversial. The provision of familial status for some of these groups may have been premature, as the phylogenetic relationships of the major clades of ranids are still unclear (Ford & Cannatella 1993; Hedges & Maxson 1993; Ruvinsky & Maxson 1996; Grant *et al.* 1997; Vences 1999; Emerson *et al.* 2000a). With the exception of the arthroleptids and petropedetids, the monophyly of most of the above-mentioned clades is generally accepted, barring some uncertainty surrounding the placement of the occasional taxon (e.g. *Hemisus*, *Leptopelis*, *Aglyptodactylus*). Recent evidence from the analysis of molecular data shows that the rhacophorids and mantellids are embedded in the larger family Ranidae, suggesting that they are best considered as subfamilies thereof (Ford & Cannatella 1993; Glaw *et al.* 1998; Vences 1999; Emerson *et al.* 2000a).

The family Ranidae is almost cosmopolitan in distribution and contains about 20% of all extant amphibian species (Bossuyt & Milinkovitch 2001); and is a dominant component of the amphibian fauna in most of the Old World (Poynton 1964; Duellman & Trueb 1986). The simplest and oldest taxonomic scheme for the Ranidae, as expressed in Frost (1985), recognizes three subfamilies. The first of these, the Raninae, is almost certainly paraphyletic (Ford 1990; Ford & Cannatella 1993) and 'displays taxonomic confusion on a grand scale' (Frost 1985:451). The second subfamily, the Mantellinae, is confined to Madagascar and some Indian Ocean islands. Finally, the third subfamily, the Petropedetinae, is restricted to sub-Saharan Africa.

The classification of the Ranidae is still in a state of flux, mostly due to major rank changes implemented by Dubois (1986, 1992), who did not present any discussion of the phylogenetics underpinning these changes (Frost 2002). Most of these changes are reflected in Duellman's (1993) additions and corrections to Frost's (1985) catalogue. This arrangement recognizes the Ranidae as containing seven subfamilies (Table 1), few of which have been subjected to any form of cladistic tests to determine monophyly and content (Inger 1996). Regardless of the phenetic nature of Dubois' arrangement, it has managed to impart a degree of order to the taxonomic chaos that was the Ranidae, and provides testable hypotheses of relationship (Inger 1996). Many of the newly erected genera and subgenera, especially those that have been split

[1] Author and year of citation for names listed in the text can be found in Tables 1 and 2, and Appendix 1. Only if not present there are they listed in the text.

from the large and undoubtedly paraphyletic genus *Rana* appear to be well founded and are likely to stand up to rigorous phylogenetic testing. Some of the new subfamilies, for example the Ptychadeninae and Pyxicephalinae, are well supported by known synapomorphies (e.g. Clarke 1981, 1983; Ohler 1996) and are most probably monophyletic. Others, for example the Dicroglossinae, are likely to be para- or even polyphyletic, and may even render some otherwise legitimate groupings paraphyletic. Frost's (2002) updated classification recognizes Dubois' (1986, 1992) subgeneric changes, but places his subfamilies at equivalent family level until further evidence comes to light, leaving those genera previously included in the subfamily Raninae as the contents of the family Ranidae.

As Glaw *et al.* (1998) point out, there has to date been no comprehensive, large-scale analysis of ranid relationships. Clarke's (1981) influential study of the osteology of the African Raninae remains the only detailed morphological study dealing with this group (Sanchiz 1998). However, it is limited by its *a priori* assumption of monophyly of the subfamily Raninae, as well as being geographically restricted to African taxa. The taxonomy of the Asian ranids has recently received some attention from molecular systematists, but this work is still conducted predominantly at lower systematic levels, or has focused on geographically and taxonomically restricted subsets of the Ranidae (e.g. Tanaka *et al.* 1996; Tanaka-Ueno *et al.* 1998a, 1998b; Emerson *et al.* 2000b; Marmayou *et al.* 2000; Richards *et al.* 2000; Kosuch *et al.* 2001; Jiang & Zhou 2001a, 2001b). However, some molecular studies on ranid higher level phylogeny are being published (Bossuyt & Milinkovitch 2000; Emerson *et al.* 2000a). Within the family Ranidae, there is a need to identify the major monophyletic clades and generate rigorous hypotheses of their relationships based on synapomorphy. Only then can one identify the appropriate rank and content for such clades, and ultimately allow them to be used to test biogeographical and ecological hypotheses concerning these frogs.

The present study focuses primarily on relationships of the taxa currently classified in the ranid subfamily Petropedetinae[2]. The Petropedetidae was raised to familial rank by Dubois (1992) without discussion, but was not listed as such in Duellman (1993), who simply noted this action of Dubois under comments, implying his rejection of this formally-proposed rank. Familial recognition for this group is reflected in the latest on-line catalogue of Frost (2002), but is not used here.

The Petropedetinae have received scant systematic attention in their own right. The validity of many of the monotypic genera, accounting for eight of the thirteen genera, remains questionable. The taxonomic history of the genera included in the Petropedetinae reflects the uncertainty surrounding their phylogenetic position. Many of these genera have historically been moved around extensively within the Ranoidea. The subfamily Cacosterninae Noble, 1931

[2] The name Phrynobatrachinae has also been used for this group. This name is now recognized as a junior synonym of the name Petropedetinae, after a motion to conserve the name Phrynobatrachinae was denied by the International Commission on Zoological Nomenclature (Dubois 1982; Anon 1995, 1999).

was erected to include the genera *Cacosternum* and *Anhydrophryne*, and placed in the family Brevicipitidae (now the Microhylidae). This proposed relationship of the cacosternids with the brevicipitids was based on the shared loss of elements of the pectoral girdle, the greatly dilated sacral diapophyses, reduced palatines and the large frontoparietal fontanelle. Latsky (1930a, 1930b) investigated the validity of the Brevicipitidae, and concluded that *Cacosternum* and *Anhydrophryne* were more closely related to the Ranidae than to the Brevicipitidae. Parker (1934) did not treat these genera as part of the Microhylidae. Laurent (1940) referred *Cacosternum* and *Anhydrophryne* to the Ranidae, but kept them in a distinct subfamily, the Cacosterninae, and included the genus *Microbatrachella*.

Noble (1931) erected the subfamily Petropedetinae for the genera *Petropedetes* and *Arthroleptides*. Parker (1935) noted that various species of '*Arthroleptis*' (which were subsequently transferred to *Phrynobatrachus*), *Dimorphognathus* and his new genus, *Phrynodon*, all share the presence of femoral glands, a medial lingual process and expanded fingertips in some taxa with Noble's (1931) Petropedetinae. In addition, *Phrynodon* and *Dimorphognathus* share the character of small sexually dimorphic mandibular tusks present in the males, with *Petropedetes natator*. Parker (1935) considered these characters as evidence of a close relationship between these taxa, and placed them all in the same subfamily. Laurent (1940) concurred that *Phrynobatrachus*, *Arthroleptella* and *Dimorphognathus*, all of which were formerly classified in the Arthroleptidae, should be classified alongside *Petropedetes* in the Phrynobatrachinae [Petropedetinae]. Later, Laurent (1961:199) expressed doubt as to the distinctness of the subfamily Petropedetinae from the Raninae, stating that 'the Phrynobatrachinae [Petropedetinae minus the cacosternids] agree almost in every respect with the Raninae except in size and vomerine teeth, which are lacking [in the Petropedetinae]'.

Poynton (1964) placed the genera *Phrynobatrachus*, *Arthroleptella* and *Dimorphognathus*, together with the additional genus *Natalobatrachus*, in the subfamily Phrynobatrachinae of the Ranidae, together with his newly-described genus, *Nothophryne*. Poynton's reasoning for incorporating the Cacosterninae into this group is not clear, but may have been due to particular character states of both the cacosternids and of the petropedetids being present in his newly described genus *Nothophryne* ('*Notho*' = mongrel). Following Noble (1926b) and Laurent (1941a), Poynton argued that the Cacosterninae was diphyletic, with one lineage containing *Microbatrachella* and *Cacosternum*, and the other containing *Anhydrophryne* and *Arthroleptella*. Poynton stated that both lineages were derived from primitive *Phrynobatrachus* stock, and he was presumably attempting to avoid the retention of a plethora of small subfamilial names within what he perceived to be a single lineage. Opinions differ on whether or not to accept Poynton's (1964) merging of the Petropedetinae and the Cacosterninae (Poynton 1964; Kuhn 1965; Liem 1970; Lynch 1973; Duellman & Trueb 1986; Blommers-Schlösser 1993).

Breeding systems in the Petropedetinae are strikingly diverse. These range from normal, fully aquatic development, through various stages of reduction of the aquatic life stages and concomitant larval specialization, to direct development completely independent of standing water (Hewitt 1919; Laurent 1961; Amiet 1981). Examples of the latter are *Anhydrophryne* and *Arthroleptella*, which have direct development, while *Natalobatrachus* and many *Phrynobatrachus* species lay their eggs out of water (Wager 1931). Various parental care strategies have also evolved in the *Phrynobatrachus* lineage, with either the male or female parent guarding the eggs in particular species (Perret 1966; Amiet 1981, 1991). Male-male combat also occurs in some species of *Petropedetes* (Sanderson 1936), *Arthroleptides* and in *Phrynodon* (Amiet 1981, 1991), with a resultant development of a suite of secondary sexual characteristics in the form of male armaments (e.g. metacarpal spines, odontids). In addition, a marked ecological trend towards exploiting the dwarf frog ecological niche (less than around 15 mm snout-vent length) is seen in the genera *Cacosternum*, *Microbatrachella*, *Arthroleptella* and in some species of *Phrynobatrachus*, the latter genus having radiated spectacularly. A distinct specialization towards breeding in temporary waters is also evident in *Cacosternum* (van Dijk 1977). These breeding systems and behavioral strategies make the Petropedetinae an attractive subject for students of the evolution of anuran breeding systems and ecology, providing that a phylogeny for the group becomes available.

The phylogenetic placement of this subfamily, or its component clades, amongst the ranids is currently unknown. As mentioned above, a wide range of hypotheses of relationships of the petropedetids to other ranoid frogs have been proposed in the past. Some of these appear reasonable, but others seem unfounded. Various petropedetine genera have in the past been associated with the brevicipitid microhylids (Noble 1931) on the basis of what are now known to be plesiomorphic character states. Some taxa were originally classified in the family Arthroleptidae, based solely on the presence of terrestrial breeding (e.g. *Arthroleptella*, some *Phrynobatrachus* species). The petropedetids have also been included peripherally in what has historically been one of the most perplexing and contentious issues in anuran systematics, i.e. the question of the phylogenetic position of the Dendrobatidae (Noble 1926a, 1931; Griffiths 1959a; Ford 1990, 1993; Grant *et al.* 1997). The genus *Cacosternum* has also been noted to have affinities with the enigmatic Seychelles family, the Sooglossidae, on the basis of an identical morphology of the os sesamoides tarsale, which occurs elsewhere in the Anura only in the Pipidae Gray, 1825 (Nussbaum 1982). Recently, Blommers-Schlösser (1993) proposed that many of the Asian ranids should be placed in the subfamily Petropedetinae, which she proposed as being diphyletic, based on a few ostensibly labile characters. *Cacosternum* has recently featured prominently in molecular investigations into the paraphyly of the burrowing genus *Tomopterna* (Vences 1999; Vences *et al.* 2000a), itself one of the most enigmatic taxa in the ranid subfamily Raninae (Clarke 1981). Since no all-encompassing phylogeny of the ranids

exists, and no previous work has focused exclusively on the petropedetids, these assumptions of relationship all remain to be tested.

The diversity of these hypotheses is a reflection of the poor state of knowledge of ranid phylogeny. Elucidating the phylogenetic relationships of the petropedetids requires the inclusion of members of other putative ranoid clades, particularly those mentioned above, in order to falsify or corroborate these hypotheses. There is a need to improve our knowledge of the comparative morphology and relationships among the major clades of Old World Ranoidea. By its content and scope, the present study provides a minimal test of the monophyly of many of these other ranoid groups. It also assesses some aspects of the new subfamilial classification scheme proposed for the Ranidae by Dubois (1986, 1992), which has been uncritically accepted by some recent workers (e.g. Bossuyt & Milinkovitch 2000) to the potential detriment of their biogeographic conclusions. A well-corroborated phylogeny of the Ranidae and improved delimitation of the major clades could also shed more light on the question of the nature and geographical occurrence of the major ranid radiation(s). It is currently under debate as to whether the family Ranidae originated prior to the break-up of Gondwanaland (as suggested by its distribution), or on the Indian fragment of Gondwana as it drifted northwards (as suggested by Bossuyt & Milinkovitch 2001), in tropical Asia (as suggested by Laurent 1951 and to some extent by Kosuch *et al.* 2001) or on continental Africa (as suggested by Savage 1973).

In summary, this research aims to test the monophyly of the ranid subfamily Petropedetinae, and to elucidate the phylogenetic relationships of the genera to each other, and to other clades of the Ranoidea. Although not attempting to construct a comprehensive phylogeny of the entire Ranidae, this study has to address some of the persistent questions regarding the phylogeny of the Ranidae in order to achieve resolution regarding the Petropedetinae.

MATERIALS AND METHODS

Taxonomic Sampling

This investigation was undertaken using an exemplar approach, with species used as terminals, as this involves using only verifiable and observable data, rather than hypothetical states or character combinations as used in the alternate method, *viz.* groundplans (Yeates 1995; Wiens 1998; Prendini 2001). The aim of the exemplar approach is to test the monophyly of particular clades, rather than assuming it. The chosen exemplars act as 'placeholders' for their respective clades: if they are truly representative of genuine monophyletic clades, then the relationships obtained by the analysis between those taxa will mirror the relationships between the monophyletic clades. An attempt was made to include exemplars of all postulated ranoid families and subfamilies, as no *a priori* knowledge of the relationships of any of these groups to the Petropedetinae can reliably be assumed in the absence of a cladistic analysis. An attempt was made to obtain molecular and morphological data for all of the selected exemplars, but tissue from some taxa was unavailable for sequencing. Some presumably crucial taxa were represented solely by morphological data. As the African subgenera of *Rana*, e.g. *Afrana*, *Strongylopus* and *Amietia*, are all distinctive and considered by local workers (e.g. Channing 1979; Passmore & Carruthers 1995; Channing 2001; Kosuch *et al.* 2001) to be generically distinct from *Rana*, as represented by *R. temporaria* Linnaeus, 1758, all subgenera of Dubois (1986, 1992) are treated here at generic rank for consistency. The subfamilial classification of the Ranidae (*sensu* Dubois) is followed, although his elevation of the petropedetids, mantellids and rhacophorids to full familial rank is not. Dubois' classification is used here as a working hypothesis within the Ranidae, and will therefore be subject to some degree of testing during this analysis.

Outgroup

The use of an archeobatrachian taxon as the outgroup would possibly have presented problems of homology assessment due to gross morphological and molecular dissimilarity with the ranoids. All previously conducted phylogenetic analyses could not adequately resolve the basal node of the Ranoidea, or have obtained conflicting results (Duellman & Trueb 1986; Hedges & Maxson 1993; Hay *et al.* 1995; Ruvinsky & Maxson 1996; Emerson *et al.* 2000a). Consequently, choice of a primary outgroup from within this group may have led to erroneous polarities. Since the superfamily Bufonoidea is widely accepted to be outside the boundaries of the Ranoidea (Hedges & Maxson 1993; Hay *et al.* 1995; Ruvinsky & Maxson 1996), the African heleophrynid *Heleophryne* was chosen from this superfamily as the primary outgroup. The Leptodactylidae, like the Ranidae, is poorly defined and appears to share some of the

hypothesized characteristics of the Ranidae, as assessed from Ford & Cannatella (1993). The leptodactylid *Leptodactylus melanonotus* was also included to test whether its character state combinations, notably the perceived sternal differences, were sufficient to place it outside of the Ranidae in a large cladistic analysis.

Ingroup

Two taxa, the Sooglossidae and the Dendrobatidae, which have been variously regarded as bufonids, 'transitional' families (*sensu* Lynch 1973) or putatively associated with the Ranoidea (Noble 1926a, 1931; Griffiths 1959a, 1959b; Lynch 1971, 1973; Savage 1973; Ford 1990; Hillis *et al.* 1993; Ruvinsky & Maxson 1996), were included. As both of these taxa have at some time been suggested to be related to the petropedetids, and because the present study contains a larger sample of the ranids proposed to be related to the dendrobatids by Griffiths (1963) than Ford's (1990) study did, their inclusion here is warranted. Many petropedetine genera were originally included in the Arthroleptidae, and share similarities in breeding systems with these frogs, hence inclusion of the Arthroleptidae was considered necessary. All genera of the Astylosterninae were represented by one species, and three species of the Arthroleptinae were included. The Hyperoliidae were thought to be closely related to the Arthroleptidae by Laurent (1951, 1973, 1986), and were thus represented here by three species. The Microhylidae were represented here because some cacosternids were historically included in this family on the basis of many shared character states, although many of these have subsequently been demonstrated to be plesiomorphic (Lynch 1971, 1973; Trueb 1973). The microhylids are also widely held to be basal within the Ranoidea, and their exclusion could thus compromise the elucidation of correct basal relationships. The Hemisotidae, represented here by a single species, was thought to be closely related to the microhylids by Blommers-Schlösser (1993), Wu (1994) and Emerson *et al.* (2000a), but not by Parker (1934), Channing (1995) or van Dijk (2001). The familial status of the rhacophorids and mantellids was refuted by recent work (Emerson *et al.* 2000a), which unequivocally considers them as sister taxa within the family Ranidae. Although neither of these taxa have previously been hypothesized to be closely related to the petropedetids, they were included for completion of sampling.

At least two to three exemplars were included as representatives of all hypothesized subfamilies of the Ranidae (*sensu* Dubois 1986), excepting the Ranixalinae, for which only one exemplar could be obtained. Emphasis was placed on including all African genera of the Ranidae. Choice of these taxa was determined by the availability of specimens for examination and tissue for DNA extraction. All currently recognized monotypic genera of the subfamily Petropedetinae were included in the present study. More than one species of each petropedetine genus was included where possible, as a minimal test of generic monophyly.

Table 1. Classification of the family Ranidae Rafinesque-Schmaltz, 1815 after Dubois (1986, 1992), compiled from Duellman (1993) and Frost (2002). The number of species in each genus is indicated in parentheses and, where applicable, subgenera in brackets. Genera represented by at least one exemplar in the present study are underlined. Asterisks represent genera or numbers of species differing from that indicated in Duellman (1993).

Subfamily Dicroglossinae Anderson, 1871

Tribe Ceratobatrachini Boulenger, 1884

Ceratobatrachus Boulenger, 1884 (1), *Discodeles* Boulenger, 1881 (5), *Ingerana* Dubois, 1987 '1986' (8), *Palmatorappia* Ahl, 1927 (1), *Platymantis* Günther, 1859 (37), *Taylorana* Dubois, 1987 '1986' (2).

Tribe Conrauini Dubois, 1992

Conraua Nieden, 1908 (6).

Tribe Dicroglossini Anderson, 1871

Euphlyctis Fitzinger, 1843 (4), *Occidozyga* Kuhl & van Hasselt, 1822 (17), *Phrynoglossus* Peters, 1867 (8).

Tribe Limnonectini Dubois, 1992

Hoplobatrachus Peters, 1863 (5), *Limnonectes* Fitzinger, 1843 [88+ species in 3 subgenera: *Bourretia* Dubois, 1987; *Feyervaria* Bolkay, 1915; *Limnonectes* Fitzinger, 1843].

Subfamily Petropedetinae Noble, 1931

Ericabatrachus Largen, 1991 (1).

Tribe Cacosternini Noble, 1931

Anhydrophryne Hewitt, 1919 (1), *Arthroleptella* Hewitt, 1926 (7*), *Cacosternum* Boulenger, 1887 (9*), *Microbatrachella* Hewitt, 1926 (1), *Nothophryne* Poynton, 1963 (1), *Poyntonia* Channing & Boycott, 1989 (1).

Tribe Petropedetini Noble, 1931

Arthroleptides Nieden, 1910 (3*), *Dimorphognathus* Boulenger, 1906 (1), *Natalobatrachus* Hewitt & Methuen, 1913 (1), *Petropedetes* Reichenow, 1874 (7), *Phrynobatrachus* Günther, 1862 (66), *Phrynodon* Parker, 1935 (1).

Subfamily Ptychadeninae Dubois, 1987 '1986'

Hildebrandtia Nieden, 1907 (3); *Lanzarana* Clarke, 1983 (1); *Ptychadena* Boulenger, 1917 [40 species in 2 subgenera: *Ptychadena* Boulenger, 1917; *Parkerana* Dubois, 1984].

Subfamily Pyxicephalinae Bonaparte, 1850

Aubria Boulenger, 1917 (3*); *Pyxicephalus* Tschudi, 1838 (2).

Subfamily Raninae Rafinesque-Schmaltz, 1814

Amolops Cope, 1865 [34 species in 4 subgenera: *Amolops* Cope, 1865; *Huia* Yang, 1991; *Meristogenys* Yang, 1991; *Amo* Dubois, 1992]; *Batrachylodes* Boulenger, 1887 (8); *Chaparana* Bourret, 1939 (6); *Micrixalus* Boulenger, 1888 (7); *Nanorana* Günther, 1896 [2 species in 2 subgenera: *Altirana* Stejneger, 1927; *Nanorana* Günther, 1896]; *Paa* Dubois, 1975 [25+ species in 4 subgenera: *Eripaa* Dubois, 1992; *Gynandropaa* Dubois, 1992; *Paa* Dubois, 1975; *Quasipaa* Dubois, 1992]; *Rana* Linnaeus, 1768 [222 species in 33 subgenera: *Afrana* Dubois, 1992; *Amerana* Dubois, 1992; *Amietia* Dubois, 1987 '1986'; *Amnirana* Dubois, 1992; *Aquarana* Dubois, 1992; *Aurorana* Dubois, 1992; *Babina* Van Denburgh, 1912; *Chalcorana* Dubois, 1992; *Clinotarsus* Mivart, 1869; *Eburana* Dubois, 1992; *Glandirana* Fei, Ye & Huang, 1990; *Humerana* Dubois, 1992; *Hydrophylax* Fitzinger, 1843; *Hylarana* Tschudi, 1838; *Lithobates* Fitzinger, 1843; *Nasirana* Dubois, 1992; *Nidirana* Dubois, 1992; *Odorrana* Fei, Ye & Huang, 1990; *Pantherana* Dubois, 1992; *Papurana* Dubois, 1992; *Pelophylax* Fitzinger, 1843; *Pseudorana* Fei, Ye & Huang, 1990; *Pterorana* Kiyasetuo & Khare, 1986; *Pulchrana* Dubois, 1992; *Rana* Linnaeus, 1758; *Rugosa* Fei, Ye & Huang, 1990; *Sanguirana* Dubois, 1992; *Sierrana* Dubois, 1992; *Strongylopus* Tschudi, 1838; *Sylvirana* Dubois, 1992; *Trypheropsis* Cope, 1866; *Tylerana* Dubois, 1992; *Zweifelia* Dubois, 1992], *Staurois* Cope, 1865 (3).

Subfamily Ranixalinae Dubois, 1987 '1986'

Indirana Laurent, 1986 (9); *Nannophrys* Günther, 1869 (3); *Nyctibatrachus* Boulenger, 1882 (11).

Subfamily Tomopterninae Dubois, 1987 '1986'

Tomopterna Duméril & Bibron, 1841 (7); **Sphaerotheca* Günther, 1859 '1858' (7); **Laliostoma* Glaw, Vences & Böhme, 1998 (1).

Table 2. Classification of additional ranoid and bufonoid genera represented in the present study by at least one exemplar.

Family Arthroleptidae Mivart, 1869
- Subfamily Arthroleptinae Mivart, 1869
  - *Arthroleptis* Smith, 1849; *Cardioglossa* Boulenger, 1900.
- Subfamily Astylosterninae Noble, 1927
  - *Astylosternus* Werner, 1898; *Leptodactylon* Andersson, 1903; *Nyctibates* Boulenger, 1904; *Scotobleps* Boulenger, 1900; *Trichobatrachus* Boulenger, 1900.

Family Mantellidae Laurent, 1946
- *Mantella* Boulenger, 1882; *Mantidactylus* Boulenger, 1895.

Family Dendrobatidae Cope, 1865
- *Colostethus* Cope, 1866; *Dendrobates* Wagler, 1830; *Mannophryne* LaMarca, 1992.

Family Heleophrynidae Noble, 1931
- *Heleophryne* Sclater, 1899.

Family Hemisotidae Cope, 1867
- *Hemisus* Günther, 1859 '1858'.

Family Hyperoliidae Laurent, 1943
- Subfamily Hyperoliinae Laurent, 1943
  - *Hyperolius* Rapp, 1842.
- Subfamily Kassininae Laurent, 1972
  - *Kassina* Girard, 1853.
- Subfamily Leptopelinae Laurent, 1942
  - *Leptopelis* Günther, 1859 '1858'.

Family Leptodactylidae Werner, 1896 '1838'
- Subfamily Leptodactylinae Werner, 1896 '1838'
  - *Leptodactylus* Fitzinger, 1826.

Family Microhylidae Günther, 1858 '1843'
- Subfamily Brevicipitinae Bonaparte, 1850
  - *Breviceps* Merrem, 1820.
- Subfamily Phrynomerinae Noble, 1931
  - *Phrynomantis* Peters, 1867.

Family Rhacophoridae Hoffman, 1932 '1858'
- Subfamily Rhacophorinae Hoffman, 1932 '1858'
  - *Chiromantis* Peters, 1855; *Philautus* Gistel, 1848.

Family Sooglossidae Noble, 1931
- *Sooglossus* Boulenger, 1906.

The largest sample was taken from the genus *Phrynobatrachus*, which was represented by seven exemplar species, although this corresponds to only 10% of its described species. Genera of the Ranidae represented in the present study are underlined in Table 1. Non-ranid taxa included in the present study are indicated in Table 2.

Morphological Data Collection

Voucher Specimens and Preparation

Voucher specimens examined for morphological data collection are listed in Appendix 1. All character states were coded preferentially from adult males, unless another semaphoront is specified. Minimal dissections were performed on whole specimens; these were usually only a lateral incision to sex the specimen and determine the character state pertaining to the testes, and

a longitudinal incision in the skin of the venter to assess the condition of the musculus cutaneous pectoralis.

All osteological material examined was double-stained (alizarin red and alcian blue) and enzymatically cleared. Skeletons were prepared using the method of Dingerkus & Uhler (1977), as modified in Drewes (1984) by incubating the enzyme-assisted digestion stage at the optimal enzyme temperature (35.5 °C for the bovine pancreatic trypsin used). Specimens were skinned and sexed beforehand, the skin was often left on the hands to prevent the disarticulation of the phalanges (L. S. Ford, personal communication). Many of the larger muscle masses were removed from large specimens, notably the calf and thigh muscles, and some of the muscles of the pectoral region. The removed skin, organs and muscle tissue were retained separately for future study or redetermination. After the rehydration series and before the 3:1 KOH: glycerine step, a 0.5% KOH step was inserted for large specimens only. Large specimens were placed in the sunlight for all of the KOH: glycerine steps, with the occasional addition of a few drops of 10 volume H_2O_2. Some large or older specimens were difficult to clear enzymatically, the latter type due to dehydration or alteration of the tissue composition with time. In these cases, length of time in the KOH: glycerine steps were increased, up to about two months. Limited disintegration occurred in some of the older specimens as a result, but if the tissue fails to clear, the usefulness of the preparation is drastically reduced, whereas osteological information is usually still obtainable from disarticulated specimens. Specimens were not disarticulated for coding, except the occasional removal of the pectoral girdle and lower jaw.

Rare specimens and additional specimens of some species were X-rayed onto Ilford Pan FP4 black and white 9 x 11.5 cm film using a dental X-ray apparatus (25 kV, 4 mA). These were developed using Agfa Rodinal© developer as per instructions, and printed commercially onto black and white high contrast film. X-rays were digitally scanned and processed using Corel PhotoPaint v. 10 (Corel Corporation Ltd.). Digital images will be deposited in the collection of the TMSA.

Morphological Characters

An abridged list of the 192 phylogenetically informative morphological characters used in the analysis, including definitions of the states observed for these in the set of chosen exemplar taxa, is presented in Table 3. The characters were drawn from the following sources: 52 from the osteology of the skull, 13 from osteology of the vertebral column, 25 from osteology of the pectoral girdle and forelimbs, 18 from osteology of the pelvic girdle and hindlimbs, 22 from the hyolaryngeal apparatus, 45 from external morphology, 15 sexually dimorphic characteristics from osteology or external morphology, and one character each from the breeding system and muscles. Of the included characters, 89 were binary and 103 were multistate. Composite coding (*sensu* Maddison 1993; Strong & Lipscomb 1999) was used in preference to binary coding

where possible, in order to minimise the occurrence of inapplicable or missing entries (Maddison 1993; Pleijel 1995; Wilkinson 1995; Strong & Lipscomb 1999; Lee & Bryant 1999). Terminology generally follows the two most recent comparable works dealing with the Ranoidea, *viz*. Ford (1990) and Wu (1994).

Criteria for recognizing characters and the definitions of states are discussed in Appendix 2. Although the process of primary homology assessment inherently contains some element of subjectively, because different researchers may perceive character states slightly differently (Hawkins *et al.* 1997; Hawkins 2000; Wiens 2001), every effort was made to use standardized states. To facilitate comparison with the findings of previous researchers, the history of usage of each character is referenced as fully as possible in Appendix 2, with an asterisk identifying those characters which are not presented identically to those in that reference. Since many of the characters used are well known in anuran systematics, only characters considered not adequately explained in previous works and not self-evident, are explained in detail in Appendix 2 or illustrated in Figures 1–19. In Appendix 2, distinction is made between synapomorphies that occur only once in the tree, termed 'unique', and those that occur elsewhere in the tree, in order to provide more information regarding their relative homoplasy in the discussion. However, whether a unique character has reversed or not is not implied by this usage (*sensu* Kluge & Farris 1969) and all character states that support a clade are listed, regardless of their tendency for reversal or transformation. Terminology regarding characters and states is similar to that used by Ford (1990), the number following a 'c' is the character number, followed by a colon, and then the state number of that character (e.g., c2:1 refers to state 1 of character 2). The original works of Cannatella (1985) and Tyson (1988) were not seen. In these cases, the information on correspondence of characters presented in Appendix 2 is taken from that provided in Ford (1990) and Wu (1994).

Characters were assumed to be logically independent, even if they may not be so biologically. Character polarities were determined via outgroup comparison (Watrous & Wheeler 1981; Farris 1982; Maddison *et al.* 1984; Nixon & Carpenter 1993) with reference to *Heleophryne purcelli*, which is coded consistently as zero in the matrix for ease of visually determining the state considered plesiomorphic by the analysis in the resulting matrix and character optimizations. All morphological multistate characters were treated by the analyses as non-additive, i.e. unordered (Fitch 1971), whereby the minimum distance between all pairs of character states could be as low as one step. Unfalsifiable *a priori* hypotheses regarding character state order were not incorporated, rather character congruence was allowed to determine the order (Hauser & Presch 1991; Slowinski 1993; Hormiga 1994).

Table 3. Abridged character list, giving states only. For references to previous usage, explanations and illustrations, and morphological character optimizations onto the equally-weighted hypothesis, refer to Appendix 2.

0. Atlantal intercotylar distance: (0) widely separated, at least one cotyl width apart (Lynch type I); (1) juxtaposed but distinct, very narrowly separated by a notch (Lynch type II).

1. Atlas, neural arches: (0) fused; (1) failing to completely unite, dorsal gap present.

2. First and second presacral vertebrae: (0) normally ossified and separate; (1) neural spine of the first vertebra appears flattened and extends posteriorly, overlapping the anterior portion of the second vertebra to which it is fused, forming a dorsal bone bridge centrally between the first and second vertebrae; (2) neural spine strongly overlaps the second vertebra from the first, but no fusion of the first to the second vertebra occurs.

3. Vertebral column, eighth vertebra, length of transverse processes: (0) much shorter than those of the fourth vertebra; (1) roughly equal in length to those of the fourth vertebra.

4. Vertebral column, eighth vertebra, orientation of transverse processes in frontal plane: (0) orientated laterally, perpendicular to spine; (1) slight anterolateral orientation, approximately 20° – 30°; (2) acute anterolateral orientation, approximately 45° or more.

5. Vertebral column, shape in dorsal view of posterior four vertebrae: (0) square, minimal space between vertebrae; (1) rectangular, gap between vertebrae greater than half their width.

6. Vertebral column, dorsal view of posterior four vertebrae, margins: (0) very strong V-shaped indent in anterior margin, reaching approximately half of the vertebral width; (1) anterior and posterior margins parallel, no large indent.

7. Neural spines on vertebrae two to four: (0) absent; (1) present; (2) extreme dorsal and posterior development of neural spines which may be totally fused in up to the first four vertebrae.

8. Fusion of eighth presacral and sacral vertebrae: (0) not fused; (1) fused.

9. Fusion of first (atlas) and second presacral vertebrae: (0) fused; (1) unfused.

10. Ossification of suprascapular cartilage: (0) limited, so that only the proximal section is ossified and forms a Y-shaped flange of mineralisation with the cleithrum, with the fork facing dorsally; (1) heavily ossified, 1/3 to 2/3 of blade, forming one rounded, rectangular or triangular flange with the cleithrum.

11. Vertebrae five to eight, ventral view; shape of centrum and base of transverse processes: (0) centra cylindrical or sub-cylindrical, bases of the transverse processes not laterally expanded; (1) centra rectangular-shaped, with a small gap between the bases of the transverse processes; (2) centra diamond-shaped, well developed lateral expansion of the bases of the transverse processes.

12. Vertebrae five to eight, attachment of zygapophyses: (0) on lateral (mid) portion of centrum, which thus gives the curvature of the centrum (and the initiation of the base of the transverse processes) an evenly graded appearance in ventral view; (1) on dorsolateral surface of centrum, thus giving the centrum's curvature a sharply cylindrical appearance in ventral view, and leading to a sharp distinction between the bases of the transverse processes and the centrum.

13. Vertebra eight, centrum: (0) procoelous; (1) diplasiocoelous.

14. Coccyx, dorsal ridge (crista dorsalis): (0) absent or greatly reduced, less than half the length of the coccyx; (1) around half the length of the coccyx but well developed; (2) longer than half the length of the coccyx and well developed.

15. Coccyx, anterior process (canalis coccygeus): (0) absent; (1) present.

16. Coccyx, length relative to precoccygeal vertebral column length: (0) approximately one vertebral length shorter; (1) equal to the vertebral column; (2) more than one vertebral length shorter.

17. Coccyx, transverse processes: (0) present anteriorly, often as small vestiges; (1) absent.

18. Ilium, dorsal protuberance: (0) oval and inconspicuous; (1) projected laterally and tending to be spike-like, can be small, sharp and triangular or slightly rounded; (2) large spike- or flange-like, not oval or adpressed to shaft.

19. **Ilium, height of crest along dorsal surface measured centrally:** (0) absent; (1) 0.5 to 1 times height of ilium; (2) 1 to 2.5 times height of ilium, very well developed and squared off posteriorly.
20. **Sacral diapophyses, expansion:** (0) ratio of distal end to proximal region (base) is greater than two (strongly dilated); (1) ratio of distal end to proximal region is greater than one but less than two (slightly dilated); (2) ratio of distal end to proximal region is equal to one (undilated).
21. **Sacral diapophyses, distal ends:** (0) distinctly flattened (dorsoventrally compressed); (1) cylindrical or nearly so in lateral view.
22. **Sacral diapophyses, anterior margin:** (0) angled posteriorly; (1) angled transversely (perpendicular to the spine), even if due to dilation; (2) directed anteriorly, due to rounded (axe-shaped) type of sacral diapophysis dilation.
23. **Clavicles, width:** (0) slightly tapering along whole length, meeting the procoracoid cartilage medially; (1) narrowing sharply, half the length of the coracoids; (2) slightly ossified expansion medially.
24. **Clavicles, nature:** (0) stout and thick; (1) reduced and thin; (2) absent.
25. **Clavicle orientation:** (0) strongly or slightly bowed, pointing distinctly anteromedially and contacting only the procoracoid cartilage; (1) bowed slightly but roughly at right angles to the main to body axis; (2) straight and perpendicular to body axis.
26. **Clavicle-coracoid, contact:** (0) clavicle not touching coracoid, separated by long procoracoid cartilage; (1) procoracoid cartilage ossified and indistinguishably fused to the coracoid, which expands strongly towards the clavicle medially: coracoid appears fused to clavicle in this manner for about 1/5 to 1/4 of the latter's length; (2) clavicle descends medially and is fused to coracoid for approximately the medial 1/3 of is length; (3) only point contact anteromedially via short procoracoid cartilage.
27. **Overlap of the medial borders of the coracoids:** (0) epicoracoids elaborated into posterior epicoracoid horns which overlap medially, usually fused in the interclavicle region (arciferal condition); (1) epicoracoid cartilages fused medially, coracoids slightly angled ventrally and one side of coracoid overlapping the other medially, overlapping coracoid is usually fenestrated at its medial edge (modified firmisternal condition, or pseudoarciferal condition); (2) epicoracoid cartilage fused medially (firmisternal condition); (3) firmisternal, with fused epicoracoid cartilages and extremely long procoracoid cartilages.
28. **Coracoid, shape:** (0) evenly constricted from medial edge to centre, trumpet-shaped; (1) strong constriction just after medial edge, T-shaped; (2) weaker constriction just after medial edge, broader medially than state 1.
29. **Dilation of coracoid:** (0) lateral and medial edges of coracoid about the same width, medial edge less than 1.3 times width of lateral edge; (1) medial edge of coracoid dilated and distinctly wider than lateral edge, more than 1.4 times its width.
30. **Coracoid, posterior margin (excluding extreme medial section):** (0) straight; (1) curved; (2) sigmoid.
31. **Medial edges of both coracoids:** (0) always single; (1) often bifurcated or nicked.
32. **Omosternum style:** (0) minute cartilaginous peg, occasionally absent; (1) present and cartilaginous, large; (2) present and well ossified; (3) always absent.
33. **Metasternum:** (0) cartilaginous and broad, sometimes with slight calcification; (1) narrow bony stylus; (2) absent.
34. **If metasternum ossified, shape:** (0) short, hourglass-shaped plate, expanded at both ends; (1) long, narrow and tapering markedly anteriorly to posteriorly, length up to 3.5 times maximum width; (2) long, narrow and tapering markedly anteriorly to posteriorly, length more than 4 times maximum width.
35. **Xiphisternum, shape:** (0) large, rounded; (1) small peg, usually triangular; (2) large triangular with distinctly serrated distal edge; (3) roughly X-shaped, two expansions of cartilage attached to a short inflated mineralised section; (4) large inverted U-shaped plate; (5) rectangular with a smooth distal end; (6) large anchor shape; (7) narrow and divided, i.e. two long rectangular projections which are expanded distally; (8) rectangular with strongly serrated distal end.

36. **Xiphisternum, posterior fenestra:** (0) absent; (1) present on posterior peripheral margin; (2) present centrally on plate, cartilage fused posterior to fenestra.
37. **Sphenethmoid, ventral portion:** (0) fused, single; (1) paired.
38. **Ventral sphenethmoid, extension of ossified anterior portion (antrum pro lobo olfactoria):** (0) reduced and narrow, adpressed to braincase; (1) covering about 1/2 the distance from palatines (or anterior edge of orbit) to premaxilla; (2) covering 2/3 or more of the distance from palatines (or anterior edge of orbit) to premaxilla.
39. **Ethmoid cartilage, septum nasi:** (0) thin, nasal capsules close together; (1) thick, nasal capsules medially separate.
40. **Palatines:** (0) present and well developed; (1) reduced, thin sliver of bone only; (2) absent.
41. **Palatines:** (0) present, touching the sphenethmoid but not nearly meeting medially; (1) present, nearly meeting at the midline over the sphenethmoid, medial portion can be slightly expanded.
42. **Vomer, anterior process:** (0) absent; (1) present.
43. **Vomers, position and reduction:** (0) not reduced, centre of vomer not lateral to articulation of the maxilla and premaxilla; (1) reduced, vomers placed laterally, with centre of vomer lateral to articulation of premaxilla and maxilla.
44. **Vomer, anterior process:** (0) short or absent, separated by a small or large gap from articulation of premaxilla and maxilla; (1) long, passing dorsally to articulation of premaxilla and maxilla; (2) long, but curving anteriorly and laterally and passing dorsally to the anterior end of the maxilla.
45. **Vomer, postchoanal process:** (0) horizontal; (1) vertical; (2) oblique; (3) fused to hyperossified sphenethmoid.
46. **Vomer, posterior (dentigerous) process:** (0) present; (1) absent.
47. **Vomer, posterior (dentigerous) process, if present:** (0) connected to main body of vomer; (1) separate from main body of vomer.
48. **Vomerine teeth:** (0) present; (1) absent.
49. **Maxillary and premaxillary teeth:** (0) present; (1) absent.
50. **Premaxilla, shape of pars palatina:** (0) medial edge greater than lateral edge; (1) medial edge equal to lateral edge; (2) medial edge less than lateral edge; (3) lateral edge slanting outwards therefore longer, and lateral section of pars palatina usually thicker than medial section.
51. **Maxilla, expansion of the pars palatina (not including the anteromedial flange):** (0) expansion of anterior 1/4 of pars palatina equals the expansion of posterior 1/4 in width; (1) anterior 1/4 more expanded than posterior 1/4.
52. **Maxilla, anteromedial flange of pars palatina:** (0) absent; (1) present; (2) present and large, veering medially, creating a strongly concave anterior margin of the maxilla which creates a large fenestra between the maxilla and premaxilla.
53. **Pterygoid, anterior ramus:** (0) in contact with or fused to the maxilla; (1) separated slightly from the maxilla by cartilage.
54. **Mandibular odontids:** (0) absent; (1) present as large thickened processes of the anterior edge of angulosplenial, more developed in males but also present in a reduced state in females; (2) small, fine, tooth- or tusk-like projections of the dentary, angled posteriorly, in adult males only; (3) irregularly-shaped jaggered fang-like odontids present for the entire length of lower jaw (false teeth).
55. **Mentomeckelian bone, relative height on medial versus lateral edges:** (0) height of medial edge is equal to height of lateral edge; (1) height of medial edge is less than height of lateral edge; (2) mentomeckelian long and fused with the angulosplenial.
56. **Mentomeckelian bone, lateral processes:** (0) absent; (1) shorter than or equal in length to mentomeckelian bones; (2) much longer than mentomeckelian bones.
57. **Angulosplenial:** (0) terminates at jaw articulation; (1) extends posteriorly to jaw articulation due to retroarticular process.
58. **Parasphenoid, shape of tip of cultriform process:** (0) rounded or serrated; (1) sharply pointed.
59. **Parasphenoid, shape of cultriform process:** (0) borders straight, process relatively wide; (1) borders biconcave, i.e. slight expansion in middle with narrower posterior section; (2)

borders not straight but slightly tapering, can be very thin; (3) borders strongly converging, strongly triangular-shaped cultriform process.

60. **Parasphenoid, length of cultriform process:** (0) reaching the anterior 1/5 of the orbit, but falling just short of the level of the palatines and planum antorbitale; (1) shorter, reaching only to about 2/3 length of orbit; (2) long, reaching the level of the palatines and planum antorbitale.
61. **Anterior ramus of pterygoid in relation to the palatines and planum antorbitale in the dorsoventral plane:** (0) falling far short of palatines, extending to approximately mid-orbital level; (1) short gap or slight overlap; (2) long, curving medially away from the maxilla towards an enlarged, wider planum antorbitale, separated from the lateral border of planum antorbitale by wide gap, palatines absent.
62. **Pterygoid, length of medial ramus:** (0) present and long; (1) reduced, short but longer than its width, or rudimentary bumps; (2) extra long and thin.
63. **Pterygoid, articulation of medial ramus:** (0) anteroventral surface of otoccipital, may be a large gap; (1) ventrolateral edge of otic capsule; (2) anterior to and adpressed to parasphenoid ala along at least 1/2 its length.
64. **Overlap of the anterior border of the parasphenoid ala and medial ramus of pterygoid in the anterior to posterior plane:** (0) point overlap (approximately 1/5) to moderately overlapping (approximately 1/4) along the length of the anterior edge of the ala, abutting; (1) close together but no contact (distinct gap), as medial ramus is more anterior; (2) strong overlap, approximately 1/2 length of anterior edge of the ala, abutting.
65. **Parasphenoid alae, in frontal plane:** (0) perpendicular to body axis; (1) pointing slightly anteriorly; (2) pointing distinctly posteriorly.
66. **Parasphenoid alae:** (0) moderately long; (1) reduced or short.
67. **Cranial exostosis:** (0) absent, or slightly on sphenethmoid and/ or otoccipitals only, occasionally on the nasals; (1) present, extensive on sphenethmoid, nasals and other skull bones.
68. **Nasals, contact with sphenethmoid:** (0) overlapping the sphenethmoid; (1) not overlapping the sphenethmoid.
69. **Nasals, median contact:** (0) separate, not in contact; (1) contact extensively on medial margin.
70. **Nasals, shape:** (0) large, triangular; (1) rectangular to round; (2) small, triangular or club-shaped.
71. **Degree of development of the otic plate of the squamosal and its relationship with the otoccipital:** (0) otic plate present, overlapping the crista parotica, even posteriorly only or the lateral border of the otoccipital; (1) overlapping most or all of crista parotica and 1/4 to 1/2 of the otoccipital; (2) otic plate rudimentary or absent, only a thin rib of bone overlaps the outside of the crista parotica; (3) otic plate rudimentary, otic ramus extends posteriorly for only about 1/2 width of lateral border of the otoccipital in an arc, otic plate overlaps the crista parotica only in this region.
72. **Otic capsule, crista parotica, cartilaginous process extending towards the suprascapula:** (0) present; (1) absent; (2) present, but part of the dorsal section of an extra large tympanum.
73. **Otic capsule, crista parotica, cartilaginous process extending towards the suprascapula, if present:** (0) short, cartilaginous; (1) very long, cartilaginous; (2) long and ossified, as is the crista parotica.
74. **Otic capsule, crista parotica, nature:** (0) cartilaginous; (1) mostly ossified.
75. **Otic capsule, crista parotica, angle:** (0) perpendicular to body axis in frontal plane; (1) angled forward in the frontal plane, assessed from the position of the anterior margin of the crista parotica.
76. **Frontoparietal fenestra:** (0) large, covering more than 1/3 the width of frontoparietal and gap, frontoparietals reduced to narrow margins only; (1) present as a small gap, not more than 1/3 the width of frontoparietal and gap, with each frontoparietal slightly reduced; (2) absent; (3) small round gap at the point of fusion of frontal and parietal.
77. **Frontoparietals, anterior margins:** (0) lateral edge extends beyond the medial edge; (1) medial edge extends as much as the lateral edge and the central portion; (2) medial edge

extends beyond the lateral edge; (3) medial and lateral edge not as anterior as the centre, leading to a heart-shaped frontoparietal arrangement; (4) lateral edges extend outwards slightly, gap for interfrontal bone, which is absent.

78. **Frontoparietal, shape:** (0) rectangular; (1) anterior wider than posterior; (2) posterior wider than anterior; (3) diamond-shaped.
79. **Squamosal, thickness of zygomatic versus otic ramus:** (0) otic ramus noticeably thicker, since distinct angular bend as it turns over the crista parotica not evident; (1) approximately equally thick, distinct angular bend onto the surface of the crista parotica evident; (2) zygomatic ramus notably expanded and exostosed.
80. **Squamosal, length of the zygomatic ramus in comparison with that of the otic ramus:** (0) zygomatic ramus longer than the otic ramus; (1) zygomatic ramus approximately equal in length to the otic ramus; (2) zygomatic ramus shorter than the otic ramus.
81. **Maxilla, shape of pars fascialis (lateral view):** (0) well developed and rectangular; (1) reduced anteriorly, strong and triangular; (2) reduced to absent, may be rectangular and short.
82. **Quadratojugal, overlap with maxilla:** (0) continuous, articulating with maxilla, slanting over each other or strongly overlapped, no reduction in quadratojugal; (1) anterior process of the quadratojugal reduced or absent, not touching the maxilla.
83. **Quadratojugal:** (0) present; (1) absent.
84. **Pars externa plectri of breeding males:** (0) large, present, rounded, covering 1/3 to 2/3 of the area inside the tympanic annulus; (1) small and rod-like, or absent; (2) extremely large, covering more than 2/3 of area inside tympanic annulus.
85. **Premaxilla, projection of pars fascialis (alary process):** (0) vertical (dorsal); (1) backwards (posterodorsally); (2) forwards (anterodorsally).
86. **Premaxilla, angle of pars fascialis (alary process):** (0) dorsally, perpendicular to pars dentalis; (1) inclined laterally outwards away from midline.
87. **Tympanic annulus:** (0) complete; (1) incomplete, rounded; (2) absent; (3) incomplete, pear-shaped, involving the squamosal as its dorsal limit, with the dorsal section of cartilage fused onto squamosal.
88. **Stapes (columella):** (0) present; (1) reduced; (2) absent.
89. **Hyoid, hyale, width from start of anteromedial process:** (0) narrow, without a flange extending to half the length of hyale; (1) wide, flange extending to half the length of hyale.
90. **Hyoid, hyale, free flange towards jaw just anterior to its angle:** (0) absent; (1) present.
91. **Medial branch of anterior process of hyale:** (0) long, straight, thin; (1) short and usually curled, relatively thick; (2) small nipple-like knob only, (3) slightly elongated, but not more than three times its width; (4) absent.
92. **Hyoid, shape of the stalk of the alary processes:** (0) narrow and pinched, blade-like; (1) thick and rounded, slightly less than or as expanded as the thick distal portion.
93. **Hyoid, alary process, width of base:** (0) equal to the stalk; (1) broader than stalk.
94. **Hyoid, distal expansion of alary process:** (0) absent; (1) present.
95. **Hyoid, shape of the distal expansion of the alary process:** (0) large rounded to trumpet-shaped or slightly triangular expansions; (1) oval, slanted posteriorly at a 45° angle to the body axis; (2) extremely small, rounded, edges can be ragged; (3) small, narrow, blade-like, slanting posteriorly at a 45° angle.
96. **Hyoid, angle of alary processes:** (0) angled anteriorly; (1) angled laterally.
97. **Hyoid, hyoglossal sinus:** (0) deeper than anterior border of base of alary processes; (1) shallow, less than or just reaching anterior border of base of alary processes; (2) shallow, but fibrous line of a deep sinus visible.
98. **Hyoid plate, calcification:** (0) not or only slightly calcified centrally, but not calcified between the thyrohyals; (1) well calcified, with large proximal expansions at the bases of the thyrohyals, resulting in the thyrohyals appearing almost fused at the posterior end of the plate.
99. **Hyoid, fibrous uncalcified suture on hyoid plate:** (0) absent; (1) present centrally, running transversely; (2) present centrally, running longitudinally and not present at extreme anterior and posterior edges of the plate.

100. Hyoid plate, shape: (0) wide, width greater than or equal to length; (1) narrow, longer than wide.

101. Hyoid, posteromedial process (thyrohyal): (0) cartilaginous stalk absent; (1) cartilaginous stalk present; (2) hyoid plate pinched above thyrohyals, posterior lateral processes originating close to base of alary processes.

102. Hyoid, posterolateral process: (0) present; (1) absent; (2) extremely reduced, small bumps only.

103. Hyoid, posterolateral processes, length: (0) long; (1) short, less than 1/3 length of posteromedial process (thyrohyal); (2) rudimentary bumps or stumps.

104. Hyoid, posteromedial process (thyrohyals), expanded flange on medial side: (0) absent; (1) present, small; (2) present, widening of thyrohyals due to distal medial expansion towards larynx, which has a concave inside edge.

105. Hyoid, posteromedial process (thyrohyals), expanded flange on lateral side: (0) absent; (1) present distally, small; (2) present medially, with curved edge.

106. Hyoid, posteromedial process (thyrohyals): (0) expanded at proximal ends only; (1) equal width, not expanded at either end; (2) expanded at both ends.

107. Hyoid, distance between posteromedial processes (thyrohyals): (0) close together, less than one times the width of the proximal expansion of the thyrohyal apart; (1) about once the width of the proximal expansion of the thyrohyal apart; (2) more than 1.5 times the width of the proximal expansion of the thyrohyal apart.

108. Cricoid ring, oesophageal process: (0) present; (1) absent.

109. Cricoid, bronchial processes: (0) present, short, not branched or latticed; (1) present, long, ending in an extensive lattice of cartilage surrounding or ramifying through the lungs.

110. Larynx, arytenoid cartilages of breeding male: (0) rounded; (1) disproportionately long and oval-shaped, relative to the width of the entire larynx.

111. Tarsal one (not naviculare): (0) absent as independent element; (1) present.

112. Tarsal two: (0) free, not fused to tarsal three; (1) fused to tarsal three.

113. Carpal state *sensu* Laurent & Fabrezi (1989): (0) A; (1) B; (2) C; (3) D; (4) E; (5) F.

114. Distal intercalary elements: (0) absent; (1) present, thick concave discs; (2) present, wedge-shaped, rounded anteriorly and slightly concave posteriorly.

115. Digital subarticular sesamoids: (0) absent; (1) present.

116. Sesamoid(s) on ventromedian surface of tarso-metatarsal joint: (0) absent; (1) present.

117. Sesamoid(s) on ventrolateral surface of tarso-metatarsal joint: (0) absent; (1) one present; (2) two present; (3) three present.

118. Sesamoid in the aponeuris palmaris: (0) none; (1) one.

119. Os sesamoides tarsale: (0) absent; (1) present.

120. Cartilagio sesamoides: (0) present; (1) absent.

121. Prehallux: (0) small, usually cartilaginous; (1) large, either ossified or cartilaginous.

122. Prepollex, length versus length of first metacarpal in mature male: (0) approximately 1/4 to 1/3 in length; (1) greater than 1/2; (2) short, ossified and tear-drop shaped, may be fused to base of metacarpal in species where this is reinforced into a fighting spike; (3) almost full length of metacarpal, curved; (4) rectangular, flat.

123. Flange (crista lateralis) on dorsolateral surface of humerus of mature male: (0) absent; (1) present proximally, large; (2) present distally, small.

124. Flange (crista ventralis) on ventral surface of humerus: (0) long, about 1/2 of length, grading into bone; (1) small, about 1/4 to a 1/3 of length, abruptly ending; (2) long, about 1/2 of length, but squared off and ending abruptly.

125. Metacarpal of the third finger of breeding male, distal tuberosity: (0) absent; (1) present.

126. Metacarpal of the first finger of breeding male: (0) no enlargement; (1) enlarged flange-like nuptial tuberosity distally, on the outer edge.

127. Metacarpal of first finger in breeding male: (0) uniformly thickened, noticeably more so than other metacarpals, not penetrating skin, not spike-like; (1) thick, enlarged into spike which may or may not penetrate skin, thus leaving the distal phalanges set off at an angle to the axis of the finger; (2) blade-like expansion at medial distal edge and on prepollex; (3) as other metacarpals.

128. Shape of tips of terminal phalanx of third finger: (0) bifurcate, T- or Y-shaped; (1) knob-like, simple; (2) sharply pointed, slightly elongated.

129. Shape of terminal phalanx of the fourth toe: (0) large T-shaped; (1) small T-shaped; (2) simple or only slightly dilated; (3) long, sharply pointed; (4) Y-shaped, arms bearing flattened oval-shaped flanges; (5) pointed, truncated (short), tip may be a very small globule; (6) long, sharply pointed, as in state 3, but tip separate from the body of the terminal phalanx and bent sharply downwards, which may or may not perforate the integument in life.

130. Medial lingual process: (0) absent; (1) type A, retractile upright cone-shaped process with alpha-type retraction; (2) type B, retractile upright rugose process with alpha-type retraction; (3) type C, elongate longitudinally reclining process with alpha-type retraction or non-retractile; (4) only a sublingual cartilaginous rudiment present.

131. If medial lingual process present, texture of surface: (0) smooth; (1) rugose.

132. If medial lingual process present, shape: (0) short, bump-like; (1) elongated.

133. If medial lingual process present, shape of tip: (0) rounded and blunt; (1) sharply pointed.

134. If medial lingual process present, orientation: (0) upright; (1) reclined posteriorly.

135. Tongue, shape: (0) maximum width greater than or equal to length at centre; (1) length at centre greater than maximum width; (2) wide, but just short of being wider than long.

136. Tongue, distal margin: (0) not indented, entire; (1) indented in centre, lobed.

137. Posterior palatial fold: (0) absent; (1) present.

138. Snout profile: (0) rounded and overshot; (1) wedge-shaped.

139. Callusing of dorsal snout of breeding males: (0) absent; (1) present.

140. Musculus cutaneous pectoris (mcp): (0) absent; (1) present as thin slip; (2) present as thick slip.

141. Breeding males, colour of testes: (0) uniformly white to off-white, no black pigment present; (1) dark, pigment present throughout or on mesorchium or dorsal sections only.

142. Breeding males, velvety nuptial pads: (0) absent; (1) on finger one only; (2) on fingers one and two; (3) on fingers one, two and three; (4) short spines on fingers one, two and three.

143. Breeding males, sub-terminal metacarpal spike: (0) absent or non-protruding; (1) present, protruding through skin.

144. Breeding males, pad of spines at base of first finger: (0) absent; (1) few, large sharp black cones in a cluster; (2) pad of small white spines, covering the entire area where nuptial pads occur on the first finger in other ranids.

145. Breeding male, length of third finger: (0) normal; (1) considerably longer than other fingers, dorsal or lateral surface of fingers two and three covered in dermal denticles.

146. Breeding males, ventral spinules: (0) absent; (1) present in the axilla and/or flanks and chest region only; (2) present over the whole ventral surface; (3) present on the inner surface of the upper arm.

147. Breeding males, hedonic glands: (0) glandular region on inside of forearm; (1) hemispherical disc-like glandular flaps near axilla; (2) absent; (3) raised cylindrical patch on dorsal surface of wrist near first finger; (4) large glandular region on inside of forearm and pectoral glands.

148. Gular gland in breeding males: (0) absent; (1) present.

149. Spicules around jawline in breeding males: (0) present, well developed; (1) absent; (2) present, fine.

150. Vocal sac breeding male, nature: (0) single medial subgular sac or no vocal sac; (1) two lateral vocal sacs, internal or external.

151. Femoral glands in males: (0) absent; (1) present; (2) less developed than in females.

152. Femoral bumps: (0) clear, granular and confined to a small region proximally, extending for less than 1/2 length of thigh; (1) absent or very faint, these may be slight parallel ridges; (2) as 0, but extending 1/2 to 3/4 length of thigh.

153. Papilla in the centre of tympanum, breeding males: (0) absent; (1) present.

154. Supratympanic ridge: (0) strong, may be glandular; (1) absent or weak; (2) strong, encircling the entire dorsal section of a large tympanum.

155. Tympanic membrane: (0) indistinct, covered by skin as thick as that on rest of head; (1) distinct, as skin over tympanum is thinned; (2) half distinct, half-covered by muscle, only a crescent visible.

156. Width of eye versus tympanum (adult male): (0) tympanum less than or equal to radius of eye; (1) tympanum greater than half but less than full width of eye; (2) tympanum greater than full width of the eye.

157. Shape of pupil: (0) vertical; (1) horizontal; (2) round.

158. Webbing between toes: (0) extensive; (1) rudimentary, 1/4 to 1/2 of longest toe; (2) trace at base, or no web.

159. Toes, if unwebbed: (0) not flanged entire length; (1) flanged entire length.

160. Dorsal digital scutes on terminal phalanx of feet: (0) absent; (1) present.

161. Relative length of first and second fingers: (0) first finger not reaching the tip of the second; (1) first finger equal in length or extending beyond the second.

162. Relative length of first and third fingers: (0) third finger longer than first; (1) third finger equal in length to first; (2) third finger substantially longer than first.

163. Relative length of second and fourth fingers: (0) second finger shorter than or equal in length to the fourth; (1) second finger longer than fourth.

164. Feet, small conical spicules on ventrolateral surfaces of soles in breeding males: (0) absent; (1) present.

165. Colour pattern on the posteroventral surface of thighs: (0) solidly dark and extending onto soles of feet or uniform; (1) reticulate blotches or broken stripes not extending onto feet; (2) mottled.

166. Tip of the terminal phalanx of the fourth toe: (0) does not terminate in a small, narrow, hard bead; (1) terminates in small, narrow, hard bead.

167. Shape of the terminal phalanx of the fourth toe: (0) deltoid or triangular disc; (1) slightly to notably enlarged semicircular disc; (2) tapering or pointed, not notably enlarged.

168. Tip of the terminal phalanx of the fourth toe: (0) with a ventral circum-marginal groove; (1) without a ventral circum-marginal groove.

169. Outer two metatarsals: (0) deeply incised and separated by web almost to the base; (1) forming part of a fleshy sole, separated only distally.

170. Inner metatarsal tubercle, length compared to that of the fifth toe (measured from the base of the subarticular tubercle to tip): (0) short, up to the same length as the fifth toe; (1) longer than fifth toe but flattened and indistinct; (2) longer than fifth toe, but expanded into a protruding digging flange.

171. Outer metatarsal tubercle: (0) absent; (1) present.

172. Tarsal fold: (0) absent; (1) present; (2) present to mid-tarsal tubercle only.

173. Lateral margin of fifth toe and metatarsal, loose flap of skin: (0) absent; (1) present; (2) absent, but strongly or weakly developed dermal seam separating dorsal and ventral surfaces of the foot.

174. Mid-tarsal tubercle: (0) absent; (1) present.

175. Heel tubercle: (0) absent; (1) small and round to spike-like; (2) not single, present in a row of three.

176. Basal (proximal) row of subarticular tubercles of feet: (0) abnormally large, tending to square; (1) large, round to oval; (2) very small and sharply defined, round to conical; (3) tubercles under the first to third digits large, those under the fourth and fifth small.

177. Subarticular tubercles of feet: (0) spherical or conical; (1) oval, long, flattened; (2) raised perpendicularly and half disc-shaped, each joined by a ridge to that of next phalanx.

178. Outer metacarpal tubercle: (0) divided, mid section smaller than outer section; (1) divided, sections equal in size; (2) divided, mid section larger than outer; (3) entire on smooth palm; (4) entire, palm of hand granular.

179. Outer metacarpal tubercle, if divided: (0) parts touching or fused; (1) parts distinctly separate.

180. Number of subarticular tubercles present on the third finger (including the basal or proximal tubercle): (0) two; (1) one.

181. Palmar supernumerary tubercles: (0) indistinct or absent; (1) distinct in one or two rows; (2) indistinguishable from granular palms.

182. Tubercle on ventrolateral surface of wrist: (0) absent; (1) present.
183. Dorsal raphe (narrow inverted skin fold) running along spine: (0) absent; (1) present.
184. Transverse fold across head behind eyes: (0) absent; (1) present.
185. Abdominal colouration: (0) uniform or slightly mottled to plain; (1) small, regular round spots; (2) irregular spots to plain; (3) small reticulations; (4) large reticulations, semi-circular, may fade to uniform in adult. (5) bull's-eye pattern.
186. Abdominal skin: (0) coarsely granular; (1) smooth; (2) showing some granulation on the posterior half of abdomen, chest region smooth.
187. Gular skin of females, texture: (0) granular or rippled; (1) smooth.
188. Additional dorsal glands: (0) none; (1) sacral gland; (2) two dorso-lateral strips of glands, continuous and complete, or incomplete and broken into paired oval glands in the lumbar and sacral regions; (3) glandular region above eyelids; (4) poorly-defined glandular patch in the inguinal region.
189. Chevron-shaped glands in scapular region, or running down length of body: (0) absent; (1) present.
190. Skin ridges on dorsum: (0) none; (1) only a few, broken or discontinuous; (2) more than six; (3) two continuous, glandular dorsolateral ridges.
191. Amplexus position: (0) inguinal; (1) male's forearms placed along female's flanks, male vent placed half a body length back from female vent; (2) cephalic; (3) weak contact or straddling; (4) gluing of male to female; (5) axillary.

Minimal polymorphism was encountered in the current data set, and in all cases was between state 0 and 1, coded as '*' in the matrix. An attempt was made to avoid 'overcoding' of absence, i.e. repetitious coding of absence for the same organ or bone, as done extensively by Wu (1994). This can have the negative effect of strongly grouping taxa that do not have a particular feature (Pleijel 1995), potentially overriding the phylogenetic signal from other characters.

Unknown determinations of the true state, or missing data, are represented in the matrix by a '?'. The primary cause of missing data was the character state not being visible on the available material, often due to the incomplete clearing of the surrounding tissue, breakage of the structure concerned, or failure of tissue to adequately take up the stain, the latter due to dehydration or decalcification, e.g. the single specimen of *Mantella* examined in the present study. In some cases, the specimen was assessed as sub-adult from the incomplete ossification of the diapophyses of the long bones and phalanges; in such cases, states of characters that are well known to be influenced by the extent of ossification were coded as unknown. Occasionally, specimens that were examined during the collections visits were unavailable for further loan, e.g. if they were being used by another researcher. In these cases, characters added subsequent to their examination were coded as unknown. This is most noticeable for *Trichobatrachus*, *Leptodactylon* and *Conraua goliath*. The osteology of *Sooglossus* was coded from the literature (Griffiths 1959b; Lynch 1973; Wu 1994), as no skeletal specimens were examined. Characters that were logically impossible to code, or not applicable, for particular taxa were coded with a '–'. The data set is only minimally affected by non-applicable codings, for example characteristics of the medial lingual process (characters 131–134), which is absent in most taxa examined. Due to its aberrant morphology and the resulting problems of homology assessment with other ranoids, many characters were coded as inapplicable for *Hemisus*. As even

incompletely coded taxa may have a major effect on phylogenetic reconstruction by showing novel character suites (Gauthier *et al.* 1988; Vrana *et al.* 1994), the value of including *Hemisus* and *Sooglossus* was deemed to outweigh the problems associated with missing or inapplicable data that their inclusion may have introduced.

Despite every attempt to avoid error, it is inevitable that there will be some errors in this matrix, or any other similar matrix. The most insidious cause of error is likely to be the small sample size of specimens examined for some taxa. In many cases, the specimens were loaned in a cleared and stained condition, thus original determinations could often not be checked, nor could the sex and breeding condition.

Molecular Data Collection

Sample Preservation, Storage and DNA Isolation

Tissue samples used for sequencing were predominantly muscle tissue, either frozen or preserved in 96% ethanol, or occasionally liver tissue preserved in 20% dimethyl-sulfoxide (DMSO) in saturated saline. All samples were collected less than one hour after sacrifice of the specimen and refrigerated until extraction. Whole genomic DNA was isolated via the standard phenol-chloroform extraction method (Maniatis 1982; Hillis *et al.* 1996), or using hexadecyltrimethylammonium bromide (CTAB) digestion buffer and excluding the phenol steps (Corach 1991).

Choice of Gene Loci

The choice of gene loci for use in phylogenetic studies is a crucial determinant of the level of insight that can be obtained from such studies (Brower & DeSalle 1994). The fragment of the 12S rDNA utilised here has been widely used in anuran systematics above the species level (Hedges & Maxson 1993; Hay *et al.* 1995; Richards & Moore 1996; Ruvinsky & Maxson 1996; Richards & Moore 1998; Emerson & Ward 1998; Vences 1999; Bossuyt & Milinkovitch 2000; Clough & Summers 2000; Emerson *et al.* 2000b, 2000b; Richards *et al.* 2000; Vences *et al.* 2000a, 2000b; Wieczorek *et al.* 2000; Kosuch *et al.* 2001). New sequences obtained are readily comparable with those obtained in previous studies. Although widespread usage does not necessarily mean that a particular gene region is suitable for phylogenetic studies at a particular level (Brower & DeSalle 1994), the gene regions chosen here have demonstrated their utility above the species level in the Anura. Although the section of 16s rDNA sequence investigated here is shorter than that conventionally sequenced in the above-mentioned papers, Parker & Kornfield (1996) reported that it appears to contain most of the variation exhibited by this gene in a wide range of taxa. Inclusion of this hypervariable section, which may contain many saturated positions, is justified because it nevertheless represents variation, much of which is

useful in resolving terminal relationships, as demonstrated for third codon positions by Vrana *et al.* (1994) and Källersjö *et al.* (1999). Both of these gene regions amplify readily in anurans. The following primers were used:

12S: 12Sa (light chain—L2519; 5'—AAACTGGGATTAGATACCCCACTAT—3') and 12Sb (heavy chain—H2916: 5'—GAGGGTGACGGGCGGTGTGT—3') of Simon *et al.* (1994);

16S: 16Svf (light chain; 5'—TACATAACACGAGAAGACC—3') and 16Svr (heavy chain; 5'—GTGATTGCGCTGTTATCC—3') of Parker & Kornfield (1996).

Polymerase Chain Reaction (PCR) Conditions

PCR reactions were conducted according to standard methods, using concentrations as given in Table 4. Reaction volumes were either 50 µl or 20 µl, and were thermocycled in a GeneAmp® PCR System 9600 (Perkin Elmer Biosystems). The following cycling protocols were used: (1) 12S. Initial denaturation step: 60 s at 94 °C; thermocycling (34 cycles): denaturation 30 s at 94 °C, primer annealing 45 s at 54 °C, extension 60 s at 72 °C; final clean-up: 300 s at 72 °C; rapid thermal ramp to 4 °C and hold. (2) 16S. Initial denaturation step: 180 s at 94 °C; thermocycling (35 cycles): denaturation 60 s at 94 °C, primer annealing 60 s at 49 °C, extension 60 s at 72 °C; final clean-up: 300 s at 72 °C; rapid thermal ramp to 4 °C and hold.

Table 4. Reaction concentrations and quantities used in polymerase chain reactions (PCR's).

Reagent	Stock concentration	Per 10 µl reaction volume	Final reaction concentration
PCR buffer	10 x	1 µl	10%
$MgCl_2$	25 mM	0.7–3 µl	1–4 mM
Taq polymerase	5 units/µl	0.05 µl	0.5 units
dNTPs	8 mM	1.0 µl	0.2 mM
Primer A	10 µM	0.12 µl	0.12 mM
Primer B	10 µM	0.12 µl	0.12 mM
Water	-	to final volume	-
DNA	-	-	± 100 ng

PCR Product Purification and Sequencing

PCR product was cleaned using Qiagen PCR purification kits (Qiagen). Cycle sequencing was performed under recommended conditions using ABI PRISM® BigDye® Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems Inc.), in quarter-reactions (10 µl). Product was cleaned through Centri-sep spin columns (Princeton Separations), refilled with Sephadex® G-100 fine (Separation Scientific), 1 g per 16 ml sterile distilled water, 0.9 ml of solution per column, pipetted while stirring to avoid settling of the gel. Spin column separation was

performed as per the Centri-sep protocol. The samples were sequenced on an ABI 377 automatic sequencer (Applied Biosystems Inc.) at the Core DNA Sequencing Facility, Department of Genetics, University of Stellenbosch. Some sequences were generated manually as in Dawood & Channing (2000).

Table 5. 12S and 16S rDNA sequences produced, specimen voucher numbers and localities. Sequences obtained by Ms M. Dupreez are marked with an asterisk(*), those obtained by Dr A. Dawood are marked with a superscript (†). Collector acronyms for molecular vouchers are listed in Appendix 1. Samples with only a collector accronym (listed in Appendix 1) do not have associated voucher specimens.

Species	12S	16S	Voucher	Locality
Afrana angolensis	15.14	15.14	RDS 926	Muzambai, Tanzania
Afrana fuscigula	M2*	M2	MA 12	Stellenbosch, South Africa
Amnirana albolabris	10.9†	10.9	TMSA 84177	Nguti, Cameroon
Anhydrophryne rattrayi	1206†	1206	AC 1206	Hogsback, South Africa
Arthroleptella landdrosia	AF330244	1204	AC 1204	Landdroskop, South Africa
Arthroleptella bicolor	AF330239	1302	AC 1302	Bainskloof, South Africa
Arthroleptides martiensseni	14.6	14.6	TMSA 84077	Armani, Tanzania
Astylosternus diadematus	AD9†	AD9	TMSA 84311	Nguti, Cameroon
Cacosternum boettgeri	8.4	8.4	ES 262	Weenen, South Africa
Cacosternum capense	10.10	10.10	TMSA 84242	Klipheuwel, South Africa
Cacosternum namaquense	12.4	12.4	TMSA 84308	Arakoop, South Africa
Cacosternum nanum parvum	9.4	9.4	TMSA 84309	Sabie, South Africa
Cardioglossa gracilis	AD13†	AD13	TMSA 84165	Nguti, Cameroon
Conraua crassipes	12.9	12.9	ZFMK 69355	Mt. Nlonako, Cameroon
Conraua goliath	M18*	-	MV	Cameroon
Dimorphognathus africanus	AD14†	AD14	TMSA 84170	Nguti, Cameroon
Hildebrandtia ornata	15.8	15.8	AC 1110	Beira, Mozambique
Hoplobatrachus occipitalis	-	M12	AC 1321	Kampala, Uganda
Hoplobatrachus occipitalis	M15	-	AC 1368	Lake Nabugalo, Uganda
Hydrophylax galamensis	1105	1105new	AC 1105	Beira, Mozambique
Hyperolius viridiflavus	-	AC1654	AC 1654	Nkuku, Zambia
Leptodactylon mertensi	15.1	15.1	MV	Nlonako, Cameroon
Leptopelis vermiculatus	14.7	14.7	TMSA 84038	Armani, Tanzania
Microbatrachella capensis	7.6	7.6	TMSA 84315	Hermanus, South Africa
Natalobatrachus bonebergi	-	14.9	ZFMK 66443	The Haven, South Africa
Nyctibates corrugatus	AD†	AD10	TMSA 84312	Nguti, Cameroon
Petropedetes cameroniensis	AD15†	AD15	LM 24	Nguti, Cameroon
Petropedetes newtoni	12.7	-	ZFMK 75590	Mt. Kupe, Nyasoso, Cameroon
Petropedetes parkeri	9.9	9.9	MV	Nlonako, Cameroon
Phrynobatrachus acridoides	1251†	AC1251	AC 1251	Mafia Island, Mozambique
Phrynobatrachus plicatus	14.11	14.11	TMSA 84101	Nguti, Cameroon
Phrynobatrachus cricogaster	9.8	9.8	MV	Nlonako, Cameroon
Phrynobatrachus krefftii	-	14.5	TMSA 84038	Muzambai, Tanzania
Phrynobatrachus natalensis	1118†	AC1118	AC 1118	Beira, Mozambique
Phrynodon sandersoni	9.7†	9.7	ZFMK 69283	Mt. Nlonako, Cameroon
Poyntonia paludicola	9.5	9.5	ES 175	Steenbras, South Africa
Ptychadena chrysogaster	M13*	-	AC 1328	Bwindi, Uganda
Pyxicephalus adspersus	13.5	13.5	ES	Glen Austin, South Africa
Scotobleps gabonicus	AD23†	AD23	TMSA 84313	Nguti, Cameroon
Strongylopus grayii	M1†	-	MA 10	Stellenbosch, South Africa
Tomopterna marmorata	AF371203	AC1539	AC 1539	Nkuku, Zambia
Tomopterna tandyi	AF371185	AC1487	AC 1487	Adelaide, South Africa

Data Analysis

Simultaneous Analysis

The analysis presented here incorporates three different data sets: morphology and two gene regions. There are both drawbacks and advantages of combining data sets obtained from different sources for analysis, which have been extensively reviewed in the literature (Kluge 1989; Bull *et al.* 1993; De Queiroz 1993; Eernisse & Kluge 1993; Kluge & Wolf 1993; Chippindale & Wiens 1994; De Queiroz *et al.* 1995; Miyamoto & Fitch 1995; Huelsenbeck *et al.* 1996; Nixon & Carpenter 1996; Page 1996). At the start of the molecular revolution in systematics, it was thought that combining morphological data sets (which mostly contain less than 200 characters) and molecular data sets (which usually contain substantially more characters, often in the order of kilobases) would lead to 'swamping' of the morphological data (Miyamoto 1985; Swofford 1991). However, empirical studies suggest that morphological data frequently contain a higher phylogenetic signal to noise ratio than do molecular data, and the opposite is often the case, even if morphological characters are less abundant (DeSalle *et al.* 1992; Donoghue & Sanderson 1992; Eernisse & Kluge 1993; Wheeler *et al.* 1993; Chippindale & Wiens 1994). The 'total evidence' or 'simultaneous analysis' maximises explanatory power, in addition to allowing the emergence of secondary signals (Kluge 1989; Kluge & Wolf 1993; Chippindale & Wiens 1994; Nixon & Carpenter 1996; Cognato & Vogler 2001). The simultaneous approach is thus considered preferable and is adopted here. As such, the results of the independent morphological and molecular analyses are not presented or discussed separately, since these are considered to inevitably be inferior to the results obtained from analysis of all available data simultaneously.

Composite Terminals

Although every effort was made to obtain data from all three data sets for the same exemplar species, this was not always possible. Taxa for which one or more of the molecular data sets were missing could affect the analysis by increasing the number of most parsimonious trees (MPT's) due to the 'wild card' or 'joker' effect, and hence the instability of the result to the addition of new data (Nixon & Carpenter 1996). In a few cases, it was possible to combine the morphological data of one exemplar species with molecular data from GenBank for one or both gene regions of a congener or assumed closely related species, to form a composite chimaeric terminal. All available information was used to avoid the generation of a non-monophyletic terminal, at least at the level of resolution required by this analysis. These terminals were then labelled at the highest inclusive taxonomic level, for example the morphological data of *Breviceps rosei* were combined with data from both gene regions from an unknown species of *Probreviceps* Parker, 1931, forming a composite terminal named Brevicipitinae. The above

approach is highly dependent on correctly identified sequences. All cases in which this was done are explicitly stated in Table 7.

Table 7. Data sets used to construct composite terminals.

Taxon	Morphology	12S	16S
Brevicipitinae	*Breviceps rosei*	*Probreviceps* sp.	*Probreviceps* sp.
Arthroleptis	*A. stenodactylus*	*Arthroleptis* sp.	*Arthroleptis* sp.
Cardioglossa	*C. leucomystax*	*C. gracilis* Boulenger, 1900	*C. gracilis*
Colostethus	*C. inguinalis*	-	*C. pratti* (Boulenger, 1899)
Dendrobates	*D. speciosus*	*D. pumilio* O Schmidt, 1857	*D. pumilio*
Heleophryne	*H. purcelli*	*H. natalensis*	*H. purcelli*
Kassina	*K. senegalensis*	*K. maculata* (Duméril, 1853)	*K. senegalensis*
Leptodactylon	*L. ventrimarmoratus*	*L. mertensi* Perret, 1959	*L. mertensi*
Leptodactylus	*L. melanonotus*	*L. pentadactylus*	*L. pentadactylus*
Nanorana	*N. parkeri*	*N. pleskei* Günther, 1896	-
Philautus	*P. surdus*	*P. petersi* (Boulenger, 1900)	*P. petersi*
Platymantis	*P. corrugatus*	-	*P. vitiensis* (Girard, 1853)
Ptychadena	*P. mascareniensis*	*P. crysogaster* Laurent, 1954	*P. crysogaster*
Sooglossidae	*Sooglossus sechellensis*	*Nesomantis thomasseti* Blg, 1909	*Nesomantis thomasseti*

Tree Reconstruction Method

'Pluralism' (*sensu* Giribet *et al.* 2001a), whereby many available methods (conventionally distance methods, maximum likelihood and parsimony) are all used on the same data set, and concordance of results taken as confirmation that the result is correct or robust, is unscientific and uncritical. Concordance does not equate to correctness (Felsenstein 1981b; Shull *et al.* 2001; Giribet *et al.* 2001a). In addition, if the results are incongruent, it is unclear what criteria would then be used to select a particular hypothesis from among the alternatives. Pluralism shows a disregard for the philosophical and operational differences between the various analytical methods (Giribet *et al.* 2001a), and ignores the fact that the outcome may be due to the choice of parameters utilised, not the method *per se.* Choice of a single analysis algorithm should be made beforehand on philosophical grounds, and justified accordingly. Parsimony (Kluge & Farris 1969; Farris 1983) using all available data (Kluge 1989) is here considered to be the best available method for information content, robustness and accuracy.

Pairwise distance algorithms, such as Neighbour Joining (Felsenstein 1984, Saito & Nei 1987), which group taxa by overall similarity, are invalid for inferring phylogenetic relationships (Farris 1981, 1985, 1986, 1990; Siebert 1992; Farris *et al.* 1996; Hillis 1996; Swofford *et al.* 1996; Goldstein & Specht 1998). Overall similarity does not differentiate between shared derived character states (synapomorphy), which are informative of evolutionary relationships, and shared primitive character states (symplesiomorphy), which are not.

The other widely used method for inferring phylogenies is maximum likelihood (Felsenstein 1973, 1981a, 1981b, 1983; Huelsenbeck & Rannala 1997; Huelsenbeck & Crandall 1997 amongst others, see Whelan *et al.* 2001 for a review). Maximum likelihood (ML) has been criticised (Farris 1986, 1999; Wheeler 1990, 1992; Carpenter 1992; Siebert 1992; Williams

1992; Wenzel & Carpenter 1994; Siddall & Kluge 1997; Goldstein & Specht 1998; Siddall 1998; Giribet & Wheeler 1999b; Siddall & Whiting 1999; Sanderson & Kim 2000; Farris *et al.* 2001; Kluge 2001), primarily on the following grounds. The results are dependent on the correctness of the models of evolution that are assumed, which, in order to simplify the analyses, are often necessarily unrealistic. Maximum likelihood sacrifices the fit of the data for conformity to the specified model of evolution (but see Sullivan & Swofford 2001). Like distance measures, ML does not consider gap information; in doing so it is less explanatory, because it dismisses *a priori* some of the historical information in the data (Wheeler *et al.* 1993; Giribet & Wheeler 1999b).

Another principal problem with ML is that existing likelihood models (excepting 'parsimony' models, which equate to parsimony analysis), cannot currently be used to analyse morphological data. This is because the evolution of these data is not as simple or nearly as well understood as that of molecular data. Although some attempts are being made towards rectifying this via the development of new models (e.g. Lewis 2001), the paucity of basic knowledge regarding morphological evolution will unfortunately persist. As morphological data will undoubtedly remain the backbone of organismal classification systems, the inability of ML to deal with this data type is problematic. Parsimony is the method of choice used here, due to the existing algorithms' ability to analyse morphological data effectively. The preferred use of a simultaneous analysis of all available data is another justification for using parsimony over ML, since simultaneous analysis is merely a logical extension of parsimony. As with any other method, parsimony has its problems. However, the circumstances under which it can fail are simple and well understood, unlike those of other methods. The most notable failing of parsimony is the phenomenon of long-branch attraction (Felsenstein 1978; Hendy & Penny 1989; Swofford & Olsen 1990; Huelsenbeck & Hillis 1993; Steel *et al.* 1993; Huelsenbeck 1995; Kim 1996; Steel & Penny 2000). However, this can be circumvented by careful taxon sampling to 'break' long branches, and by including basal exemplars of all putative clades (Williams 1992; Graybeal 1998; Prendini 2001). Despite all reasonable attempts at minimizing it, some long-branch attraction may still have occurred here, given the scope of the present study and the completely unknown nature of the relationships of the taxa concerned.

The Parsimony Ratchet

The existence of local optima, or 'islands of trees' (*sensu* Swofford 1990; Maddison 1991), which are defined as a group of tree topologies in which each topology is no more than a single rearrangement away from another topology in the set, has been recognized as a problem in phylogenetics for some time. Local optima can usually be avoided using traditional search strategies, such as incorporating random addition sequences followed by tree-bisection-reconnection (Kitching 1992). However, this method is ineffective on large data sets (over about

70 terminal taxa), because the existence of many local optima considerably decrease the possibility that a given replication will find the global optimum (Goloboff 1999). Large data sets require an approach that analyses different parts of the tree separately, sequentially improving sections that are suboptimal without worsening those that are already optimal.

One such novel strategy designed specifically for large data sets is the 'parsimony ratchet' of Nixon (1999a), which was used for analyses here. This method results in search times from 20 to 200 times faster than those of conventional methods of random addition sequence, Wagner trees, subtree-pruning-regrafting (SPR) or tree-bisection-reconnection (TBR) (Nixon 1999a; Giribet & Wheeler 1999a). The parsimony ratchet does not attempt to find multiple trees during swapping, but simply concentrates on finding the shortest trees possible. It provides better results on large data sets than simple branch swapping or random addition sequences because it samples many local optima (tree islands), retaining fewer trees from each local optimum and thereby provides a more accurate estimate of the true consensus than collecting many trees from fewer islands (Nixon 1999a).

The method proceeds as follows:

i) A starting tree is generated, typically by randomly ordering the taxa, calculating a Wagner tree, and then implementing TBR branch swapping.

ii) The weights of a selected subset of the characters are then randomly increased. The proportion of characters to be reweighed is user-defined, but is recommended to be 5–25% of the total informative characters. The weighting can be increased or set to zero.

iii) Branch swapping is then performed on the current tree, using the perturbed weights to calculate length, holding only a few trees, and concluding with a single 'optimal' tree. Any type of swapping strategy can be used in this step, but it is typically TBR.

iv) The artificial weights are then dropped, and the original character weights restored. Swapping on the trees found using the artificially inflated weights commences, until an optimal tree is located for the unperturbed data.

v) Another random set of characters are then reweighted and swapping commences again on the tree, continuing the cycle described from the second step.

Steps ii to v represent a single cycle, with the number of iterations at each step, and the number of cycles, being defined by the user. The ratchet thus finds shorter trees more rapidly by avoiding the time spent searching on new starting trees that are much less optimal than the last tree swapped. The reweighed characters favour topologies that are potentially not in the same island as the current tree (Giribet & Wheeler 1999a). A demonstration of the effectiveness of the ratchet was presented by Nixon (1999a) via a reanalysis of the large data set of Chase *et al.* (1993), a 500 taxon by 1428 character data set of chloroplast *rbc*L data for seed plants. This data set ran for three and a half months when reanalysed on three Sun workstations (Rice *et al.* 1997) using PAUP (Swofford 1993), and could only find a tree of 16220 steps. The parsimony

ratchet in NONA found a tree 2 steps shorter (16218 steps) in approximately 150 hours using Pentium II class computers, which were estimated to be no more than twice the speed of the Sun workstations used by Rice *et al.* (Nixon 1999a; Goloboff 1999).

Fixed Sequence Alignment

Multiple alignment is conventionally employed to assign provisional homologies among nucleotides, which are then tested in phylogenetic analysis. Sequence alignment is a problematic procedure, both philosophically and empirically. The algorithm used by fixed alignment programs, an extension of that of Needleman & Wunsch (1970), is almost entirely intractable for large numbers of sequences, requiring storage and computational power increasing by a factor of the length of each successively added sequence (n^m, where n is the length of the sequence and m the number of sequences). This intense level of computational complexity necessitates the use of heuristic shortcuts in order to be workable (Wheeler 1994). Multiple alignment programs take shortcuts by first clustering the sequences by overall similarity, then aligning pairs according to their perceived similarity from the resulting distance guide tree. This cluster can then be aligned to the next most similar sequence or cluster of aligned sequences. However, the relative alignment of the sequences is kept constant; once a gap is inserted, it remains in that position. The fixed nature of aligned sequences makes the procedure highly dependent on the order in which the sequences are accreted, and multiple accretion orders may yield unique, yet equally optimal, multiple solutions. Thus, the use of the same data and parameters can yield non-unique solutions (Wheeler 1994; Lutzoni *et al.* 2000).

Gaps, representing insertion-deletion events (indels), are inserted by the alignment programs to create correspondence between sequences of unequal lengths, which is commonly the case for sequences from widely disparate or higher-level taxa such as those used here. The placement and number of gaps inserted, which then remains immutable, is dependent on functions chosen *a priori* by the investigator. The appropriate values for the cost of gaps and substitution events are unknown, and there is no empirical way to measure what these should be in the absence of a predetermined phylogeny (Wheeler *et al.* 1995). Moreover, whether or not an indel is to be postulated should depend on the phylogeny in question, and that a phylogeny should be evaluated according to how many substitutions and how many indel events it requires postulating (Wheeler 1995, 1999). As such, the analysis should simultaneously consider the substitutions and indels required by alternative phylogenies instead of taking them as given from a fixed alignment.

Initially, the data in the present study were subjected to a conventional pair-wise multiple sequence alignment in the program Clustal X (Thompson *et al.* 1997). The scoring matrix used for the alignment was the Identity matrix, with a gap opening and gap extension costs arbitrarily set to 60 and 30 respectively. This results in a string of gaps being downweighted, a commonly

implemented strategy that is analogous to treating them as a single evolutionary event. However, this treatment is contrary to the assumption of character independence (Giribet & Wheeler 1999b). The resulting alignments were adjusted by eye using the program GeneDoc v. 2.6.001 (Nicholas & Nicholas 1997). Adjusting the alignment by eye is another widely used procedure, but is highly subjective, and is neither repeatable nor scientific (Gatesy *et al.* 1993; DeSalle *et al.* 1994; Shull *et al.* 2001). The results of this alignment procedure, provided in Appendix 3 for 12S and Appendix 4 for 16S, were rejected. Substantial length variation was found to occur in unaligned sequences (12S: $n = 63$, $\bar{x} = 338$ bp, Range 286–376 bp, S.D. = 14.2 bp; 16S: $n = 61$, $\bar{x} = 152$ bp, Range 138–158 bp, S.D. = 4.4). This length variation greatly reduces the confidence that can be placed on the homology statements inferred from the alignments. It is obvious from Appendices 3 and 4 that the alignment in particular regions is suboptimal. The conventional approach to this problem is to exclude any difficult regions, but this amounts to loss of information and is arbitrary and unscientific (Gatesy *et al.* 1993).

Direct Optimization

An alternative approach was taken to circumvent the use of multiple sequence alignments. Sequence data were analysed using the direct optimization (DO) method, described by Wheeler (1996). This method directly assesses the number of sequence transformations (evolutionary events) required by a phylogenetic topology without using a fixed sequence alignment. This is achieved through a generalisation of existing character optimization procedures to include insertion and deletion events, in addition to base substitutions. Thus, this method treats indels (gaps) as processes rather than patterns implied by multiple sequence alignments. Direct optimization works by creating parsimonious hypothetical ancestral sequences at internal cladogram nodes. As in multiple alignment, evolutionary base substitution events in sequences are treated with cost functions. The main difference between multiple alignment and DO is that evolutionary differences in sequence length are accommodated in the latter method not by the use of gap characters, but rather by allowing indel events between sequences, i.e. gaps appear not as states but as transformations linking ancestral and descendent nucleotide sequences (Wheeler 1996).

The majority of phylogeneticists operating at higher taxonomic levels (where alignment is more crucial) continue to ignore problems associated with fixed multiple alignments (Lutzoni *et al.* 2000). Direct optimization is not yet used widely, possibly because it is extremely computer intensive, as demonstrated by the analysis of Giribet *et al.* (2001b) recently published in *Nature* (September 2001), which required the equivalent of 42 years of standard computer processing time. Direct optimization is gaining in popularity, and studies that have used the method include Chavarría & Carpenter (1994); Whiting *et al.* (1997); Wheeler (1997, 1998); Wheeler & Hayashi (1998); Carpenter & Wheeler (1999a, 1999b); Edgecombe *et al.* (1999); Giribet (1999);

Janies & Mooi (1999); Sorenson *et al.* (1999); Giribet & Ribera (2000); Giribet *et al.* (2000, 2001b); Wahlberg & Zimmerman (2000); Cognato & Vogler (2001); Frost *et al.* (2001) and Shull *et al.* (2001). For a detailed discussion of some of the uncertainties associated with the DO method, see Shull *et al.* (2001).

Character Weighting and Sensitivity Analysis

Character weighting is a controversial subject, and most phylogenetic analyses are conventionally conducted with all characters weighted equally (sometimes termed 'unweighted' analyses). Treating every character as equally important in a phylogenetic analysis is a theoretical standpoint justified by philosophical arguments that this is the least assumption-laden approach (Kluge 1989, 1997; Siebert 1992; Brower 2000). On the other side of the debate, the rationale for the use of differential character weighting is the presumption that not all characters are equally informative of phylogenetic relationships (Brown *et al.* 1982; Neff 1986; Wheeler 1986; Wheeler & Honeycutt 1988; Sharkey 1989; Miyamoto *et al.* 1994). In practice, phylogenetic analysis of most data sets indicates that some characters are homoplasious. Thus, the analysis itself demonstrates that not all characters are equally informative of phylogenetic relationships, and they are thus not all necessarily deserving of equal weights (Farris 1969, 1983; Williams & Fitch 1989; Goloboff 1993). Goloboff (1993) presents a strong argument that if the data are properly weighted, the results obtained should always be preferred, regardless of the result under equal weights. Weighted parsimony has also been shown to perform better than unweighted parsimony in most simulation studies and experimental phylogenies (Hillis *et al.* 1994). The use of differential weighting has also been justified on the grounds that it can provide a criterion for choosing amongst multiple MPT's, as in Carpenter (1988, 1994) and Scharff & Coddington (1997). In addition, weighting via multiple cost ratios (parameter sets) can be used to gauge how the analysis parameters affect phylogenetic conclusions.

Perturbing the data (via weighting) under a single tree reconstruction method facilitates the differentiation of robust relationships, which are supported under a wide range of parameter values, from unstable relationships, which appear only under particular parameter values. This approach has been termed 'sensitivity analysis' (*sensu* Fitch & Smith 1983; Wheeler 1995) and is used to explore the data. This is an essential part of the phylogenetic reconstruction process to avoid the adoption of hypotheses supported only by unique combinations of parameter values (Giribet & Wheeler 1999b; Giribet & Ribera 2000). In the current analysis, the standpoint was taken that the equally-weighted hypothesis should be adopted on the basis that this represents the least assumption-laden approach, but the effect of weighting was also explored, in order to assess the robustness of the equally-weighted result.

There are two alternative ways in which differential character weighting can be accomplished (Neff 1986); by setting the individual character weights before analysis (*a priori*

weighting) or by allowing the analysis to do this (*a posteriori* weighting). For the sensitivity analyses conducted here, *a priori* weighting was used. A parameter space of two analytical variables was explored, *viz.* insertion: deletion cost ratio (gap cost), and transition: transversion cost ratio (change cost), as in Wheeler (1995), Edgecombe *et al.* (1999) and Giribet & Ribera (2000). The sets of differential values assigned to these are termed the 'parameter sets', and are arbitrarily chosen before analysis. The use of different parameter sets may result in different tree topologies. One of the main concerns regarding this type of weighting approach is that there are potentially limitless sets of parameters to chose from. However, in practice certain sets are found to be optimal for certain taxa, such as gaps: transversions: transitions (gaps: tv: ts) ratios of 211, 411 and 221 for arthropods (Wheeler 1995; Wheeler & Hayashi 1998).

When the transition-transversion ratio was set to a value other than unity, the insertion-deletion cost was set according to the cost of transversions. Where the costs of gaps to transversions to transitions are set to unity, the analyses are equivalent to those conduced under equal weights. There are constraints on the range of values of these parameters for nucleotide character transformation, which are determined by the 'triangle inequality' (Farris 1981, 1985), as pointed out in Wheeler (1993, 1995). Firstly, character transformations must be symmetrical ($i \rightarrow j = j \rightarrow i$). Secondly, the transversion-transition cost ratio must be at a minimum of 0.5 (although there is no upper bound for this ratio). This prevents transversions from being so cheap as to mediate all change. Thirdly, as with the transversions, the cost of gaps must be at least half the cost of a change (character transformations), which again can vary upward without bound (Wheeler 1995).

Weighting was implemented by invoking Sankoff-style step-matrices (Sankoff 1975), the format of which consists of five lines each with five integers signifying the transformation costs among molecular character states as follows:

A→A	A→C	A→G	A→T	A→Gap
C→A	C→C	C→G	C→T	C→Gap
G→A	G→C	G→G	G→T	G→Gap
T→A	T→C	T→G	T→T	T→Gap
Gap→A	Gap→C	Gap→G	Gap→T	Gap→Gap

For example, parameter set 221 means that the gap cost is set to twice the highest change cost, in this case the transversion cost, which is set to twice the transition cost. The ratio 221 thus implies costs for gaps, transversions and transitions of 4, 2 and 1 respectively.

The step matrix which specifies the costs of the molecular state transformations in 221 would thus be as follows:

0 2 1 2 4
2 0 2 1 4
1 2 0 2 4
2 1 2 0 4
4 4 4 4 0

In total, 12 parameter sets were analysed, with the maximum weighting in any of these being 16. The combinations were (gaps: tv: ts): 111, 121, 141, 211, 221, 241, 411, 421, 441, 110, 210 and 410. The parameter set 111 is equivalent to equally weighted analysis. These parameter sets were analysed for the molecular data alone, and for two sets of simultaneous analyses (each running all 12 parameter sets), with the cost of the morphological data set as equal to the change cost or equal to the gap cost. Since four analyses theoretically utilize the same parameter values, only 20 analyses are presented. The step matrices used are provided in Appendix 5.

When exploring data in this manner, it is essential that an optimality criterion is specified beforehand, by means of which a preferred hypothesis can be chosen from amongst the set of hypotheses generated by different parameter sets, since an arbitrary choice of a 'preferred' tree is not defensible epistemologically (Giribet & Wheeler 1999b). The widely implemented Incongruence Length Difference (ILD) metric (Mickevich & Farris 1981, Farris *et al.* 1995) can be used in the context of sensitivity as an optimality criterion, to identify the optimal parameter set that produces the most corroborated topology. This would be the one which maximises character congruence between the individual partitioned data sets (Wheeler 1995; Whiting *et al.* 1997; Wheeler & Hayashi 1998; Edgecombe *et al.* 1999). Although the ILD metric was calculated, and indicated a 'preferred hypothesis' on the criterion of character congruence, this topology was not used to infer phylogenetic conclusions. In the current analysis, the weighted analyses were merely used in the context of sensitivity to identify robustly versus weakly supported clades present on the equally-weighted tree.

Analysis Software Employed

All analyses which included molecular data employed DO and were conducted using the program POY v. 2.0 (Gladstein & Wheeler 1997-2001). Analyses were run over a 20 week period on five 500 MHz Pentium III computers at the Geographical Information Systems facility, Information Technology Services, University of Cape Town. In order to speed up the analyses, the jackboot option of POY was used, which conducts 'parsimony jack-knifing' (Farris 1995, 1997, Farris *et al.* 1996) and the resulting 50% majority rule consensus of all trees obtained was converted to a constraint file, used for further more intensive searches. Outputs of POY (parenthese trees), were processed using the program JACK2HEN v. 4.22 (Farris 1995,

available with the POY software), to create group inclusion character matrices from the POY output. These were read into HENNIG86 v. 1.5 (Farris 1988) to obtain unweighted tree lengths, and to enable the trees to be read by WinClada v. 0.9.9+ (Nixon 1999b) for presentation. Separate analyses of the morphological data set in isolation, for the purposes of calculating ILD values, were conducted in the program NONA v. 2.0. (Goloboff 1997) with all characters weighted equally. Complete command lines used in POY, JACK2HEN and NONA, and a brief description of the function of relevant POY commands are provided in Appendix 6.

Characters were optimized onto the equally-weighted topology using WinClada v. 0.9.9+ (Nixon 1999b), for discussion in Appendix 2. Ambiguous optimizations were preferentially resolved using accelerated transformation (Acctran). Acctran was preferred to delayed transformation (Deltran) optimization as it favours secondary loss (reversals) over parallelisms (convergence) to explain homoplasy (Farris 1970; Swofford & Maddison 1987, 1992; Swofford 1990) and therefore maximises homology (Griswold *et al.* 1998).

The use of statistical tests, such as non-parametric bootstrapping, was avoided as an estimator of confidence for the nodes, because these tests merely reflect how well the data responds to perturbation. In addition, they may be misleading in the context of phylogenies, because phylogenetic facts are historically unique and thus have no associated probabilities of occurrence (Carpenter 1992; Bremer 1994; Wenzel & Carpenter 1994; Goldstein & Specht 1998). Branch support, or decay indices (Bremer 1988, 1994; Donoghue *et al.* 1992), were calculated to assess the relative degree of support for each node in the program POY.

RESULTS

The morphological data matrix collated in the present study is presented in Table 8. Separate morphological and molecular results are not shown, because combining all available evidence provides the most explanatory phylogenetic hypothesis, which implies that they would be considered inferior. The topologies generated under the 20 different sensitivity parameter sets using direct optimization are provided in Appendix 7.1–7.20. The analysis results were sensitive to the choice of analysis parameters employed for this data set, although the content of the major clades was fairly consistent. The major difference was usually in the placement of the major clades relative to each other.

The overall strict consensus tree, produced from all of the individual strict consensus trees from 20 analyses (Fig. 18), is almost completely unresolved. This tree is presented to demonstrate those clades which are retrieved under all analysis conditions, i.e. the most robust relationships obtained utilizing these data, in which the highest confidence can be placed.

Table 8. Continued

	0 5 10 15 20 25 30 35 40 45 50 55 60 65 70
Leptopelis vermiculatus	01110001011000212111210002320110 20-7202001100100000110000011012100001 01
Limnonectes blythii	11010011011011210102200002320110210?10?001101100002111100000210100000 10
Mannophryne trinitatis	00110011010100112111200012120100 20-110111011-01-1001100011011010100000 1
Mantella aurantiaca	000100110 1?10?110111101002120110211100210001 0?1-11?000010000010 1?10000
Mantidactylus femoralis	0??10??10100112101???2?000212011021161001001112 00?01110011000210100001 00
Microbatrachella capensis	00002110011201001111001112322111111601000011000010311100100201111010102
Nannophrys ceylonensis	01011000011001202111000012320110111610000110100000112031100120010001010
Nanorana parkeri	11?10011010201112101200002310110210??000000000000111?000?0001000000110
Natalobatrachus bonebergi	00111010011201110102210002120100211610010011-01-1010000010000101100000 1
Nothophryne broadleyi	00011110010201011110101-2-32011021021000001000 1-1011110010010100100010 2
Nyctibates corrugatus	01010001011000 2?10220?20213001020-8000001100100001101001011212100000 11
Pantherana pipiens	11010001011011211102210002120110210410000010000000111100000021010000010
Petropedetes cameronensis	01110110010201111112200002120?10210210000110020100111101100101010000102
Petropedetes natator	01010011 01?201110112210012120100210 21??001100000001011 2??00021010000101
Petropedetes newtoni	01110011010001111112200002320110210210000110000100101101100101010000102
Petropedetes parkeri	01110011010001111112200002120110210210000110000100111101100101010000002
Philautus surdus	01110110011201111101200012120110212100100010020000311001?00101010000102
Phrynobatrachus acridoides	01011010011201210102210012120110210310001011-01-1021100010000101100001 1
Phrynobatrachus cricogaster	00011??001120121?10221001212011021031 01?1011-0??10??100010000101 1?00101
Phrynobatrachus dendrobates	01011011011201210102210012120110210310110011-0001010100110000101120001 1
Phrynobatrachus krefftii	000110?10112012101022100121201102103100000 11-01-1021100110011101120000 1
Phrynobatrachus natalensis	01011010011201211112210012120110210310000011-01-1021100010000101120000 1
Phrynobatrachus plicatus	000110?00112012111022100121201102103100000 11-01-1021100110000101120001 1
Phrynobatrachus versicolor	01011111011201211102210012?2010021031011 0011-0001010100110001101120000 1
Phrynodon sandersoni	01010010011201210102200012120100211110010011-01-1010102110010101120010 1
Phrynoglossus laevis	01011011011201212102210002310110210610000110000010300002-11321000000010
Phrynomantis bifasciatus	01002000010011002110001-2-32000130-401002-100?1-1101110120030100121010 2
Platymantis corrugatus	01110?11010001211102210002310110211610000110120000111001100021010000010
Poyntonia paludicola	00011110011201111101101113230111210600000010000010300100001101111000001
Ptychadena anchietae	1101111111100-211102210--1220110211400102-10020000101100100022010000002
Ptychadena mascareniensis	0001111111100-211102210--1220110211400102-10020000101100000022010000002
Pyxicephalus adspersus	1?0100?10110112 1?1022100 0?3?0110211400200110 1?00001??0110011?1022001010
Scotobleps gabonicus	11010001011001212102200002130010 20-8000001100100001100001001012110000 10
Sooglossus sechellensis	0???1??001???0???00100200000000000-5100?2-1???1-1?1??00--00?0?0????0011
Staurois natator	01110010010011212111210002120100211710110011001-1011100010002101020000 2
Strongylopus grayii	11011101011011211102200002120110211410000100020000100100100021010000102
Tomopterna marmorata	00211001011001212121210002120110211610200110110010011000100121010000002
Tomopterna tandyi	01211001011001210121210002120111211610200110110000011000100121010000002
Trichobatrachus robustus	0?0100?10110012 1?1022000023201?020-??02001?01?0?0011?00010012 1?10000010

Table 8. Continued

	71	76	81	86	91	96	101	106	111	116	121	126	131	136	141
Afrana angolensis	00000200100001100000201100100000000210000030000001110000323													0----2100020	
Afrana fuscigula	00000200100001100000201100100000000200000030000001100000323													0----2100020	
Amnirana albolabris	00100210100001 01?0000113010211000011?00113000000011010030													10----210002?	
Amolops ricketti	01-00210100001010000001??000000000020 00?1130000000031201													0000----2101020	
Anhydrophryne rattrayi	21-00210011001110010211101100020010010000030000001000100													3124----1101111	
Arthroleptella hewitti	21-00210011001110000211101100020 01?0100003000000*000100													311?----1101011	
Arthroleptella landdrosia	21-00210011101100000211101100100110010010030002011000100													312?----1100011	
Arthroleptella lightfooti	21-00210012101100000211101100100110010010030002011000100													312?----1100011	
Arthroleptides martiensseni	02-00200111001000000101100000000000010000030000001121100													10021000----2100020	
Arthroleptis stenodactylus	01-00220021 00?1130000?????00111-00120001010100000001003010													----0100000	
Arthroleptis variabilis	01-00220021001113000010100000111-00120001010100000100100312													30100010000?	
Astylosternus diadematus	01-00240110000103000001110100011-00120 0?100010000001001003													160----0100000	
Aubria subsigillata	10210210200001100000211100000000002000011400000011000003													120----1100020	
Batrachylodes vertebralis	01-00220020001100010-?1??000010000001101113000000001001003													000----1001120	
Breviceps rosei	01-01012002100 0?*0??4000-10111000002011000400100011000003													120----1010000	
Cacosternum boettgeri	21-01022012111001010311101100110110112001003011311000010													03124----1100011	
Cacosternum capense	21-01002011011000010101100100010000120010030001110002101													3120----1100011	
Cacosternum namaquense	21-0102201111-00221010110110001000012001003001111000210													13120----1100001	
Cacosternum parvum	21-01122022110000000311101100110101120010030000110002100													3124----1100?1	
Cardioglossa gracilis	01-00220021001000000011101000 1?1-11000001000100000 1?0100													3020----110?00?	
Chiromantis xerampelina	01-00201120001000000 1000-01000001000000001320000010100103													040----0100000	
Colostethus inguinalis	01-00210021002213010010101100020001101010040102100000100													3000----1001001	
Colostethus trinitatis	01-00210021002213010011101100020000 10?0100400021000001003													000----1001000	
Conraua crassipes	11-10210101001000000211100002000000200000030000000100000													3120----210002?	
Conraua goliath	1????210?0100100000021110000000?002??00?13000000?100?003													120----210002?	
Dendrobates pumilio	01-00210?2100221300000110110012000010001004001210000010													03000----1001001	
Dendrobates speciosus	01-00210?2100221300000110110012000010001004001210000010													03000----1001001	
Dimorphognathus africanus	01-00210010001010000211101100020120000010050000000100100													3013011000 20	
Discodeles bufoniformis	00000220100001100000?111000110000000000011140100000100200													315110-0210102?	
Ericabatrachus baleensis	01-00200021010003000001100100000000210010150000010000000													31230111111000??	
Euphlyctis cyanophlyctis	?????210101001000010211 10??000000002?000?130000000100?003													230----1100020	
Heleophryne purcelli	00000000000000000000000-00000000000000000000000000000000													0000----0000000	
Hemisus marmoratus	01-01220022101??22004000-12110000000011001501100011000003													120----1011000	
Hildebrandtia ornata	30110200100001100000200131000000000210000030000001110000													3120----110002?	
Hoplobatrachus occipitalis	???10210101001000000211100000000000211000030000000100200													3230----210002?	
Hydrophylax galamensis	00100210100001 01?0100011301021000001110111300000001101003													010----2100020	
Hyperolius viridiflavus	01-00210020010003010001020100111-00121010002000000110110													3150----0100?0	
Kassina senegalensis	01-00222020010000010001 1??100111-00121010002100000100110													3010----1100000	
Leptodactylon ventrimarmoratus	0???024??0000?1?30000??????00?10???12???100010000011 1?000													120----010000?	
Leptodactylus melanonotus	00010210100001001000200100010000000201000 0?0102000101100													2230----1100000	

Table 8. Continued

	71	76	81	86	91	96	101	106	111	116	121	126	131	136	141
Leptopelis vermiculatus	01-00201110011100000000120000101-0000001000200000011001031													50----0100000	
Limnonectes blythii	10210210101000000000?11100100000000010000??300000011001003230----2100020														
Mantella aurantiaca	01-0021002?00?21?0??????????0????0020???1132?020001001003040----110002?														
Mantidactylus femoralis	00000210110001017000101100100000100200007032000001100100304100001101020														
Microbatrachella capensis	21-00102?11011100010201101100110100121010030000000020003124----1100011														
Nannophrys ceylonensis	01-00210-000010000????1??0100000000010000?030?000000021003 1?0----1100020														
Nanorana parkeri	21-11332111???10?????????????????000002?????040???000??00010230----2100020														
Natalobatrachus bonebergi	01-00210020001010000201100100000100000010030012*111001013000----1101010														
Nothophryne broadleyi	01-00102111011100000201107100020001220010030000100012100312301111100010														
Nyctibates corrugatus	01-00120020001003000000110100012200120001000100000100100312 0----0100000														
Pantherana pipiens	00000200100001100000101100100000000200000130000000110000323 0----2100020														
Petropedetes cameronensis	01-00200111001000000011300000000000100000300000010211001002100001 0002?														
Petropedetes natator	01-00200101001010000?011300000000000100000?000000100010030 00----0101020														
Petropedetes newtoni	02-00200111001000000101130000000000000010030000001021100100210002100020														
Petropedetes parkeri	01-00200111001000000001100000000000010000030000001021100100210002100020														
Philautus surdus	01-00200120000000000000-0100000110000000132000000000110304100000100 00?														
Phrynobatrachus acridoides	01-00210020001010000211101100020122000001150000000100100301301011100 0??														
Phrynobatrachus cricogaster	01-00210?100?10?00002??1??10000012 20?00???500000001001003013011111 0002?														
Phrynobatrachus dendrobates	01-00210110001010000211101100000220011011130000000100100301301011101 02?														
Phrynobatrachus krefftii	01-00210010001010000211101100000222010001130000000100100301301111101020														
Phrynobatrachus natalensis	01-00210020001000010211101100020122010011150000000100100301301011100001														
Phrynobatrachus plicatus	01-00210110001010000211101100000122000011150100000100100301301111102?														
Phrynobatrachus versicolor	01-00210110001010 0??211101100000220010001130000000100100301301011102?														
Phrynodon sandersoni	01-00210111 0?111000021110110000022201101013000000010010030030101110102 0														
Phrynoglossus laevis	01-01222100001000000211100011000000000?1301000001001003000----200002?														
Phrynomantis bifasciatus	01-01002022000001000410101000000000011100041000001100100300 0----0111000														
Platymantis corrugatus	00000211120001110000211101011000011000000040100000000100315110-0210102?														
Poyntonia paludicola	01-00202011000000010211101100000100210010030000000100000312 4----1000011														
Ptychadena anchietae	20100200100001000000200131000000110211010030000001010100323 0----1100021														
Ptychadena mascareniensis	20100200100001000000200131000000110211010030100001010100323 0----1100021														
Pyxicephalus adspersus	1????2?3200001?000020110000000?002??0?1140000001 10??003120----1100020														
Scotobleps gabonicus	01-00240110001103000001110000010100120 0?10001000001001003160----0100000														
Sooglossus sechellensis	?????11???10?10122001101010000000000200 01??30?01?10000??03220----100000?														
Staurois natator	01-00200122001010000001 0-0100102210220001140000000041201300110-0110101?														
Strongylopus grayii	00000200100001100000201100100000000000000030000001100000323 0----2100020														
Tomopterna marmorata	01-00232020001000011211101000000002 1?0101300000011000??120----110002?														
Tomopterna tandyi	01-00232020001000011211101000000002100101300000011000013120----1100020														
Trichobatrachus robustus	0???022??0000?1?30000??????00?10???12???100010000101?000160----110000?														

Table 8. Continued

	142 147 152 157 162 167 172 177 182 187
Afrana angolensis	10000201002001110-0100011210001200101110004110015
Afrana fuscigula	10000201002001110-0100011210001200101110000004110015
Amnirana albolabris	10000101102001110-0100000100010000111101000210035
Amolops ricketti	00200202002000010-0000000000100000111101000000000?
Anhydrophryne rattrayi	00000202000011012000000002110000001001100003110005
Arthroleptella hewitti	10000201000011012000000002110000001001100003110005
Arthroleptella landdrosia	00000202002010012000000002110100001020110000110005
Arthroleptella lightfooti	00000202002010012000000002110100001020110000110005
Arthroleptides martiensseni	40001200112121212-1100000001100200101101000021000 5
Arthroleptis stenodactylus	00010201000010012001210002112000001010010100000000?
Arthroleptis variabilis	00000201000010012001210001012000001010010100000000?
Astylosternus diadematus	10000201002001002-0101020111000000002 0??000011100?
Aubria subsigillata	0000020?021011110-0110001210001200201100000421000 5
Batrachylodes vertebralis	00003202012010012000000000011100001120011100100 00?
Breviceps rosei	00000201001010-12-0101000211210000102001010001000 4
Cacosternum boettgeri	10000201001010-1200000000211010002020010002111005
Cacosternum capense	20000201000010-1210000000211200002000010002112005
Cacosternum namaquense	20000201002010-12100000002112*0000200001000211200 5
Cacosternum parvum	10000201001010-120000000021 10*0000101101000211100 5
Cardioglossa gracilis	00010201002011012001210001012000001020010000210 00?
Chiromantis xerampelina	20000201002000010-0000000100000200?04-02000000000?
Colostethus inguinalis	00000201002012012011000001010122101 03-000000110002
Colostethus trinitatis	00000201002012012011000001010122101 03-000000110002
Conraua crassipes	10000202001000100-0110001210001100201100001011000 5
Conraua goliath	10002202001 00?000-0110001210001100201100001011000 5
Dendrobates pumilio	00000201002012012010000001010122101 03-000000110002
Dendrobates speciosus	00000201002012012010000001010122101 03-000000110002
Dimorphognathus africanus	00000301011000?11-0000000101012211102000100011010 5
Discodeles bufoniformis	00000202002000010-0100000101110000111001000000000?
Ericabatrachus baleensis	00000201011010-1201000000101000000--311?0001?10005
Euphlyctis cyanophlyctis	1000?202101000110-0110011210001100202000000411000 5
Heleophryne purcelli	00000000000000000-0000000000000000000000000000000
Hemisus marmoratus	00000201001010-0210101000211200000203-000*101?0000
Hildebrandtia ornata	30000202102011111000010112102002001011000000210005
Hoplobatrachus occipitalis	1000?202101001110-0110001210001100202000001411000 5
Hydrophylax galamensis	10000101102001110-0100011110010200111101000021003 5
Hyperolius viridiflavus	000000110 0?010-10-000000100000100304-020000010001
Kassina senegalensis	00000011002010002-0000000211010000303-010000010001
Leptodactylon ventrimarmoratus	0010120?0010100020011000010100000000?0?0000110000?
Leptodactylus melanonotus	40000201002011012101000002110110001 03-010000110025

Table 8. Continued

	142 147 152 157 162 167 172 177 182 187
Leptopelis vermiculatus	00004010020111O1-0000000101200000101002010000000?
Limnonectes blythii	00002010010000O-0110011210101100111100001011000S
Mantella aurantiaca	00002010120100120000000010101000010??000000110003
Mantidactylus femoralis	00002010120000O-0000000100000201101101000001000З
Microbatrachella capensis	10000202001010-1000000000210000000102010000З110005
Nannophrys ceylonensis	00001202112001002000000002111000001211000110000000?
Nanorana parkeri	00002010010010??0-0110001210000000207?000003113007
Natalobatrachus bonebergi	10000202002011110-0000000000000001101001000011010S
Nothophryne broadleyi	10000202000010-1200000000211000000102111000211000S
Nyctibates corrugatus	10000201002010001-0101020111010100002007000000000?
Pantherana pipiens	10000201?02001110-0100011210011100101101000021003S
Petropedetes cameronensis	00002011112001011-1000000001000200101100010021000?
Petropedetes natator	10002011112000010-1000000000100200112100000000000?
Petropedetes newtoni	01001201112121212-1000000001000200101100000021000?
Petropedetes parkeri	01001200112121212-1100000001100200101101000021000?
Philautus surdus	10002010020000O-00000001000002007040210000000?
Phrynobatrachus acridoides	1000020?001011011-0000000101010211102000100010010S
Phrynobatrachus cricogaster	100002010?1000011-0000000101012211102000100511010S
Phrynobatrachus dendrobates	10002010120001l1-0000100001012011102000000010010S
Phrynobatrachus krefftii	10002010110001l0-0000100100012011102100?000110105
Phrynobatrachus natalensis	10002010110000l1-0000000211012211102000100011000S
Phrynobatrachus plicatus	?0002010110011l1-0000000100012?101020001000110105
Phrynobatrachus versicolor	?0002010120001l1-0000100101012011102000000100105
Phrynodon sandersoni	10002010110000l1-000000000101221*102100000011000S
Phrynoglossus laevis	00002010010010?10-0100001100001200201100001000000?
Phrynomantis bifasciatus	00002010010l0-22-0000000101200000103-0000000?1005
Platymantis corrugatus	0000?2010020010l2-0110000101110002102001100000000?
Poyntonia paludicola	00002010010l0-1200000000211200000203-100001114005
Ptychadena anchietae	30002021020111l0-0000011210001200102101000021002S
Ptychadena mascareniensis	30002021020111l0-0000011210001200102100000021002S
Pyxicephalus adspersus	20002010010111l1-0100001211200000201100000411001S
Scotobleps gabonicus	00002010100000O1-0100020111010000001001000011000?
Sooglossus sechellensis	00002010010010?12-0000000101110000--3-1000001?0000
Staurois natator	10002010010010l0-0000000000110000101100000000000?
Strongylopus grayii	20002010020110l2-0100010211001200101101000011000S
Tomopterna marmorata	20002010020100111010100021120000120210100001100OS
Tomopterna tandyi	20002010020100101010101021121000020210100001100OS
Trichobatrachus robustus	0010120?002000001-0110000111000100007070?1000010000?

Figure 18. Strict consensus of 20 individual strict consensus trees obtained by analysis of data under each parameter set, showing groups universally retrieved by all analyses.

Figure 19. Fifty percent majority-rule consensus of 20 individual strict consensus trees obtained by analysis of data under each parameter set, showing groups retrieved by more than half of all analyses.

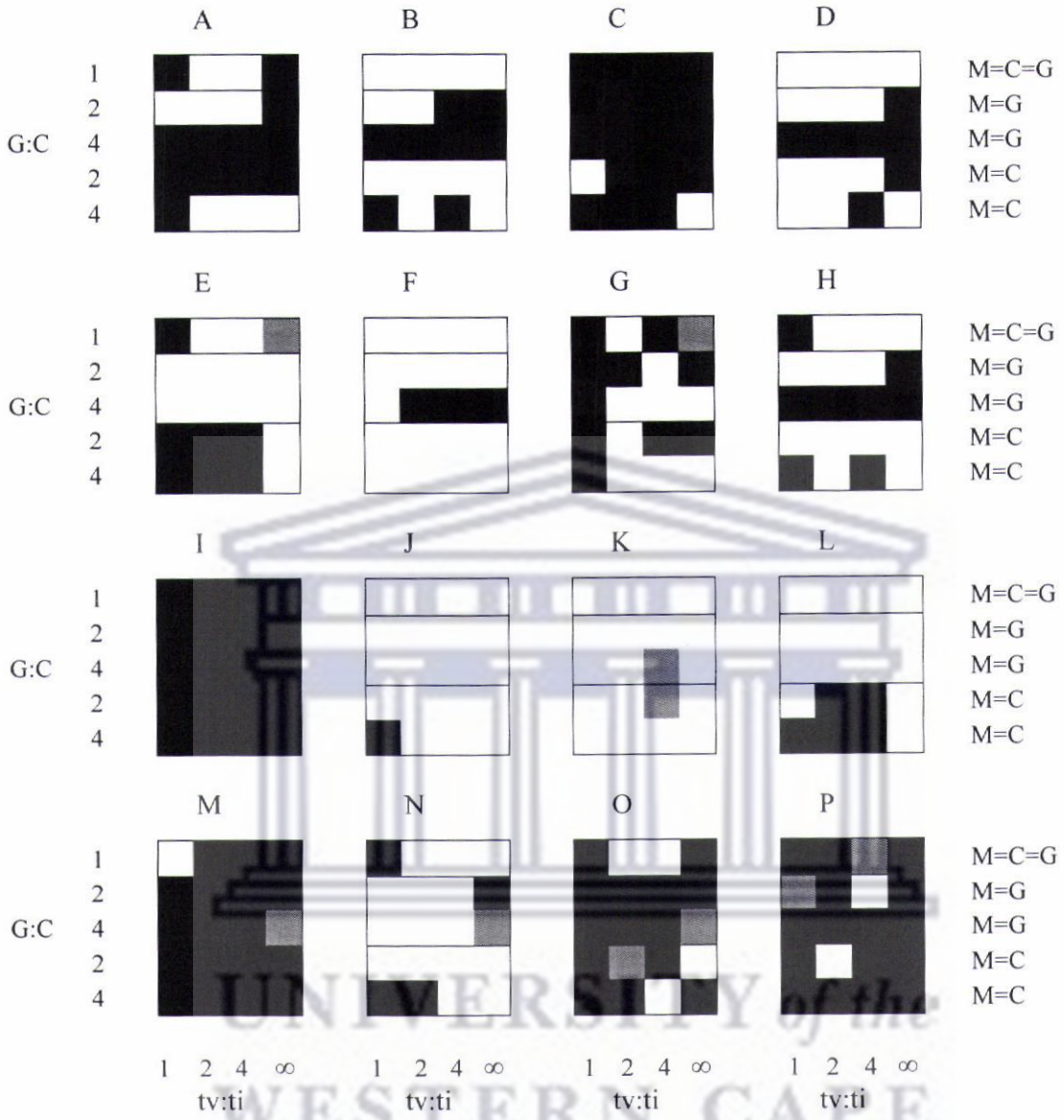

Figure 20. Gallery of analysis space plots for selected groups postulated as monophyletic in the literature. White = monophyletic, grey = unresolved but congruent with potential monophyly, black = non-monophyletic. **A.** Bufonoidea including sooglossids, dendrobatids, heleophrynids and leptodactylids. **B.** Ranoidea excluding dendrobatids. **C.** Ranidae excluding rhacophorids and mantellids. **D.** Ranidae including rhacophorids and mantellids. **E.** Hyperoliidae including *Leptopelis*. **F.** Hyperoliids and arthroleptids. **G.** Arthroleptidae. **H.** Mantellids. **I.** Petropedetinae. **J.** Cacosternids. **K.** Phrynobatrachids. **L.** Petropedetids. **M.** (Phrynobatrachids + Cacosternids). **N.** (Tomopterninae + Cacosternids). **O.** (Cacosternids + Tomopterninae + Phrynobatrachids). **P.** (Rhacophorids + Mantellids). Consistently monophyletic and consistently paraphyletic groups not illustrated, except the Petropedetids (I). M = morphology, tv = transversions, ti = transitions, ∞ represents infinity.

Table 9. Numerical summary of the 20 analyses under different weighting parameter sets, showing the calculations of the Incongruence Length Difference (ILD). Parameter set 410G was found to have the lowest character incongruence between morphological and molecular data sets.

PS	G/C max	Tv/ Ti	Mor Wei	No. trees	L Comb	L Mor	L Mor*Wei	L Mol	Σ (MM)	ILD
110G	1		1	8	3347	1679	1679	1441	3120	0.0678
111G	1	1	1	1	5113	1679	1679	3181	4860	0.0495
121C	1	2	2	2	8178	1679	3358	4431	7789	0.0476
141G	1	4	4	4	14543	1679	6716	7085	13801	0.051
210C	2		1	4	3507	1679	1679	1623	3302	0.0585
210G	2		2	2	5290	1679	3358	1623	4981	0.0584
211C	2	1	1	6	5335	1679	1679	3420	5099	0.0442
211G	2	1	2	2	7100	1679	3358	3420	6778	0.0454
221C	2	2	2	2	8906	1679	3358	5084	8442	0.0521
221G	2	2	4	1	12371	1679	6716	5084	11800	0.0462
241C	2	4	4	2	15942	1679	6716	8321	15037	0.0568
241G	2	4	8	1	22786	1679	13432	8321	21753	0.0453
410C	4		1	4	3926	1679	1679	2027	3706	0.056
410G	4		4	5	9120	1679	6716	2027	8743	0.0413
411C	4	1	1	1	5827	1679	1679	3842	5521	0.0525
411G	4	1	4	1	11051	1679	6716	3842	10558	0.0446
421C	4	2	2	1	9758	1679	3358	5878	9236	0.0535
421G	4	2	8	1	20259	1679	13432	5878	19310	0.0468
441C	4	4	4	1	17672	1679	6716	9828	16544	0.0638
441G	4	4	16	6	38419	1679	26864	9828	36692	0.045

PS = parameter set; G = gap cost; C = change cost; Tv = transversion cost; Ti = transition cost; Mor = morphology; Mol = molecular; Wei = weight; L = length; Comb = combined analysis; MM = separate molecular analysis plus separate morphology analysis.

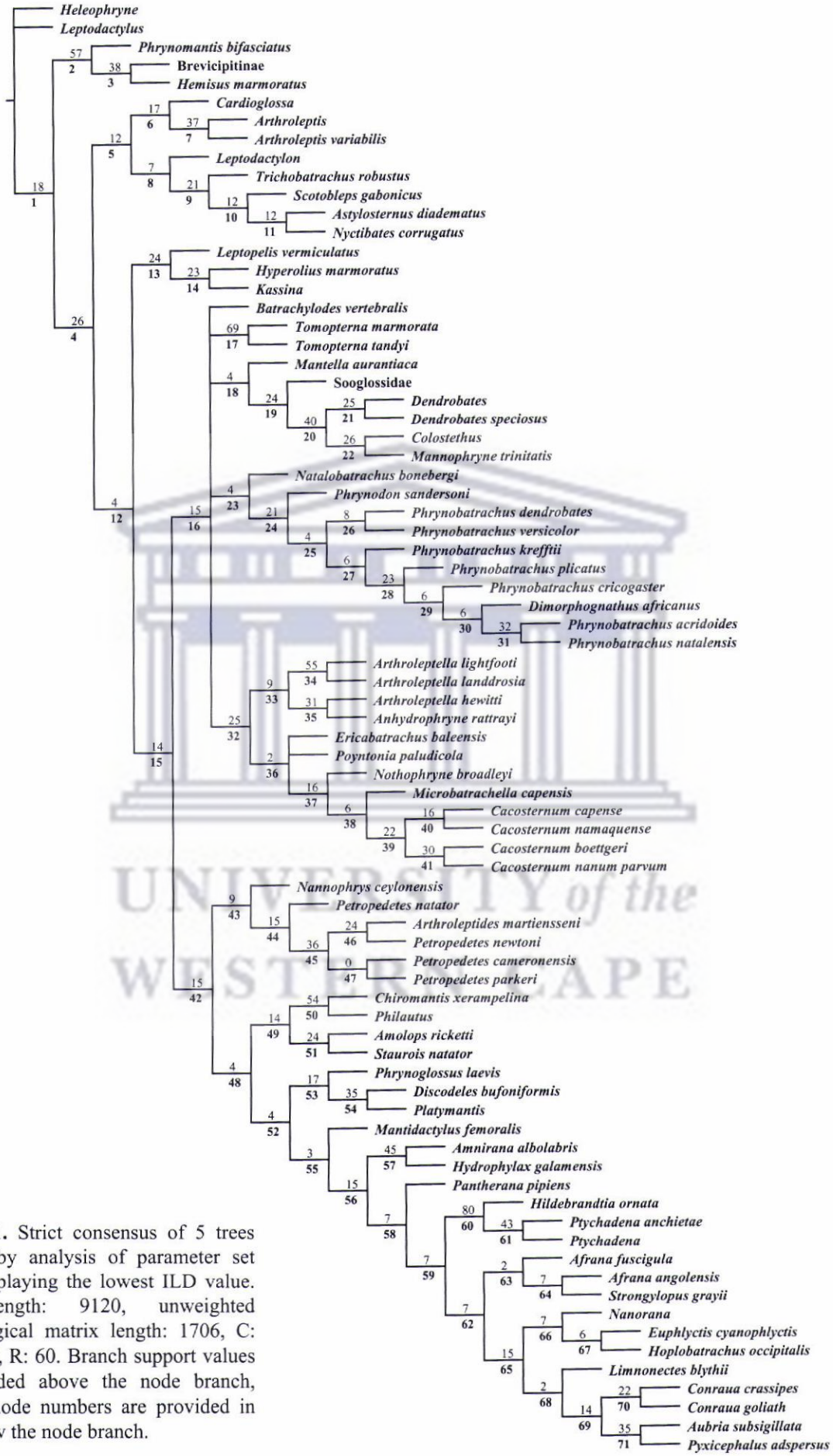

Figure 21. Strict consensus of 5 trees obtained by analysis of parameter set 410G, displaying the lowest ILD value. Total length: 9120, unweighted morphological matrix length: 1706, C: 20, Ci: 20, R: 60. Branch support values are provided above the node branch, whereas node numbers are provided in bold below the node branch.

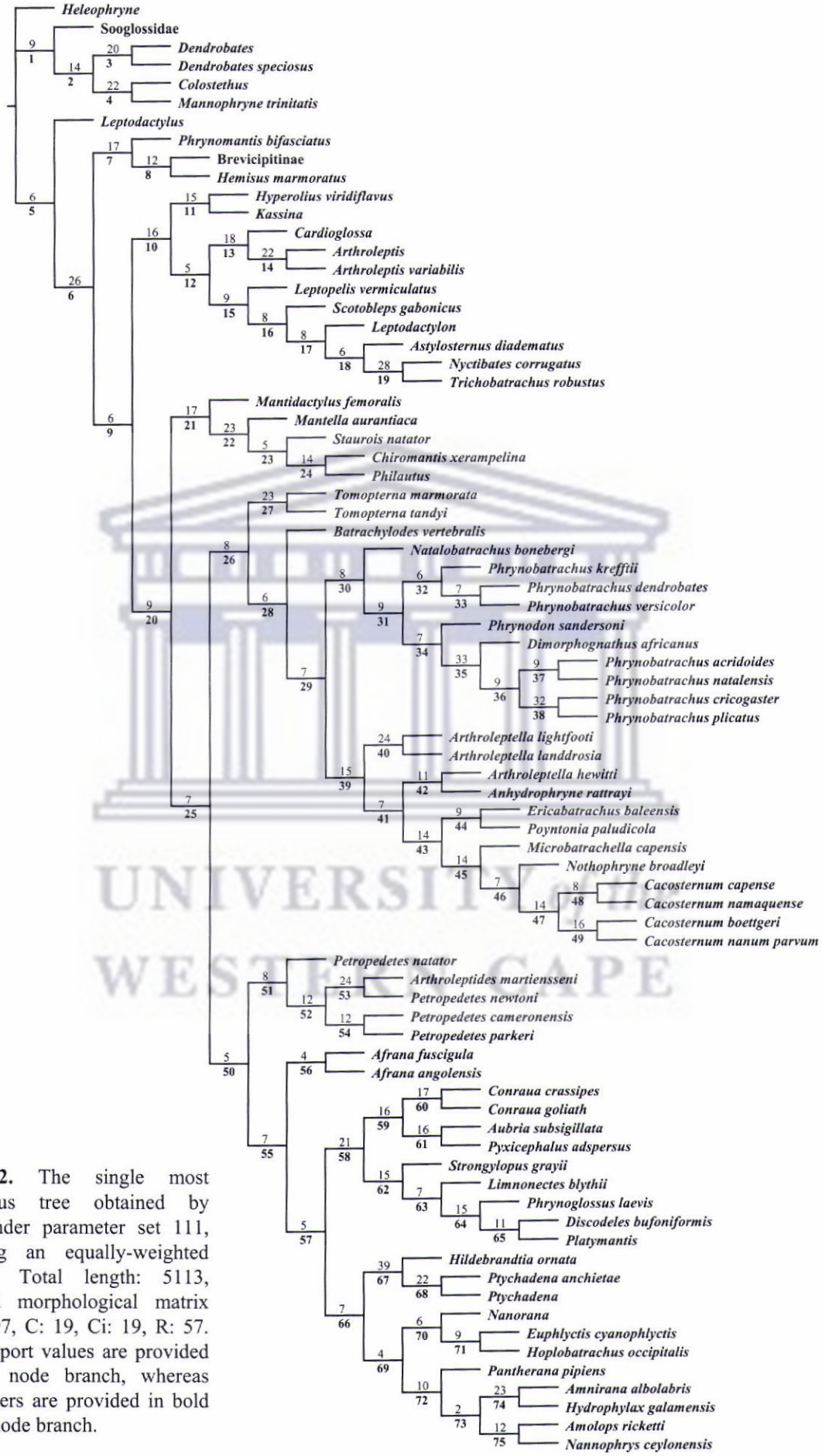

Figure 22. The single most parsimonious tree obtained by analysis under parameter set 111, representing an equally-weighted hypothesis. Total length: 5113, unweighted morphological matrix length: 1797, C: 19, Ci: 19, R: 57. Branch support values are provided above the node branch, whereas node numbers are provided in bold below the node branch.

Table 10. Number of steps, consistency index (ci) and retention index (ri) of each morphological character, according to the equally-weighted topology (Fig. 22). Character numbers are bolded, the line below this shows the number of steps of that character, the second line below shows the ci of that characters and the third line below shows the ri of that character.

0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
8	11	9	6	15	10	10	12	1	2	9	11	10	6	12	6
12	9	22	16	13	10	10	16	100	50	11	18	10	16	16	16
61	54	50	54	60	47	55	69	100	50	57	73	43	61	61	50
16	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**
22	2	14	11	12	14	10	3	10	4	15	9	2	8	14	10
9	50	14	18	16	7	20	66	20	50	20	33	100	12	14	10
48	66	53	73	50	56	60	83	68	60	66	33	100	30	40	10
32	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**
9	4	11	20	14	3	20	10	9	8	9	8	12	16	10	2
33	50	18	40	14	33	10	10	22	12	11	12	16	18	10	50
33	89	64	70	47	0	37	40	53	75	20	69	28	35	59	50
48	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**
9	4	17	17	15	11	7	15	11	2	11	19	16	7	7	8
11	25	17	5	13	9	42	13	18	50	9	15	12	28	28	25
76	50	39	33	35	65	50	48	43	75	23	57	62	68	58	62
64	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**
8	11	6	2	17	17	19	8	9	4	5	4	9	22	12	11
25	18	16	50	5	5	10	37	22	50	20	25	33	18	25	18
83	43	37	50	44	33	63	66	56	60	33	62	33	52	40	70
80	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**
17	12	4	4	10	17	11	11	3	12	1	13	13	8	4	8
11	16	25	25	20	11	9	27	33	8	100	30	7	12	25	37
69	70	50	66	38	44	58	50	0	26	100	72	61	50	50	50
96	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**
10	11	3	4	10	9	5	12	8	8	16	16	11	1	12	10
10	18	33	50	10	22	40	16	25	25	12	12	9	100	8	10
70	67	60	66	47	69	57	54	64	40	67	66	28	100	64	59
112	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**
14	12	5	10	5	8	2	5	10	10	12	9	15	3	6	7
7	33	40	10	20	37	50	20	10	10	33	22	13	33	16	42
48	70	50	47	33	50	87	50	62	68	42	46	35	50	16	42
128	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**	**141**	**142**	**143**
15	24	11	2	2	3	1	14	5	1	13	2	7	6	21	2
13	25	36	50	50	33	100	14	20	100	7	50	28	16	19	50
69	60	68	83	87	50	100	60	60	100	40	0	84	66	50	0
144	**145**	**146**	**147**	**148**	**149**	**150**	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**
3	2	7	5	1	13	4	10	18	2	16	18	10	7	20	4
66	50	42	80	100	15	25	20	11	50	12	11	20	28	10	25
0	0	20	66	100	38	75	52	51	50	57	46	60	54	57	40
160	**161**	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**	**175**
3	11	8	6	1	11	5	18	14	14	17	16	10	15	2	5
33	9	25	16	100	18	20	11	7	7	11	6	20	13	50	40
77	69	45	44	100	25	73	60	64	51	34	50	66	60	91	66
176	**177**	**178**	**179**	**180**	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**	**191**
11	6	18	10	4	20	4	6	6	9	15	12	6	3	6	6
27	33	22	10	25	10	25	16	16	55	13	8	66	33	50	83
60	33	66	68	66	43	57	16	16	71	55	42	50	71	50	85

DISCUSSION

The strict consensus of the results of analyses conducted under all 20 parameter sets (Fig. 18) indicates that the ubiquitously present groupings are mostly those between sister species, demonstrating the high variability of the results of the sensitivity analyses at higher levels. This lack of resolution of strict consensus tree can be attributed to the range of analytical parameters used (see Wheeler 1995 for a similar example), and not because there is no signal in the data. The fifty percent majority-rule consensus of analyses conducted under all 20 parameter sets (Fig. 19) indicates those groupings that appeared under most analysis parameters, and thus differentiates groups retrieved only under particular parameter sets from more generally supported relationships. All topologies obtained displayed at least one local taxon placement considered to be suspect in light of the morphology of the organisms. This can be expected in any large analysis where sampling is incomplete, because particular pivotal taxa required to stabilise relationships may be missing. Questionable relationships identified by the sensitivity analysis include a relationship of *Strongylopus* to the fanged ranids (*sensu* Emerson & Ward 1998), *Mantella* to the dendrobatids creating a non-monophyletic Mantellidae, *Leptodactylus* nested within the Ranidae, and *Amolops* and *Staurois* not being closely related. In one analysis, *Ericabatrachus* grouped with the dendrobatids and sooglossids and, in another, the dendrobatids were found nested within the Ranidae. However, the sensitivity analyses all confirmed that the Petropedetinae is not monophyletic and identified the same three component clades thereof, which was the main focus of the present study.

From this point forward, the discussion focuses on each putative clade postulated in recent classifications, or novel placements obtained in this analysis. A brief taxonomic history, focusing particularly on the putative relationships of each of these groups to the petropedetines (if applicable), is presented. The morphological synapomorphies identified for these clades, according to the equally-weighted topology and amongst the current taxon set, are also discussed.

Dendrobatids and Sooglossids

Although the monophyly of the Dendrobatidae is well corroborated and supported by many unique synapomorphies (Myers & Ford 1986; Weygoldt 1987; Ford 1990; Myers *et al.* 1991; Ford & Cannatella 1993; Fig. 18), their phylogenetic position within the Neobatrachia remains controversial. Dendrobatids have been suggested to be in the superfamilies Bufonoidea or Ranoidea. The prevailing view in the older (pre-phylogenetics) literature is that the dendrobatids are more closely related to the bufonid frogs than they are to the ranoid frogs, i.e. the 'leptodactylid hypothesis' of Noble (1922, 1926a, 1931), as advocated by Lynch (1971, 1973). A recent morphological study of microhylid relationships (Wu 1994) and analyses based solely (Ruvinsky & Maxson 1996; Vences *et al.* 2000b), or primarily (Emerson *et al.* 2000a) on

molecular data appear to favour the leptodactylid hypothesis. The alternative hypothesis of dendrobatid relationships, i.e. the 'ranoid hypothesis' of Griffiths (1959a), was not generally accepted until Ford's (1990) large-scale phylogenetic analysis of Neobatrachian relationships based on osteological characters showed the family Dendrobatidae to be embedded in the Ranoidea. As Ford (1993) points out, ambiguity and error in the literature has resulted in the same lines of morphological evidence being used by proponents of the two different viewpoints to support their preferred hypotheses. Ford & Cannatella (1993) provide a comprehensive discussion of the competing hypotheses of dendrobatid relationships, and observe that the character state distribution of the dendrobatids does not refute its placement in the Ranoidea. Rather, this suggests that, as with the microhylids, the dendrobatids are not nested within Laurent's (1979, 1986) Ranidae or Hyperoliidae.

The present study offers a new perspective on this problem, because it employs a comprehensive morphological data set in a simultaneous analysis with molecular data, and includes a larger sample of ranoid frogs than any previous phylogenetic analysis. The gallery of analysis space plots (Figs 20A, B) shows that both the Bufonoidea (the leptodactylids and *Heleophryne*, as defined to include the dendrobatids and sooglossids) and the Ranoidea (including the microhylids) were rendered paraphyletic under some sets of analysis parameters, due to the unstable position of the sooglossids and the dendrobatids. The results of the sensitivity analysis generally place the dendrobatids at the base of the ranoid tree (Fig. 19), with the sooglossids in most cases found to be the sister taxon of the dendrobatids. The suggestion that the dendrobatids and the sooglossids are derived from the same lineage is is a novel arrangement, and idicates that perhaps they should both be regarded as 'transitional' families (*sensu* Lynch 1973) until further evidence comes to light. However, the frequent placement of *Leptodactylus* as the sister to this couplet (occasionally with the position of *Leptodactylus* and the sooglossids reversed) could be taken as evidence slightly in favour of the 'leptodactylid hypothesis'. However, this may also simply be a sampling artifact, caused by the paucity of other leptodactylids in these analyses.

A sister group relationship between the phrynobatrachids and dendrobatids, as suggested by Griffiths (1959a), was only retrieved by two of the sensitivity analyses, although the possibility of this was present in another unresolved topology (410G, which just happens to be that topology with the lowest character incongruence). Ford's (1990) study indicated the families Dendrobatidae and Arthroleptidae to be sister taxa, but this arrangement was not retrieved by the current analysis. As noted by Ford (1990), the omission of the Astylosterninae from her analysis may have been problematic. The present study found that the astylosternids strongly link the arthroleptids to the hyperoliids, presumably excluding a dendrobatid-arthroleptid relationship.

On the equally-weighted topology, three synapomorphies were identified that supported the Ranoidea excluding the dendrobatids and sooglossids (node 9), but none of these character states were found to conflict with the notion that the dendrobatids may be included in the ranoid lineage, congruent with Ford & Cannatella's (1993) above-mentioned observation. These characters were undilated sacral diapophyses (c20:2); the pars palatina of premaxilla having equally expanded medial and lateral edges (c50:1); and the width of the base of the stalk of the alary processes of the hyoid being broader than the stalk (c93:1). However, none of the synapomorphies that united the sooglossids with the dendrobatids on the equally-weighted topology are unique. These included the presence of a posterior fenestra in the xiphisternum (c36:1); absence of palatines (c40:2), which also occurs in the microhylids and Ptychadeninae; absence of the posterior process of the vomer (c46:1); the pars palatina of premaxilla having equally expanded medial and lateral edges (c50:1); rectangular to round nasals (c70:1); the pars fascialis of the maxilla being strong and triangular (c81:1); the alary processes of the premaxilla inclined laterally (c86:1); the alary processes of the hyoid angled laterally (c96:1); and the arytenoid cartilages of breeding males being long and oval (c110:1). The condition of the medial borders of the coracoids (c27) was coded differently for these two groups, and thus had no influence in grouping them together. Additional work is required to verify the above conclusions.

Arthroleptids and Hyperoliids

The Arthroleptidae was raised to familial status by Dubois (1981), after historically being regarded as two subfamilies, the Astylosterninae and Arthroleptinae, in either the Ranidae or the Hyperoliidae. Dubois (1986) subsequently transferred the hyperoliids to an enlarged family Arthroleptidae, which has nomenclatural priority over the Hyperoliidae. Dubois (1992) again revised his opinion, changing the rank of each of the Arthroleptidae, Astylosternidae and Hyperoliidae to families, perhaps to avoid the problems associated with possible paraphyly of the astylosternines (Frost 2002). Whilst most workers accept the status of the Hyperoliidae, the status of the arthroleptids is highly contentious. Many workers do not agree with familial status for even the Arthroleptinae and Astylosterninae together in one family, the Arthroleptinae. For example, J. D. Lynch (in Frost 1985:14) comments that, 'the recognition of this family is premature given that no phylogenetic justification or diagnosis has been presented'. Ford & Cannatella (1993) treated the Arthroleptidae as a metataxon, as no unique synapomorphies of the group had been identified up to then. Grant *et al.* (1997:16) state that 'conclusions about the content of this genus [*Arthroleptis*] and its familial separation from petropedetine ranids seem more based on authoritarianism than on character analysis and should be revisited.'

Laurent (1940, 1973 and elsewhere) consistently rejected the inclusion of the petropedetids with the arthroleptids, a viewpoint that is supported by the present analyses. Not one of the

sensitivity analyses suggested a close relationship between any of the clades in these two groups. Laurent (1951) noted that *Leptopelis* has strong similarities with the astylosternids, and his views have again been borne out by recent molecular studies, which place *Leptopelis* outside the Hyperoliidae (Vences 1999; Emerson *et al.* 2000a). This is consistent with results of the present study, where the both the hyperoliid and the arthroleptid lineages were often rendered paraphyletic by the position of *Leptopelis* at the base of the astylosternids (Figs 20G, E). The Arthroleptidae excluding the Hyperoliidae was not retrieved as monophyletic by all sensitivity analyses, although the monophyly of these two groups together was retrieved in nearly all cases (Fig. 20F).

The sensitivity analyses thus support the recognition of one monophyletic family to include the hyperoliids and arthroleptids, as advocated by Dubois (1986), which would take the familial name Arthroleptidae. Many synapomorphies exist for this composite clade or family. The only unique character for the broadly defined Arthroleptidae (including the hyperoliids) is the absence of the posterior lateral process of the hyoid (c102:1), although these are present in most astylosternids (absent only in *Astylosternus* and reduced in *Nyctibates*). Although ambiguously optimized on the topology, the xiphisternum shape being rectangular with strongly serrated distal end (c35:8) appears to be unique to this lineage amongst the taxa examined here. Other non-unique synapomorphies include: the biconcave shape of the cultriform process of the parasphenoid (c59:1); rectangular to round nasals (c70:1); a long narrow hyoid plate (c100:1); the presence of a cartilaginous stalk of the thyrohyal (c101:1), which reverses to absent in *Leptopelis*, and occurs elsewhere only in *Microbatrachella*, *Cacosternum* and *Amnirana*; the thyrohyals not being expanded at either end (c106:1) and a pointed, short truncated shape of the terminal phalanx of the fourth toe (c129:5), which changes many times in the lineage, including to a unique state 8 in the astylosternids.

From past studies of the hyperoliids and arthroleptids (Liem 1970; Laurent 1979, 1986; Drewes 1984; Channing 1989), the following characters have been suggested to be synapomorphic for the hyperoliids (Ford & Cannatella 1993): the presence of a musculus dentomentalis; the absence of nuptial pads; the presence of claw-shaped terminal phalanges; the absence of the posterolateral process of the hyoid; a vertical pupil and a cartilaginous sternum. Muscular characters have not been examined for the arthroleptids or astylosternids, but it is likely that most of the putative hyperoliid synapomorphies also occur in these groups. The absence of nuptial pads and a cartilaginous metasternum are shown to be plesiomorphic by this analysis, as are the carpal and tarsal characters which were often postulated in the past to be synapomorphic for some of these taxa. The analysis suggests that vertical pupils are independently and secondarily derived in the astylosternids and in *Kassina*. This character state cannot therefore be considered as synapomorphic for either the classically defined Hyperoliidae, for the Arthroleptidae or for the Arthroleptidae including the hyperoliids. Claw-shaped terminal

phalanges also occur in many Raninae, and the only state of this phalangeal character unique to this lineage is where the tip is detached from the body of the terminal phalanx and curves sharply downwards (c129:6), which occurs only in three astylosternids. This state is distinctly different from the 'claw shaped' protruding phalanges recorded in the literature for *Ptychadena* (Parker 1936; Perret 1966). As noted by Ford & Cannatella (1993), definition of this character is notoriously difficult and has varied widely in the literature, requiring standardization.

Microhylidae and Hemisotidae

The microhylid lineage was found to be basal in the ranoid lineage, which is consistent with the views of Laurent (1940) regarding its position in the Ranoidea, and with the perception of a superfamily Microhyloidea by Dubois (1986). Unfortunately, little else can be deduced from this analysis due to poor sampling of this diverse lineage. However, the analysis does shed some light on the relationships of *Hemisus*. Parker (1934) was not convinced that *Hemisus* should be classified with the microhylids, and neither were Channing (1995) nor van Dijk (2001). Parker (1934) excluded *Hemisus* from his monograph of the family, since de Villiers (1933:257) had pronounced it 'quite definitely a terrestrial Ranid', while Laurent (1979) proposed familial rank for the Hemisotidae. Recent molecular and morphological work (Blommers-Schlösser 1993; Wu 1994; Emerson *et al.* 2000a) indicates that *Hemisus* should be treated as a brevicipitid microhylid, a group which Wu (1994) considered deserving of familial status as the 'Brevicipitidae'. However, Vences (1999) found *Hemisus* to be more closely related to the astylosternids and hyperoliids than to the microhylids, on the basis of partial sequence data from the 16S mitochondrial gene analysed with Neighbour Joining. Chromosome data from Morescalchi (1973, 1981) and Bogart & Tandy (1981) show that both the microhylids and *Hemisus* have the plesiomorphic condition of 12 pairs of chromosomes ($2n = 24$) whereas the arthroleptid lineage shows a derived state, and thus offers no further clarification of this point.

The results of the current analysis are unequivocal on this issue, with the microhylid lineage (*Phrynomantis* (*Hemisus* + Brevicipitinae)), being retrieved under all analytical parameters (Fig. 18). The exact position of the three genera relative to each other may not be correct here, given the sparse taxon sampling of microhylids, but in no analysis under the wide range of parameter values explored did an arthroleptid–*Hemisus* relationship occur. Among the broad cross-section of ranoids examined here, four uniquely synapomorphic characters support the placement of *Hemisus* with the microhylids. These include the presence of posterior palatial folds (c137:1); the lateral processes of the mentomeckelian being very well developed (c56:2); the bronchial processes of the cricoid being latticed and ramifying through the lungs (c109:1); and the medial branch of the anterior process of the hyale absent (c91:4). Other non-unique synapomorphies of this clade include: the orientation of the transverse processes of the eighth vertebra being acutely anterolateral (c4:2), which transforms in *Hemisus*; the dorsal ridge of the coccyx absent

exclude the rhacophorids and mantellids, was found to be almost always paraphyletic (Fig. 20C), while the Ranidae, defined to include these two groups, was found to be almost always monophyletic (Fig. 20D). Thus, the sensitivity analyses vindicate Laurent's (1951) standpoint that the rhacophorids should be included in the Ranidae, although the equally-weighted hypothesis demonstrates that the (mantellids + rhacophorids), including the genus *Staurois*, occur outside of, and basal to, the Ranidae.

Laurent (1979, 1986) characterised the Ranidae as having a bony sternal style, the second distal carpal fused to other carpals, second distal tarsal fused to other tarsals and the tongue notched posteriorly. The presence of the musculus cutaneous pectoris was noted by Tyler (1971) to be a possible synapomorphy of the Ranidae. Ford & Cannatella (1993) dismissed Laurent's (1986) tarsal and carpal characteristics, and concluded that only the bony sternal style and notched tongue were synapomorphic of the Ranidae, although they noted that the musculus cutaneous pectoris could be a synapomorphy for this family. The present analysis demonstrates that the presence of the musculus cutaneous pectoris (c140:2) is a unique synapomorphy for the Ranidae, although it can be thick or thin, and is absent in a few taxa in this group (four species examined here). A notched tongue (c136:1) was found to occur in the Arthroleptidae (including hyperoliids), *Leptodactylus* and *Phrynomantis*, and is thus not considered to be a synapomorphy of the Ranidae, although it occurs in all ranids examined except *Batrachylodes*, *Poyntonia* and *Phrynoglossus*.

A bony metasternum (c33:1) would be unique for the Ranidae, were it not present in *Leptodactylus*. This character state appears to be absent in *Ericabatrachus*. Nevertheless, it was demonstrated to constitute a non-unique synapomorphy of this family. A long cultriform process of the parasphenoid reaching the palatines (c60:2) was identified as a synapomorphy of the Ranidae, but it reverses twice to falling just short of the palatines (state 0) in the (phrynobatrachids + cacosternids) and in the petropedetids. The analysis also recognized a reversal to extensive webbing (c158:0) and the outer metacarpal tubercle, if divided, the sections thereof distinctly separate (c179:1) as synapomorphic for the Ranidae, but these change often and sporadically in this family and cannot be regarded as defining features.

Mantellids and Rhacophorids

A sister group relationship of the rhacophorids and mantellids was previously demonstrated by Ford (1990), Blommers-Schlösser (1993) and Emerson *et al.* (2000a) and was also retrieved here by the sensitivity analysis. This is not reflected in Fig. 20P due to the inclusion of *Staurois* in, or exclusion of *Mantella* from, this clade in many analyses. The findings of these sensitivity analyses suggest that the taxonomic scheme listed in Duellman (1993) is erroneous regarding the rank of these taxa relative to the Ranidae. Neither of these taxa should be regarded as separate families, unless the Ranidae itself is redefined, possibly similar to the scheme presented

in Frost (2002). Even in this case, justification as to why they should be regarded as separate ranked groups, when they are clearly one lineage, must be presented.

The two included exemplar rhacophorids, *Chiromantis* and *Philautus*, were found to be sister taxa by all analyses, although the two included exemplar mantellids were not (Figs 18, 20H). This was predominantly due to the movement of *Mantella* in concert with the dendrobatids under some extreme weighting, e.g. in four analyses (410G, 441G, 411G, 210G), *Mantella* was found to be the sister to the sooglossids plus dendrobatids, which might be viewed as a spurious result caused by either sampling errors from too few exemplar taxa and specimens thereof, or the convergence of many osteological characters of *Mantella* and the dendrobatids due to the common feeding strategy of microphagy (see Vences *et al.* 1998). A relationship between *Mantella* and the dendrobatids was dismissed by Daly *et al.* (1984, 1996) and Ford (1990). Monophyly of the mantellids was questioned on the basis of morphological data (Daly *et al.* 1996), and has not yet been satisfactorily demonstrated by published molecular studies (e.g. Richards & Moore 1998; Richards *et al.* 2000).

Although a close relationship between the mantellids and the rhacophorids is gaining widespread acceptance, their relationship to other ranid taxa remains to be clarified. The current sensitivity analysis suggests that the Asian genera *Amolops* and *Staurois* are particularly closely related to the mantellids and rhacophorids, as are the petropedetine genera *Petropedetes* and *Arthroleptides*. The placement evident in the equally-weighted topology, whereby *Staurois* falls outside the Ranidae with the mantellids and rhacophorids, is most likely a reflection of its strong affinity with these Asian taxa. The position of the clade outside the Ranidae is probably spurious, given that the genus *Amolops* is strongly affiliated to *Staurois*, and were historically classified in the same genus.

Ford & Cannatella (1993) stated that if the hyperoliids are not the sister group of the rhacophorids, which all present sensitivity analyses demonstrate, then the presence of the intercalary element must be a synapomorphy of the (rhacophorids + mantellids). The presence of wedge-shaped distal intercalary elements (c114:2) is shown here to be a non-unique synapomorphy of these two groups, being found elsewhere only in hyperoliids. Blommers-Schlösser (1993) and Glaw *et al.* (1998) identified two potential synapomorphies of the mantellids: Y-shaped terminal phalanges and the lack of a strong amplexus during mating (Duellman & Trueb 1986). Y-shaped terminal phalanges, qualified by noting the presence of flattened oval flanges on the branches of the arms (c129:4), were found to be uniquely synapomorphic for the (rhacophorids + mantellids), but do not occur in *Staurois*. Weak amplexus (c191:3) has been criticised as a potentially synapomorphic character because it requires more precise definition (Daly *et al.* 1996), but was nevertheless used here and found to be synapomorphic for (rhacophorids + mantellids) by default, due to this character being coded as unknown in *Staurois* and the rhacophorids. Another non-unique synapomorphy for the

(rhacophorids + mantellids) is a shallow hyoglossal sinus (c97:1), a widespread character state. The three remaining synapomorphies supporting this grouping that were identified by the equally-weighted analysis change state in the rhacophorids, *viz*. thick septum nasi (c39:1), changing to thin in the rhacophorids; reduced lateral vomers (c43:1), changing to not reduced and central in the rhacophorids; and alary processes of the premaxilla inclined laterally (c86:1), changing to perpendicular in the rhacophorids. More research needs to be conducted in order to identify morphological synapomorphies of these two groups, which display a strong sister group relationship based predominantly on molecular data.

Raninae

The subfamily Raninae of the Ranidae has long contained most of the problematic taxa that do not fit into any of the other purportedly better defined subfamiles. Dubois (1986, 1992) recently elevated many putative groups to subfamilial status without considering their relationships to one another. The current analysis shows that three of these subfamilies, the Ptychadeninae, Dicroglossinae and Pyxicephalinae, are embedded in the Raninae, rendering it grossly paraphyletic under all parameter sets. Recognition of the subfamily Ptychadeninae was always partly responsible for this, as was recognition of the subfamily Dicroglossinae into which the Pyxicephalinae was often embedded. Paraphyly of the subfamily Raninae was also caused by the consistent placement of *Staurois*, *Amolops*, or both, nearer to the rhacophorid-mantellid lineage, and the placement of *Batrachylodes* nearer to this clade, or to the phrynobatrachids.

One unique synapomorphy was discovered for the subfamily Raninae (including the subfamilies Ptychadeninae, Dicroglossinae and Pyxicephalinae), *viz*. the terminal phalanx of the fourth toe terminates in a small, rounded but narrow, hardened bead (c166:1). However, this character state is obviously absent from specialised arboreal taxa that have developed digital discs (such as *Platymantis*, *Discodeles*, *Amnirana*, *Nannophrys*, *Amolops*), and in the anomalous genus *Strongylopus*. In association with this, the shape of the tips of the terminal phalanx of the third finger being sharply pointed and slightly elongated (c128:2) and the shape of terminal phalanx of the fourth toe being long and sharply pointed (c129:3) occur in most ranids, except in many of the above-mentioned arboreal taxa. A digital pad on the toes, with a circum-marginal groove, is usually absent (c168:1), except in taxa with expanded toe tips. The above synapomorphies can reasonably be regarded as part of the same ecological syndrome. The taxa that did not display these synapomorphic character states include the above-mentioned five taxa. With the exception of *Amnirana*, all of these taxa were placed elsewhere in some sensitivity analyses. The sensitivity analyses indicated that the (*Phrynoglossus* (*Platymantis* + *Discodeles*)) clade may be the basal group of the Ranine clade, and that *Nannophrys* and

Amolops may be related to the petropedetids, rhacophorids and mantellids in a clade outside of the Raninae.

The atlantal intercotylar distance being very narrow, with the cotyls separated by a notch (c0:1), is generally, with few exceptions, consistent in the Raninae. Other synapomorphies include the attachment of the zygapophyses on vertebrae five to eight on the dorsolateral surface, giving a cylindrical appearance to the vertebrae in ventral view (c12:1); a cartilaginous process extending from the crista parotica towards the scapula (c72:1); the flange on the ventral surface of the humerus reversing to around half the length of the humerus (c124:0); the width of half of the eye versus the width of the tympanum in adult males being greater than half, but less than the full, width of eye (c156:1); the first finger being equal in length or extending beyond the second (c161:1); and the presence of a tarsal fold (c172:1), except in sporadic taxa and from node 73 onwards. The latter character occurs elsewhere only in *Leptodactylus*.

Dicroglossinae and Pyxicephalinae

The exemplars of the subfamily Dicroglossinae included in the present analysis (*Conraua*, *Discodeles*, *Euphlyctis*, *Hoplobatrachus*, *Limnonectes*, *Phrynoglossus* and *Platymantis*) were not found to form a monophyletic group under any of the 20 parameter sets investigated. In all analyses, the Dicroglossinae was rendered paraphyletic by either it containing the subfamily Pyxicephalinae, the inclusion of the ranine genera *Nanorana* or *Nannophrys*, or by the position of *Phrynoglossus*, *Platymantis* and *Discodeles* being separated from the remaining genera, usually by many taxa of the subfamily Raninae. In a few cases, other taxa from the ranid subfamily Raninae were responsible for dicroglossine paraphyly. In their work on fanged ranid phylogeny, Emerson & Berrigan (1993) and Emerson *et al.* (2000b) have also demonstrated that phylogenetic relationships in the Digroglossinae contradict the taxonomic classification of Dubois (1986, 1992).

In all cases, the Asian genera *Platymantis* and *Discodeles* were found to be sister taxa. In the majority of cases, the genus *Phrynoglossus* was found to be sister to this couplet. In all but two analyses, the genera *Hoplobatrachus* and *Euphlyctis* were found to be sister taxa. The genera *Pyxicephalus*, *Conraua* and *Aubria* form a monophyletic clade on the equally-weighted tree, as they do on most trees resulting from the sensitivity analysis. No unique synapomorphies were identified for the (Pyxicephalinae + *Conraua*), but four synapomorphies are almost unique. The postchoanal process of the vomer fused to the hyperossified sphenethmoid (c45:3), occurs elsewhere only in *Hoplobatrachus*; the presence of large mandibular odontids (c54:1) occurring elsewhere in *Limnonectes*, *Hoplobatrachus* and *Euphlyctis*; the otic plate of the squamosal overlapping most or all of crista parotica and 1/4 to 1/2 of the otoccipital (c71:1), which is almost unique, occurring elsewhere only in *Limnonectes*; and the crista parotica being mostly ossified (c74:1), which occur elsewhere in *Limnonectes*, *Hoplobatrachus*, *Nanorana*,

Hildebrandtia and *Leptodactylus*. Other synapomorphies of the clade containing *Pyxicephalus*, *Aubria* and *Conraua* include: the extension of ossified anterior portion of the ventral sphenethmoid covering 2/3 or more of the distance from palatines to premaxilla (c38:2); anterior ramus of the pterygoid in contact with or fused to the maxilla (c53:0); height on medial edge of mentomeckelian bone less than that on lateral edges (c55:1); cultriform process of the parasphenoid biconcave (c59:1); the terminal phalanx of the third finger knob-like (c128:1); the terminal phalanx of the fourth toe simple (c129:2); and the proximal row of subarticular tubercles of the feet very small and well-defined, round to conical (c176:2).

The osteology suggests that the 'fanged' ranids (*sensu* Emerson & Ward 1998) of Asia are closely related to the African Pyxicephalinae. The subfamily Pyxicephalinae was found by the sensitivity analyses to be closely related to the genera *Conraua* and *Limnonectes*, and possibly also (*Hoplobatrachus* + *Euphlyctis*) and *Nanorana*. The Pyxicephalinae also displays sexual dimorphism, male territoriality and parental care, bony odontids on the lower jaw and have enlarged heads, as noted by Emerson & Ward (1998) and Emerson *et al.* (2000b) to be characteristic of the southeast Asian fanged ranids. Emerson *et al.* (2000b:136) state that their 'molecular analysis fully supports the finding from the previous morphological study [Emerson & Berrigan 1993] that the fanged frogs consitute a monophyletic group'. However, the sampling of Emerson & Berrigan (1993) and Emerson *et al.* (2000b) was insufficient to demonstrate this with respect to the above-mentioned African taxa. Similarly, Kosuch *et al.* (2001) retrieved a sister genus relationship between *Conraua* and *Limnonectes* in their Neighbour Joining analysis of 16S, and a sister genus relationship between *Pyxicephalus* and *Limnonectes* in a combined Neigbour Joining analysis of 16S and 12S, but still advocate intercontinental dispersal to explain the distribution of *Hoplobatrachus*. The current study suggests that a monophyletic clade of 'fanged' ranids (*sensu* Emerson & Ward 1998) exists, but that it should include the African fanged ranids. The rank of this clade remains to be determined, but it would probably take its name from the genus *Pyxicephalus*, depending on its final content. The fanged ranids may or may not contain the genus *Phrynoglossus* (previously in *Occidozyga*), which appears to be more closely related to (*Platymantis* + *Discodeles*).

Ptychadeninae

The monophyly of the Ptychadeninae, i.e. (*Hildebrandtia* + *Ptychadena*), is strongly supported and was retrieved by all sensitivity analyses (Fig. 18). A high degree of confidence can be placed in the validity of this clade (Bogart & Tandy 1981; Clarke 1981), which probably includes the genus *Lanzarana* Clarke, 1983. There are at least four unique non-homoplastic morphological synapomorphies of the Ptychadeninae. These include fused eighth presacral and sacral vertebrae (c8:1); the clavicles descending and fused to the coracoids (c26:2); the anterior ramus of pterygoid being long and curving medially away from the maxilla (c61:2); and the

sensitivity analyses refuted Blommers-Schlösser's (1993) transferral of *Nannophrys* to the 'Cacosterninae'. The true affinities of *Nannophrys* remain to be determined in a larger analysis.

Tomopterninae

Clarke's (1981) osteological study on the African Raninae found *Tomopterna* to be isolated within the 'Raninae' as he had treated it. The main character on which this was based was the presence of a spike-like ilial process, combined with the lack of ilial flanges, which obfuscates the coding of the former character. In Clarke's analysis, the monophyly of the traditionally defined Raninae was not questioned, and thus *Tomopterna* was found to be outside of the main clade of Raninae. Clarke's findings were subsequently taken by Dubois (1992) as justification to raise a new subfamily of the Ranidae, the Tomopterninae, again without considering the possibility that the genus may be more closely related to ranids outside Clarke's Raninae. Two unique synapomorphies were identified for the Tomopterninae, *viz.* the neural spine of the first and second presacral vertebrae overlapping but not fused (c2:2), and a free flange or projection present centrally, facing towards the jaw (c90:1). Other synapomorphies occurring in only a few other taxa include: a heart-shaped frontoparietal arrangement (c77:3), which occurs elsewhere only in *Nanorana*; the posterior of the frontoparietals being wider than the anterior (c78:2), which occurs in some cacosternids, microhylids and a few other taxa; and the toes unwebbed but flanged the entire length (c159:1), which occurs elsewhere in *Cacosternum*, *Hemisus* and *Leptodactylus*. The equally-weighted hypothesis identified fourteen additional synapomorphies for *Tomopterna* (see Appendix 8).

The subfamily Tomopterninae, as erected by Dubois (1986), was recently demonstrated to be paraphyletic (Vences 1999; Vences *et al.* 2000a), its only genus, *Tomopterna*, being found to comprise three distinct clades which are now regarded as separate genera. The Indian genus (*Sphaerotheca*) is related to *Fejervarya*, while the Madagascan genus (*Laliostoma*) is related to *Aglyptodactylus*, and the African genus *Tomopterna* is related to *Cacosternum* (Vences *et al.* 2000a). Recognition of the Tomopterninae thus renders the Dicroglossinae and the rhacophorids or mantellids paraphyletic (the latter depending on the placement of *Aglyptodactylus*–see Blommers-Schlösser & Blanc 1991; Glaw *et al.* 1998; Emerson *et al.* 2000a for discussions of this controversy). The overall similarity of these three genera is due to convergence caused by their burrowing habits, which makes them superficially similar to even the spadefoot toads of the Americas (genus *Scaphiopus* Holbrook, 1836). This may explain why the African members were classified in the burrowing genus *Pyxicephalus* for many years. The sister group relationship of *Tomopterna* to the cacosternids was supported in the current study by both molecular and morphological data. The geographical and ecological range of *Tomopterna*, i.e. its 'arid corridor' distribution (*sensu* van Zinderen Bakker 1967; de Winter 1971; Poynton 1995) and ability to survive in hyperarid ecosystems of southern Africa, are shared with

Cacosternum boettgeri. The strong ecological constraints on its morphology that are maintained by its burrowing habit may be partly responsible for obscuring the relationships of *Tomopterna* for decades.

Petropedetinae

In the only phylogenetic analysis which has included some members of the Petropedetinae, Ford (1990) concluded that the subfamilies Raninae and Petropedetinae were intermingled, rendering both para- or polyphyletic with respect to each other. Familial status was subsequently proposed for the 'Petropedetidae' by Dubois (1992). The premature elevation of this assemblage to familial rank has compounded the problems and confusion evident in ranid taxonomy, because it appears to support this demonstrably paraphyletic assemblage. A rigorous hypothesis of relationship based on synapomorphy should be a prerequisite for rank changes at this taxonomic level. In the current study, a monophyletic 'Petropedetidae' was not retrieved under any of the 20 parameter sets analysed here, which is sufficient to refute its familial status.

An examination of the characters that have been used in the past to justify the grouping of the cacosternids and petropedetids shows that these are either plesiomorphic or plastic features. Some of these are known to be correlated to particular ecological strategies and occur in many different groups of frogs. Examples of these characters are found in Blommers-Schlösser's (1993) analysis of ranid relationships, which utilized 15 characters to determine the relationships among the firmisternal frogs, and seven characters to determine relationships between the Ranidae, Rhacophoridae and Mantellinae[3]. Remarkably, given the paucity of her data, she concluded that the Petropedetinae was paraphyletic, although the analysis that led her to this conclusion was not presented, nor were the exact terminals that she used in each of the two analyses explicitly stated. Blommers-Schlösser (1993) perceived the Cacosterninae as comprising *Cacosternum*, *Microbatrachella, Anhydrophryne, Nothophryne, Arthroleptella* and the Sri Lankan ranid *Nannophrys*. This corresponds to a group of taxa which possess dilated sacral diapophyses and reduced ossification of the omosternum and procoracoid-clavicular bar. Dilated sacral diapophyses display many subtley diverse forms (Emerson 1979, the present study c20–22) and occur in many Neobatrachian groups (Lynch 1973). The character of dilated sacral diapophyses has in the past been used to incorrectly ally the cacosternids with the microhylids (Noble 1931). Reduction in ossification of the omosternum and procoracoid-clavicular bar is known to be correlated to small size (Trueb 1973) and again occurs in many disparate ranids. Hence, both of these characters are widespread and cannot be used in isolation to determine the contents of the Cacosterninae with respect to the Asian taxa that she mentions.

[3] These numbers exclude the binary characters in which one state occurred only in a single taxon included in the analysis (autapomorphies).

Blommers-Schlösser's (1993) concept of the Petropedetinae consists of the genera *Arthroleptides*, *Dimorphognathus*, *Natalobatrachus*, *Petropedetes*, *Phrynobatrachus* (in part, but which part is not stated), *Phrynodon* as well as some assorted Asian genera (*Staurois*, *Batrachylodes*, *Palmatorappia*, *Platymantis*, *Ceratobatrachus*, *Discodeles*, and tentatively *Micrixalus*, *Occidozyga* [including *Phrynoglossus*?] and *Elachyglossa* Andersson, 1916). This was based on the plesiomorphic character state of widely-separated atlantal cotyls, and two derived (and correlated) characters of T-shaped terminal phalanges and expanded digital pads with circum-marginal grooves. The latter is well-known to be correlated with an arboreal habit (Trueb 1973), and is always supported by bifurcated terminal phalanges. Blommers-Schlösser's (1993) criterion for inclusion in the Petropedetinae was thus essentially the presence of expanded digital discs, which may explain how she managed to divide a cohesive monophyletic genus like *Phrynobatrachus* into two parts, which she subsequently placed in different subfamilies of the Ranidae.

The tendency towards terrestrial breeding evident in some petropedetine genera is, in reality, a suite of characters manifesting themselves at various levels of specialization. Although these characters were not examined in the current study, they are unlikely to be synapomorphic at the level of the Petropedetinae, given the diversity of breeding strategies employed by the taxa concerned. Egg-laying out of water is a common anti-predation strategy, while guarding of egg clutches by parents is similarly widespread and probably linked to desiccation avoidance once the former strategy is employed (Amiet 1981). These strategies appear to have evolved many times in many disparate anuran lineages, and many prominent authors (Orton 1957; Laurent 1961; Lynch 1973; Inger 1996) have expressed doubts regarding the overriding emphasis placed in the past on specialised life histories in determining anuran relationships. The femoral glands and medial lingual process alluded to by Parker (1935) are widespread in the Ranoidea (Grant *et al.* 1997; Glaw *et al.* 2000), although absent in many taxa considered to belong to the Petropedetinae. The absence of vomerine teeth is a condition known to occur sporadically in many ranids (Lynch 1973), and is not a defining feature of the Petropedetinae. This condition does not occur in the type genus, *Petropedetes* (Noble 1931), and can vary intragenerically, e.g. in *Tomopterna* (the present study).

The sensitivity analyses conducted here recognize three separate monophyletic clades of genera formerly included in the Petropedetinae, which are referred to hereafter simply as the cacosternids, the petropedetids and the phrynobatrachids, as the appropriate rank for these clades cannot be determined until a considerably more detailed knowledge of ranid relationships is attained. These three clades do not appear to be closely related, and as such, further references to this 'subfamily' or 'family' are avoided. However, the sensitivity analyses seem to support the notion of the cacosternids and phrynobatrachids being closely related, if not a monophylum due to the possible inclusion in this clade of the genera *Tomopterna* and *Batrachylodes*. While

the affinites of *Tomopterna* are clearly with the cacosternids, the true affinities of *Batrachylodes* remain obscure as this taxon consistently displaced around the tree under different analysis parameters. This may be due to poor sampling of the taxa to which it is likely to be related, such as *Micrixalus*, *Indirana* or the Ranixalinae, but the possibility of *Batrachylodes* being related to petropedetids or phrynobatrachids cannot be dismissed at present.

The equally-weighted tree suggests that the cacosternids and phrynobatrachids are sister taxa, but does not identify any unique synapomorphies supporting this grouping. The following character states were identified as non-unique synapomorphies: neural spines on vertebrae two to four absent (c7:0); posterior process of the vomer absent (46:1), which is not consistent within the clade; short gap or slight overlap between the anterior border of the parasphenoid ala and the medial ramus of pterygoid in the anterior to posterior plane (c64:1); nasals rectangular to round (c70:1); and a shallow hyoglossal sinus (c97:1).

Phrynobatrachids

The group of genera referred to here as the phrynobatrachids (*Phrynobatrachus*, *Natalobatrachus*, *Dimorphognathus* and *Phrynodon*) was consistently retrieved as a monophyletic group except in analyses under two parameter sets where it was unresolved but consistent with monophyly (Figs 19, 20K). Chevron-shaped glands in the scapular region (c189:1) are a unique synapomorphy of the phrynobatrachids, although these are absent in two species. A small round heel tubercle (c175:1) is almost unique, occurring in *Mantidactylus* and in one species of *Tomopterna*. The phrynobatrachids also display a large indel in their 16S sequences between bp positions 60–79 on the alignment presented in Appendix 4. Other non-unique synapomorphies of the phrynobatrachids include expansion of anterior 1/4 of the pars palatina of the maxilla equalling the expansion of the posterior 1/4 in width (c51:0), transforming within the genus to state 1; the alary process of the premaxilla inclined laterally away from the midline (c86:1); and nuptial pads in breeding males being present on finger one only (c142:1).

Phrynobatrachus contains approximately 65 species, 15 of which are known only from the type localities, many of which may not be valid. Some indication of the diversity of *Phrynobatrachus* is obtained from evidence that at least three different chromosome numbers were found in the genus when six different species were examined (Bogart & Tandy 1981), while at least two different carpal arrangements (Laurent & Fabrezi 1989) and two distinct morphologies of the medial lingual process (Grant *et al.* 1997) are present in the genus. The inclusion of only seven *Phrynobatrachus* species here nevertheless demonstrated a remarkably tight cohesion of the members of this genus on morphological grounds. The monophyly of *Phrynobatrachus* is compromised only by recognition of the genus *Dimorphognathus*, which is deeply nested inside the former, justifying the synynomy of *Dimorphognathus* with

Phrynobatrachus. Within *Phrynobatrachus*, *Dimorphognathus* is closely related to *P. natalensis* and *P. acridoides*, which all have 18 chromosomes (Bogart & Tandy 1981). All sensitivity analyses demonstrated *Phrynobatrachus dendrobates* and *P. versicolor* to be sister taxa within this taxon set.

Although embedded within *Phrynobatrachus* in the equally-weighted hypothesis, *Phrynodon* was usually found to be the sister to *Phrynobatrachus* in the sensitivity analyses, with *Natalobatrachus* always basal to the entire phrynobatrachine clade. The latter genus lacks many of the important features of *Phrynobatrachus*, hence it may be most appropriately considered as a valid monotypic genus. A recent paper on a new reproductive mode in *Phrynobatrachus alticola* (Rödel & Ernst 2002) demonstrates that the reproductive mode of *Phrynodon* is not unique, but is rather probably synapomorphic for these two taxa. Due to the lack of convincing differences between *Phrynodon* and *Phrynobatrachus*, and due to the size of the *Phrynobatrachus* lineage, *Phrynodon* is probably congeneric with *Phrynobatrachus*. The action of synynomising the monotypic genera *Dimorphognathus* and *Phrynodon* with the genus *Phrynobatrachus* will ensure that future studies of the phrynobatrachids will examine these two taxa, and not disregard them as is often the case in modern revisions. *Phrynobatrachus* is in need of a thorough revision, probably more so than any other African ranid genus. This revision will need to incorporate data from conventional morphological sources as well as data from life history, behaviour, advertisement calls and gene sequences, in order to adequately address the question. Such a revision may indicate the need to split the genus *Phrynobatrachus*, in which case *Dimorphognathus* and *Phrynodon* would be available names, but are unlikely to remain monotypic.

Cacosternids

The genera *Poyntonia*, *Ericabatrachus*, *Nothophryne*, *Microbatrachella*, *Cacosternum* and the terrestrial breeding *Anhydrophryne* and *Arthroleptella*, are referred to here as the cacosternids. The present analyses do not support Poynton's (1964:137) view that the cacosternids are derived from 'a primitive *Phrynobatrachus* stock', but rather suggest that both lineages may be in the same clade, along with at least *Tomopterna*, and possibly *Batrachylodes*. The sensitivity analyses indicate that the cacosternids are possibly more basal than the phrynobatrachids and may even be the most basal clade of the broadly defined Ranidae (*sensu* Dubois 1986). The analyses refute Loveridge's (1957) synynomy of *Microbatrachella* with *Phrynobatrachus*, which was nevertheless rejected by subsequent workers, for example Poynton (1964), who argued that this synynomy was inadmissable on sternal characteristics alone.

The equally-weighted topology does not support Poynton's (1964) view of two separate lineages in the cacosternids, *viz*. the *Arthrolepella–Anhydrophryne* lineage and the *Cacosternum–Microbatrachella* lineage, although the majority of sensitivity analyses did (Fig.

19). Poynton (1964) hypothesized that *Arthroleptella* is the sister genus of the monotypic *Anhydrophryne* on the basis of breeding system and similarly reduced shoulder girdle architecture. The current analyses confirm this, but also indicate that *Arthroleptella hewitti* is the sister taxon of *Anhydrophryne*, and further suggests that it should be transferred to *Anhydrophryne* in order to preserve the monophyly of *Arthroleptella*.

The equally-weighted analysis placed *Nothophryne* as the sister genus of *Cacosternum*, although the sensitivity analyses favoured a reversal of the positions of *Nothophryne* and *Microbatrachella*. *Cacosternum* was in all cases found to represent the most derived genus of the cacosternids. *Poyntonia* was postulated to be closely related to *Cacosternum* and *Microbatrachella* (Channing & Boycott 1989), although some of the sensitivity analyses (including the equally-weighted analysis) indicated that *Ericabatrachus* is the sister of *Poyntonia*. However, most sensitivity analyses displayed a pectinate relationship with *Poyntonia* basal to *Ericabatrachus* and the rest of the cacosternids. These results are difficult to explain on biogeographic grounds. *Poyntonia* (extreme southwestern regions of South Africa), *Nothophryne* (Malawi) and *Ericabatrachus* (Ethiopia) appear to be distributed along Afro-montane forest relicts. It is plausible that many other, now extinct, taxa once existed in this lineage, which may have bridged the morphological disparities between the extant taxa. Absence of intermediate taxa from the analyses may be frustrating any attempt to retrieve relationships of these three taxa relative to one another. The lack of molecular data from both *Ericabatrachus* and *Nothophryne* might also be partly responsible.

The cacosternids are defined by one unique synapomorphy, *viz.* the clavicles narrowing sharply and being unossified towards the medial edge of the coracoids (c23:1). However, they are also supported by a further five synapomorphies that occur only in a few other taxa. These include a reversal to short transverse processes of the eighth vertebra (c3:0), which occurs in some microhylids and *Heleophryne*; the lateral edge of the pars palatina of the premaxilla slanting outwards and being longer and thicker (c50:3), occuring elsewhere only in rhacophorids and *Phrynoglossus*, but reverses in *Cacosternum*, *Nothophryne* and *Ericabatrachus*; the otic plate being a thin rib of bone overlapping the side of the crista parotica only (c71:2), which occurs elsewhere in *Ptychadena* and *Nanorana*; testes with black pigment (c141:1), occurring elsewhere only in *Ptychadena*, some dendrobatids and *Phrynobatrachus natalensis*; and two subarticular tubercles present on the third finger (c180:1), which occurs in the sooglossids and *Afrana angolensis*, and reverses in *Cacosternum*. Non-unique synapomorphies of the cacosternids include: distal ends of sacral diapophyses distinctly flattened (c21:0); anterior margin of sacral diapophyses angled transversely (c22:1); nasals not overlapping the sphenethmoid (c68:1); pars fascialis of the maxilla reduced anteriorly and triangular (c81:1); terminal phalanx of third finger knob-like (c128:1); terminal phalanx of fourth toe simple (c129:2); and toe tips without a circum-marginal groove (c168:1). The

presence of a similar os sesamoides tarsale in the sooglossids and certain cacosternids (*Cacosternum*, *Ericabatrachus* and *Arthroleptella*), is indicated by the equally-weighted phylogenetic hypothesis to have been acquired independently in each of these four taxa. Similar protective requirements of the ankle joint in small frogs probably facilitated the evolution of similar morphology in this sesamoid.

The sensitivity analyses leave little doubt that the recently described Ethiopian genus *Ericabatrachus* is closely related to the cacosternids, not the petropedetids as assumed by some workers on the basis of the presence of dorsal digital scutes (M. Klemens, personal communication). According to all interpretations, *Ericabatrachus* is a peculiar genus. The most notable external feature of the genus is a reduction in the first finger relative to the second finger, which occurs sporadically in certain microhylids, ranids and leptodactylids (Wu 1994; Myers & Ford 1986; Brown *et al.* 1997). However, *Ericabatrachus* displays novel character combinations intermediate between the cacosternids and the basal ranoids. In many of the sensitivity analyses, this genus may have contributed to the cacosternids occuring in a basal position in the Ranidae. On the equally weighted trees, 22 apomorphic state changes are postulated for the branch leading to *Ericabatrachus*. Eight of these are reversals to the plesiomorphic state and include: the transverse processes of the eighth vertebrae orientated laterally (c4:0); centrum of eighth vertebra procoelous (c13:0); undilated medial edges of the coracoids (c29:0); posterior margin of coracoid straight (c30:0); metasternum cartilaginous (c33:0); medial branch of anterior process of hyale long, straight and thin (c91:0); alary processes of hyoid angled anteriorly (c96:0); and toes with a ventral circum-marginal groove (c168:0). Fourteen other apomorphies exist for this taxon. In one instance, under extreme weighting of the morphology (411C), *Ericabatrachus* displayed a sister relationship to the sooglossids, next to the dendrobatids. The above-mentioned character states were most likely responsible for the exclusion of *Ericabatrachus* from the Ranidae in this particular analysis, as happened frequently when the morphological data alone were subject to analysis under implied weighting (not presented here), where these characters were obviously deemed to be amongst the most consistent and therefore received disproportionately greater weights than the other characters.

Petropedetids

The genera *Petropedetes* and *Arthroleptides* were found to form a monophyletic clade in the vast majority of analyses. Regardless of the relationship of the cacosternids to the phrynobatrachids, which may or may not be sister taxa, the petropedetids are isolated from both of these clades, rendering the subfamily 'Petropedetinae', as currently defined, paraphyletic. The petropedetids were found by the equally-weighted analysis to be closely related to the Raninae, and by the sensitivity analyses to the *Amolops* and mantellid–rhacophorid lineage, but

no analysis showed them to be closely related to the cacosternids or phrynobatrachids. The species of *Amolops* examined here clearly has a similar rupicolous and riparian ecology to that of the petropedetids. However, this is supported by many internal osteological features, and this similarity appears to be due to common ancestry, not convergence (*cf.* Bossuyt & Milinkovitch 2000).

One non-unique character of the petropedetids, *viz.* the presence of dorsal digital scutes (c160:1), is rare in the ranids and occurs elsewhere in this analysis only in *Ericabatrachus* and the dendrobatids. More widespread non-unique synapomorphies of the petropedetids include: dorsal ridge of the coccyx around half the length of coccyx but not reduced (c14:1); pars fascialis of the maxilla reduced anteriorly, strong and triangular (c81:1); thyrohyals more expanded at the proximal ends (c106:0); prehallux small, usually cartilaginous (c121:0); two lateral vocal sacs in breeding males (c150:1); and femoral glands present in the males (c151:1).

Petropedetes natator was found to be the basal member of the petropedetids, which form a homogeneous group. There appears to be no justification for retaining the genus *Arthroleptides*, which is nested in *Petropedetes*, thus rendering it paraphyletic. Nieden may have been unaware of the existence of *Petropedetes* (described by Reichenow in 1874) from West Africa when he described *Arthroleptides* in 1910 from East Africa, because they are more than superficially similar. They share fundamental suites of shared derived characters, such as the metacarpal spike and tympanic papillae in breeding males, and differ, according to Noble (1931), in size and the lack of vomerine teeth in *Arthroleptides*. Geographical disjunction alone is insufficient to uphold the validity of *Arthroleptides* in the face of this evidence, and this genus should therefore be synynomised with *Petropedetes*.

On Contemporary Biogeographical Scenarios

Taxonomic confusion in the family Ranidae has impeded progress in elucidating the biogeographic history of the group. Darlington (1957) suggested that the ranids originated in the Old World tropics, based on their contemporary distribution and in the absence of plate tectonic theory. Africa was traditionally assumed to be the site of the major ranid radiation, since their greatest diversity was perceived to occur there (Noble 1931; Savage 1973; Bogart & Tandy 1981; Duellman & Trueb 1986). However, the erection of a plethora of taxa from the Asian region is now challenging the notion that Africa has the greatest diversity of ranid frogs (Dubois 1992). It has been debated as to whether the Ranidae originated prior to the breakup of Gondwanaland, as suggested by the work of Darlington (1957), or on continental Africa, as suggested by Savage (1973). Recently, Bossuyt & Milinkovitch (2000) presented a molecular phylogenetic hypothesis of the Ranoidea based on 28 taxa, 20 of which were in 8 genera. On the basis of this, Bossuyt & Milinkovitch (2001) came to a novel biogeographic conclusion that the

'Raninae' and 'Dicroglossinae' lineages originated on the drifting insular block of India. Similarly, Kosuch *et al.* (2001) presented a molecular phylogeny based on 34 taxa in 20 genera. Kosuch *et al.* (2001) argue for an Asian origin of the genus *Hoplobatrachus*, and speculate that the ancestors of the African species, *Hoplobatrachus occipitalis*, must have reached Africa via dispersal. Bossuyt & Milinkovitch (2001) postulate that only a limited number of ranine frogs 'reached' Africa, e.g. *Hoplobatrachus*. Kosuch *et al.* (2001) additionally postulate that there was more or less parallel intercontinental dispersal of several anuran groups between Africa and Asia in the Neogene, possibly via contact between the Arabian Peninsula.

Despite the poor sampling of both the dicroglossine and ranine lineages in the current study, both are shown here to be grossly paraphyletic. Bossuyt & Milinkovitch's (2001) phylogenetic hypothesis failed to detect the close relationship of the fanged African ranids (*Pyxicephalus*, *Aubria*, *Conraua*) to the Asian fanged ranids (*Limnonectes*, *Phrynoglossus*), whereas Kosuch *et al.*'s (2001) analysis did, but they did not discuss it. Kosuch *et al.* (2001) acknowledge that a number of lineages comprise taxa present in Africa and Asia, e.g. the African *Amnirana–Hydrophylax* and Asian *Hylarana* clade, and the rhacophorids. They note that in several published molecular studies (not referenced by them), African and Asian ranid lineages were grouped at basal positions of the tree. However, they nevertheless still present the hypothesis that the fanged ranid clade dispersed into Africa from Asia. The studies of Bossuyt & Milinkovitch (2001) and Kosuch *et al.* (2001) present poorly sampled phylogenies that do not adequately test their assumptions. Both of the above-mentioned studies do not question the validity of the current classification scheme (*sensu* Dubois 1986, 1992) of the Ranidae and present similar lines of argument, which are accordingly discussed together below.

Bossuyt & Milinkovitch (2001) and Kosuch *et al.* (2001) present biogeographical hypotheses that rely heavily on dispersal to explain data that do not fit their hypotheses, thereby negating the need to consider alternative explanations, notably that of a Gondwanan origin. Clearly, Bossuyt & Milinkovitch (2001) subscribe to a centre-of-origin paradigm. Bossuyt & Milinkovitch (2001) state that it would require six dispersal events to be consistent with an African origin, but if it is assumed that the Ranixalinae is a derived, purely Indo-Asian lineage that evolved subsequent to the events in question (which includes three of their putative lineages), and that the dicroglossines are embedded in the Raninae, this number is reduced to only two 'lineages'.

Kosuch *et al.* (2001) also argue that it is more parsimonious to assume an Asian origin of *Hoplobatrachus*, because this would require one dispersal event (the *H. occipitalis* ancestor into Africa) than to assume an African origin. The latter is stated to require three dispersal events, *viz* one for the ancestor of *Fejervarya*, one for the (*Euphlyctis*+ *Nannophrys*) lineage, and one for the Asian *Hoplobatrachus* ancestor entering Asia. From the phylogeny that they present in Fig. 2, this would be only two for an African origin: one for the ancestor at the node leading to

actually was introduced there, nor is there any evidence that other, now extinct, *Hoplobatrachus* species did not exist on Madagascar in the past.

Thirdly, an African origin of *Hoplobatrachus* is excluded by Kosuch *et al.* (2001) because the low genetic divergence between African and Asian species does not indicate such an ancient divergence. The third point might be valid if one trusts current molecular clock calculations for the genes and the species involved, or even accepts the validity of the molecular clock *per se*. The authors themselves express concern regarding the uncertainties in the application of the different calibrations available, stating that reliable ranid calibrations are currently lacking. They also mention that doubts exist as to whether the ribosomal DNA fragments utilized actually exhibit clock-like behavior. Bossuyt & Milinkovitch (2001) also rely on assumptions of a molecular clock to calculate divergence time of some of the major lineages of frogs of the family Ranidae, not that the content of these are known with any degree of confidence.

Bossuyt & Milinkovitch (2001) present current numbers of species in the 'Raninae' and 'Dicroglossinae' in Africa and Asia as observations congruent with their hypothesis that these lineages dispersed 'out of India'. Kosuch *et al.* (2001:403) follow a similar argument, stating: 'according to Dubois (1992), the largest number of species and subgenera of this section [*Hylarana*] are found in Asia, and an Oriental origin of its African representatives may therefore be taken into consideration', again alluding to the centre-of-origin paradigm. The number of extant species does not conclusively demonstrate anything, apart from the fact that the evolutionary lineages to which these belong, whatever these may be, radiated spectacularly in Asia. This could conceivably have been made possible by the lack of competition from other ecologically equivalent ranoid forms when they arrived from Gondwanaland via the Indian plate. Using raw species numbers to support their conclusions is misleading regardless of the above point, because it is the distribution of higher clades that should be studied, not individual species. In addition, the true numbers of species and lineages in central Africa is unknown, and severely underestimated due to the paucity of systematic study of African frogs. Recent herpetological collecting expeditions are revealing the extent of this underestimation, with for example 55 species being recorded from a single locality in Gabon (Marius Burger and Alan Channing, personal communication).

Bossuyt & Milinkovitch (2001:94) state that the fossil evidence of European *Rana* is consistent with their hypothesis, since 'much older fossils [than the Oligocene] would likely have been found if the lineage originated in Africa or Eurasia'. However, Kosuch *et al.* (2001) claim that Sanchiz (1998) lists the existence of some unpublished data, indicating the possible existence of ranid remains from the Late Cretaceous from Europe. The text of Sanchiz (1998) does not imply that these unknown remains are ranids, and states that they should be considered as indeterminate Neobatrachia until studied further. However, Sanchiz (1998) does note that true ranids are known from the Cenomanian (Cretaceous) period from the Wadi Milk Formation

in Sudan (Werner 1994). Whilst an Eurasian origin of the ranids is implausible, few anuran fossils are known from Africa (Vergnaud-Grazzini 1966; Sanchiz 1998), although the region is rich in them (D. E. van Dijk, personal communication). It should be noted that a lack of fossils does not prove that they do not exist. The paucity of African anuran fossils could be ascribed to limited attention given to anuran paleontology in the region. The antiquity of the ranid lineages is highly relevant, because the 'frog fauna in any existing world land area is determined in complex fashion by the interaction of present and past ecology, geographic accessibility, long-term physiographic events, and the evolutionary history of the familial units' (Savage 1973:396). The more time that has elapsed, the more complex the interaction of these factors is expected to be. Biogeographical hypotheses based on weak phylogenetic analyses, and overly concerned with the current distributions of extant taxa, are unlikely to retrieve this complex history.

The findings of Bossuyt & Milinkovitch (2001) do not contradict the 'out of Africa' scenario developed by Savage (1973). Moreover, there is no need to postulate dispersal as Savage did to explain the distribution of some groups, e.g. the rhacophorids, if a more ancient origin of the Ranidae is assumed that is congruent with a Gondwanan origin. The phylogenies presented here and by Emerson *et al.* (2000a), show that the basal lineages of the Ranoidea are clearly Gondwanan. The current study indicates that the basal lineages of the Ranidae are either African or Asian, and demonstrates that there are taxa in many ranine clades that occur either in Africa or Asia. There is little justification for suggesting that the Raninae evolved in India and dispersed back to Africa, although the Ranixalinae (incorporating *Micrixalus* and *Nyctibatrachus*), is probably an exclusively Indo-Asian lineage. Tempting as it may seem to conclude otherwise, an African or Gondwanan origin of the lineage has not yet been conclusively refuted by any published study.

The conclusions drawn from this study regarding the biogeography of ranid frogs is that we simply do not know enough about the phylogeny of the group to be postulating new theories at present. Reliable, comprehensively sampled and rigorously analyzed phylogenies are a prerequisite before such hypotheses can be truly tested.

CONCLUSIONS AND SUMMARY

The specific questions raised regarding the monophyly and relationships of the primary focus of the present study, the ranid subfamily Petropedetinae, were addressed. The Petropedetinae (*sensu* Frost 1985) or Petropedetidae (*sensu* Dubois 1992) should not be recognized as a single evolutionary lineage, as it comprises three clades that do not form a monophyletic group. Sensitivity analyses indicated that the cacosternids may be the most basal clade of the Ranidae (*sensu* Dubois 1986). The phrynobatrachids are either sister to the cacosternids or the next most basal lineage, and are strongly supported as monophyletic. The cacosternids are more closely related to *Tomopterna* than to the petropedetid lineage. The equally-weighted analysis indicated the petropedetids to be closely related to the Raninae, but by the majority of sensitivity analyses suggested a relationship to the *Amolops* and mantellid–rhacophorid lineage. However, no analysis demonstrated that they are closely related to the cacosternids and phrynobatrachids. Justification for synynomising three genera within these clades was found.

As with many previous studies of the phylogeny of the Ranoidea, the current analyses did not unequivocally resolve the basal relationships between the major clades. The basal cladogenic events within this group are ancient and concealed by tens of millions of years of evolutionary change. Some novel insights into ranoid relationships were nonetheless obtained from the present study. The sensitivity analyses indicated that the sooglossids and dendrobatids may both be 'transitional' families (*sensu* Lynch 1973), intermediate between the superfamilies Bufonoidea and Ranoidea, whose interrelationships are presently unknown. No support was found for a sister group relationship of the dendrobatids with either the phrynobatrachids or the arthroleptids. The microhylids were found to be the basal clade in the Ranoidea, consistent with the notion that they could be placed in a separate super family, the Microhyloidea. The microhylids were found to include the hemisotids and formed a well-supported monophyletic clade. The astylosternids were found to strongly link the arthroleptids to the hyperoliids, which together form one clearly monophyletic lineage. The genus *Leptopelis* is either basal in the hyperoliid lineage or embedded in the astylosternid lineage, and is the single taxon that is primarily responsible for the non-monophyly of these clades in some of the sensitivity analyses.

The present study answered some questions regarding the evolutionary history of the Ranidae, but also served to highlight the deficiencies of our knowledge in this regard. The family Ranidae, *sensu* Dubois (1986), is in need of redefinition, but this can only be accomplished once the evolutionary relationships in this group are known with a greater degree of confidence, to avoid promulgating additional non-monophyletic higher taxon names. Some consensus on the position of the rhacophorids and mantellids is emerging from the present and previous phylogenetic analyses, which indicate that they are sister taxa and are embedded in the Ranidae (*sensu* Dubois 1986). At this point, neither should be recognized at familial rank unless

the Ranidae is completely subdivided. In that case, the rhacophorids and mantellids together should probably be recognized as a single family, which is further justified by the lack of known morphological synapomorphies for the mantellids.

Three recent subfamilies of the Ranidae erected by Dubois (1992) are embedded within each other and the older subfamily Raninae. The monophyletic Pyxicephalinae is nested within the paraphyletic Dicroglossinae, which is nested within the paraphyletic Raninae, which also contains the monophyletic Ptychadeninae. This larger monophyletic clade could in future be redefined and renamed as the true family Ranidae. Following further phylogenetic study, particular taxa demonstrably not part of this lineage might then be removed from the Ranidae and transferred to other families. These may include the Rhacophoridae, Cacosternidae, Polypedetidae, the Ranixalidae, or whatever names may be applicable, leaving the core of the Ranidae as a monophyletic lineage. Within the latter clade, it appears that the fanged Raninae of Africa and Asia (many of the Dicroglossinae and Pyxicephalinae, but also some taxa currently placed in the Raninae, i.e. *Nanorana*), may comprise a single evolutionary lineage. This lineage may be valid at the subfamilial level as the ranid subfamily Pyxicephalinae. However, further analyses, including additional taxa, are required before taxonomic emendations can be undertaken on this group. The new taxonomic framework proposed by Frost (2002) is the closest yet to the above-mentioned redefinition, but it cannot be accepted until the evolutionary relationships of these taxa have been clarified.

In addition, monophyly of many of the genera, or subgenera, of Ranidae remains to be verified, and the classification is likely to remain unstable until this is addressed. The taxonomy of many genera, particularly those formerly included in the genus *Rana*, is in need of review. This must be undertaken from an evolutionary perspective, because the pitfalls of typological classification systems have been amply demonstrated, both in the literature and in the present study. In order to achieve this, future research should avoid the approach whereby taxa from a restricted geographical region or phenetically defined groups are examined in isolation. A comprehensive large-scale phylogeny for the Ranidae, along the lines of the analysis of angiosperm phylogeny conducted by Chase *et al.* (1993), is required. This should include at least two to three species, including the type species, of all ranid genera and subgenera. This is not an impossible goal, given the pace of the accrual of molecular sequence data, particularly through the 'Tree of Life' project. However, molecular data should not be solely relied upon to attain this, and it is imperative that more morphological (organismal) data sources be explored. Organismal data sources, including myology, karyology, visceral anatomy, larval anatomy, and behaviour and ecology, contain new and informative insights into the problem of the evolution of ranid frogs. These data sources would complement the molecular sequence data, and provide essential characters for diagnosis and identification of the taxa. Preliminary molecular findings can be used to improve the sampling in more detailed morphological studies, which would

allow for a more accurate estimate of ranid frog phylogeny to be obtained. The resulting reciprocal illumination possible from combining these data types will result in a clearer definition and knowledge of evolution in the family Ranidae, and the super family Ranoidea. It is hoped that the preliminary estimate of ranid phylogeny presented here, which has concentrated on African taxa and on morphology, will stimulate other research groups to expand and test the data set and to corroborate or refute the conclusions derived from its analysis.

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Appendix 1. Taxa and material examined for morphological data collection, with localities. The type species of genera are identified by the superscript (‡). Stained and cleared specimens are identified by (*), whilst those that were X-rayed are identified by the superscript (†). Depositories for material examined are abbreviated as follows: AC, Alan Channing (Stellenbosch, South Africa); AMNH, American Museum of Natural History (New York, NY); BMNH, The Natural History Museum (London, UK); CAS, California Academy of Sciences (San Francisco, CA); CNC, Cape Department of Nature and Environmental Conservation (Stellenbosch, South Africa); ES, Elizabeth Scott (with TMSA); EVD, Eduard van Dijk (Stellenbosch, South Africa); IRSNB, Institut royal des Sciences naturelles de Belgique (Brussels, Belgium); JPB, Jim P. Bogart (with AC); JV, John Visser (with TMSA); LIVCM, National Museums and Gallerys of Merseyside (Liverpool, UK); MB, Marius Burger (Cape Town, South Africa); NMBA, National Museum (Bloemfontein, South Africa); NMSA, Natal Museum (Pietermaritzburg, South Africa); PEM, Port Elizabeth Museum (Port Elizabeth, South Africa); RAS, R. A. Stevens (with TMSA); SAMC, South African Museum (Cape Town, South Africa); TMSA, Transvaal Museum (Pretoria, South Africa); NMBZ, Natural History Museum of Zimbabwe (Bulawayo, Zimbabwe); UTACV, University of Texas at Arlington (Arlington, TX). Additional acronyms used for molecular samples are MA, Marleen Dupreez (neé Adams); MV, Miguel Vences; LM, Les Minter; RDS, Rafael de Sa. For specimen lots, the number of specimens is listed in brackets after the accession number.

***Afrana angolensis* Bocage, 1866**

Nandi Hills Town, 5 mi. SW of: CAS 152766*. MALAWI: AC 597*. SOUTH AFRICA: KwaZulu Natal: U.C.N.R.: TMSA 51868. Ngotshe Dist, Itala Game Reserve: TMSA 51861, 51863, 51864*. Mpumalanga: Malelane, 10 km W of: AC 1522. North West Province: Marakele National Park: ES 742. UGANDA: CAS 201982*.

***Afrana fuscigula* (Duméril & Bibron, 1841)‡**

SOUTH AFRICA: AC [2, 1*]. Aarbossiesplaat, Albert: TMSA 35763. Western Cape: Bainskloof: CAS-SU 9556*. Baardskeerdersbos, nr Elim: ES 735. De Wet Station, nr Worcester: TMSA 19629*.

***Amnirana albolabris* (Hallowell, 1856)**

CAMEROON: Nguti: TMSA 84176–84177†. EQUATORIAL GUINEA: Luba, Rd S of: CAS 207656†. GHANA: Eastern Region: Kade, agricultural station: CAS 103711-103714. KENYA: Western Province: Kaimosi, Kaimosi Dam: CAS 141603*. UGANDA: Kiizi [Kiiga] River: CAS 204716.

***Amolops ricketti* (Boulenger, 1899)**

CHINA: Fukien Province: Yenping/ Ch'ungan Hsien: AMNH A-28372, A-28373, A-28596, A-28598, A-28601, A-28670, A-28676, A-28680*, A-28681, A-28688, A-28697, A-28701, A-30830, A-328670.

***Anhydrophryne rattrayi* Hewitt, 1919‡**

SOUTH AFRICA: Eastern Cape: Hogsback: ES 550*, 551*, 552–560, NMSA 3497, 3499–3501, PEM 7124*, EVD N50280*, CAS 156431*, 156437*, 156439*, 156440*. Katberg Pass: PEM*. Stutterheim: NMSA 5837 [7].

***Arthroleptella hewitti* FitzSimons, 1947**

SOUTH AFRICA: KwaZulu-Natal: CAS 157024*. Midmar, 23 km from on rd to Bulwer: NMSA 6746–6749. Bannerman Hut Area, Giant's Castle Game Reserve: NMSA 6565*, 6567*, 6570–6575. Between Bulwer and Pietermaritzburg: NMSA 3469, 3473. Between Greyton and Muden: NMSA 3446. Border Forest, nr Kokstad: NMSA 3462, 3464. Bulwer: NMSA 3490. Dargle, Maritzdal: NMSA 6741. Drakensberg, Cathkin Peak: NMSA 6415, 6425 [4]; 6431 [2]. Drakensberg, Champagne Castle: NMSA 1339–1345, 1192 [3, 1*], 1350, 1352, 1391, 1348; CAS 157244*, 3465, 3466. Drakensberg, Giants Castle, nr Injasuti: NMSA 5275. Drakensberg, Langibelele Pass: NMSA 5276. Inhluzane: NMSA 3485, 3486. Karkloof: NMSA 3448, 3449, 6752, 3492, CAS 156518*. Lundys Hill, Umkomaas River: NMSA 1246 [5]. Ngoye Forest: NMSA 993. Nkandla Forest: TMSA 36334*. Pietermaritzburg: NMSA 3442, 3451, 3452, 3454, 3459, 3460, 3467, 3468, 3488.

***Arthroleptella landdrosia* Dawood & Channing 2000**

SOUTH AFRICA: Western Cape: Helderberg: AC 1715*. Landdroskop: MB 1117–1119. Jonkershoek: NMSA 3416–3419.

***Arthroleptella lightfooti* (Boulenger, 1910)‡**

SOUTH AFRICA: Western Cape: JV 4542, ES 164 [5, 3*], NMSA 5798 [7]. Muizenberg Mountains: NMSA 3428, 3431. Table Mountain: NMSA 3423–3426, 3432, 3433, 5268, 5272.

***Arthroleptides martiensseni* Nieden, 1910‡**

TANZANIA: Tanga Region: East Usambaras, Armani, 7 km SE of on the Muheza, tributary of the Zigi River: ES 704*, 723, CAS 168625–168627†, 168628*, 168629–168633†, 168681, 168682, TMSA 84077.

***Arthroleptis stenodactylus* Pfeffer, 1893**

SOUTH AFRICA: Eastern Cape: Weza-Harding: JV 4682. Kwa-Zulu Natal: Southport: TMSA 79814. St. Lucia: ES [8, 2*]. TANZANIA: West Usambaras, Muzambai Forest Reserve: ES 734.

***Arthroleptis variabilis* Matschie, 1893**

MHNG 1040.6*. CAMEROON: Nguti: LM 18, 19. Eastern Province: Boumir Camp: CAS 199162*. DEMOCRATIC REPUBLIC OF CONGO: Haut-Zaïre Province: Ituri Forest, Epula, Lenda Camp: CAS 196108. EQUATORIAL GUINEA: Vicinity of Moka Malabo, along rd cut to Moka rd: CAS 207821, 207822*, 207823–207826. FERNANDO PO: Bioco village area: BMNH 1975.310*, 1975.352*.

***Astylosternus diadematus* Werner, 1898‡**

CAMEROON: Nguti: TMSA 84311*.

***Aubria subsigillata* (Duméril, 1856)‡**

CAMEROON: Yaounda Rd, Douala: CAS 103804. CONGO: Nr Coquilhatville: CAS 113967, 113968. DEMOCRATIC REPUBLIC OF CONGO: Sankuru Province: Lodja Terr, Omaniundu: CAS 145276. GABON: MB. GHANA: Eastern Region: Tafo, Nobi Rd nr Cocoa Research Institute: CAS 144214*, 144215, 146050*.

***Batrachylodes vertebralis* Boulenger, 1887‡**

PAPUA NEW GUINEA: Kunua Coastal area: AMNH A-102866, A-102869–A-102872, A-102874, A-102878*, A-102881, A-71701, A-71727–A-71730, A-71733, A-71735–A-71738, A-71740–A-71744, A-71748, A-71750, A-71751.

***Breviceps rosei* Power, 1926**

SOUTH AFRICA: Western Cape: TMSA 26662–26664. Cape Flats Nature Reserve, nr UWC, Bellville: AC 584*, 586*, 561*.

***Cacosternum boettgeri* (Boulenger, 1882)**

NAMIBIA: Hardap Dam: ES 237*, 24*. SOUTH AFRICA: EVD [8*]. Nylsvlei: ES 173*. Wolweplaat: NMSA 3323–3327. Eastern Cape: Port Elizabeth: NMSA 5248. Umgazi: NMSA 5814 [14]. Free State Province: Glen: NMSA 5820 [2]. Welkom: ES 150*, 152*. Gauteng: Pretoria: NMSA 3305, 3320, 5251. Zebediela, nr, Sunningdale: NMSA 5245–5247. Kwa-Zulu Natal: NMSA 6478, 6479, ES 299*, 315*. Drakensberg, Cathkin Peak: NMSA 840. Drakensberg, Champagne Castle: NMSA 3322. Matatiele: NMSA 3328. Msinga Hide: NMSA 6052. Pietermaritzburg: NMSA 3342, 3343, 5253, 5254. Sithole area: NMSA 7513. Umvumu: NMSA 5255, 5256. Northern Cape: Kimberley: NMSA 267. Limpopo Province: Pietersburg: NMSA 5822 [2]. Western Cape: Pearly Beach: ES 31*, 32*.

***Cacosternum capense* Hewitt, 1926**

SOUTH AFRICA: Western Cape: PEMA 4974*, 4975*, EVD*. Malmesbury, 6 mi N of: CAS 156592*, SAMC 46158. Rosebank: NMSA AM110, SAMC 46162. Between Hopefield and Malmesbury: NMSA 3397. Darling: SAMC 50063. Durbanville: EVD 15079*. Klipheuwel: TMSA 84242. Kraaifontein: EVD 15179*. Mitchell's Plain: SAMC 50073, 50086, 50088, 50099, 50100, 50103. Stellenbosch: AC 791*, CAS-SU 9538*.

***Cacosternum namaquense* Werner, 1910**

SOUTH AFRICA: Northern Cape: NMSA 3395, ES 166*, 167*, 172*. Garies, 20 km S of: CAS 156622*, 156623*. Garies, S of: EVD 50880*. Arakoop: SAMC 46691–46696, TMSA 84308. Grootdoring, Namaqualand: TMSA 35069*. Karragab: NMSA 3394 [3]. Skouerfontein, Richtersveld: SAMC 45015, 45016. Western Cape: Bitterfontein: EVD [3*].

***Cacosternum nanum parvum* Poynton, 1963**
SOUTH AFRICA: NMSA 6426, 7421, 7468–7471. Kwa-Zulu Natal: Bannerman Hut Area, Giant's Castle Game Reserve: NMSA 6576, 6577. Drakensberg Gardens: ES 22*. Drakensberg, Cathedral Peak: NMSA 3317, 3319. Drakensberg, Cathkin Peak: NMSA 748 [8], 749 [9], 6432 [8], 6424 [2]. Drakensberg, Champagne Castle: 919, 1156 [9], 1193 [4], 1357, 5252. Drakensberg, Royal Natal National Park: ES 148*. Drakensberg, Mont-Aux-Sources: NMSA 3321. Mooi River: NMSA 1146, 5339, 5341. Van Reenen: NMSA 3385–3387. Mpumalanga: Barbeton, nr Jambili Forest: NMSA 3388–3393. Blyde River Canyon: LM [6, 2*]. Dullstroom: NMSA 5830 [2]. Sabie: TMSA 84309, ES 237*, NMSA 3384. Limpopo Province: Woodbush: NMSA 5826 [5].

***Cardioglossa leucomystax* (Boulenger, 1903)**
CAMEROON: Lolodorf: CAS 103974–103975. Nguti: LM 17*. South West Province: Korup Reserve: BMNH 1979.515*. CENTRAL AFRICAN REPUBLIC: Confluence of Chinko and Vovodo Rivers, within 10 mi. radius of: CAS 143231. DEMOCRATIC REPUBLIC OF CONGO: Haut-Zaïre Province: Ituri Forest, 1 km W of Epula: CAS 196115, CAS 196118*.

***Chiromantis xerampelina* Peters, 1854**‡
MALAWI: AC 599–600*. SOUTH AFRICA: Hazyview: AC 1517, 1518. Kwa-Zulu Natal: St. Lucia: ES. Limpopo Province: Ben Lavin Nature Reserve: ES 676, 677*, 678, 679.

***Colostethus inguinalis* (Cope, 1868)**
PANAMA: Coclé, El Balle, Río Anton: AMNH A-161112–161114, A-161115*.

***Conraua crassipes* (Buchholz & Peters, 1875)**
CAMEROON: Avundi, 35 km NNW of Ebolowa: CAS 153623, 153624*, 153625. Kribi: 103908–103914, 38858. Yaonda Rd, Douala: CAS 103805, 103806. EQUATORIAL GUINEA: Arena Blanca rd: CAS 207771.

***Conraua goliath* (Boulenger, 1906)**
CAMEROON: Eseka, 8 mi. S of: CAS 103389, 103390. Lukungg River, Bigindi, S Cameroun: CAS 8396. Nyabessan, 157 km SW of Ebolowa: CAS 153620, 153621, 153622*.

***Dendrobates speciosus* O. Schmidt, 1857**
PANAMA: Chiriquí, continental divide above upper Quebrada de Arena: AMNH A-118447*, A-118454*, A-124289, A-124293, A-124296, A-124300, A-124310, A-124318, A-124323, A-124324, A-124326, A-124327, A-124329, A-124337, A-124341, A-124343, A-124346, A-161120, A-161121*, A-161122, A161123.

***Dimorphognathus africanus* (Hallowell, 1857)**‡
CAMEROON: CAS 207783*. Nguti: TMSA 84170–84171. Sangmelima, Foulassi, Ngam: CAS 153801, 153802, 153803*. Eastern Province: Boumir Camp: CAS 199305–199307. EQUATORIAL GUINEA: Luba, 3.6 km by rd N of: CAS 207779–207782.

***Discodeles bufoniformis* (Boulenger, 1884)**
SOLOMON ISLANDS: Matalogu: CAS 109895*. Topanas: CAS 109887–109891.

***Ericabatrachus baleensis* Largen, 1991**‡
ETHIOPIA: Bale: Katcha, 12 km N of: LIVCM 1986.212.363†, 1986.212.368†, 1986.212.380*, 1986.212.381*.

***Euphlyctis cyanophlyctis* (Schneider, 1799)**
PAKISTAN: Hyderabad, 5 mi. W of Mirpur, khas: AMNH A-67570, A-67572, A-67573. Manshera: AMNH A-104985. Punjab Province: Sheikhupura: AMNH A-45826, A-45834*, A-45845, A-45847. SRI LANKA: Western Province: Sinharajah: AMNH A-23984, A-77479–A-77484.

***Heleophryne purcelli* Sclater, 1899**‡
SOUTH AFRICA: PEM A-4*, PEM [3], A-560, A563, A-2092. Bainskloof: PEM A-5057*, EVD N55680*.

***Hemisus marmoratus* (Peters, 1854)**
ES*. SOUTH AFRICA: Ben Lavin Nature Reserve: ES 659–661. Kwa-Zulu Natal: Hazyview: AC 1520. ZIMBABWE: Victoria Falls: TMSA 84095–84098.

***Hildebrandtia ornata* (Peters, 1878)**‡
AC 535† [3]. MALAWI: ES 638*. MOZAMBIQUE: Xiluvo: CAS 154656*, 154657, 154658. SOUTH AFRICA: Kruger National Park, Pafuri: TMSA 26110, 26373. Barberton Dist., f. Helena 406 JU: TMSA 60843. Phalaborwa Dist., f. Ross 55 KU: TMSA 60847. TANZANIA:

Bagamoyo District: CAS 202702, 202703.

***Hoplobatrachus occipitalis* (Günther, 1858)**

CAMEROON: Mouth of Nchit River at confluence with Mbam River, 29 km SSE of Foumbon: CAS 152599. GHANA: Legon, University of Ghana: CAS 135615*. UGANDA: Kampala, stream between Bunga Hill and Kansanga: CAS 202432. Lake Nabagabo, Kayanja marsh: CAS 204600.

***Hydrophylax galamensis* (Duméril & Bibron, 1841)**

KENYA: CAS 183788. Lake Mbaratumu, 1.5 km N Kakayuni: CAS 183789, 183790. Malindi: TMSA 35992. SOMALIA: Lower Juba River, nr Mareri: CAS 151133*. TOGO: Akposso, Aposso Elavagon: CAS 136117.

***Hyperolius viridiflavus* Rapp, 1842**

AC [5*]. SOUTH AFRICA: Eastern Cape: Hluleka Nature Reserve, Wild Coast: ES 118, 119. Madden Dam: ES 112. Nr Cintsa, +- 30 km N of East London: ES 351. Stutterheim: ES 411, 412.

***Kassina senegalensis* (Duméril & Bibron, 1841)‡**

Niangara: AMNH A-9354*. NAMIBIA: Okarara: AC 546. Waterberg Plateau Park: ES*. Klein Hamakari: AC 504, 505, 506. SOUTH AFRICA: KwaZulu-Natal: St. Lucia: ES. Mpumalanga: 10 km W Malelane: AC 1399, 1411.

***Leptodactylon ventrimarmoratus* (Boulenger, 1904)**

CAMEROON: Kala: MNHG 1524.91*, 1524.95*. Mt Kala, Yaounde: CAS 153793, 153794.

***Leptodactylus melanonotus* (Hallowell, 1861)**

MEXICO: Chiapas, Huixtla: AMNH A-160839, A-52268*, A-52270, A-52272.

***Leptopelis vermiculatus* (Boulenger, 1909)**

TANZANIA: East Usambaras, nr Amani Forest Reserve: TMSA 84038, ES 703*, 706, 717*, 718*, 719–721.

***Limnonectes blythii* (Boulenger, 1920)**

MALAYSIA: Sarawak: Mengiong River, Nanga Tekalit Camp: AMNH A-90518, A-90519. 4th Division: Tabau Camp on Sungei Pesu: AMNH A-90520, A-90521, A-90522*, A-90523–A-90525.

***Mannophryne trinitatis* (Garman, 1887)**

TRINIDAD: Northern Range, approximately 8 km airline N Arima: AMNH A-161116, A-161117, A-161118*, A-161119.

***Mantella aurantiaca* Mocquard, 1900**

MADAGASCAR: AMNH A-106561*, A-123695, A-156962–A-156964, A-73447, A-73448.

***Mantidactylus femoralis* (Boulenger, 1882)**

MADAGASCAR: AMNH A-50361*, A-50362. Antsrianana: AMNH A-157116, A-157126.

***Microbatrachella capensis* (Boulenger, 1910)‡**

SOUTH AFRICA: Western Cape: EVD [4*]. Ratelrivier, Aghulus Plain: CNC 6691*, 6692–6697, 6698*. Betty's Bay: ES 154*, 156*. Cape Flats: NMBA 441–446, CAS 154655*, 157015*. Cape Town: NMSA 3299, 3300, ES*, 159*. Faure: NMSA 3330. Kleinmond, nr Hermanus: AC 4000*, CNC 6594–6600, 6601*, 6602, 6603*.

***Nannophrys ceylonensis* Günther, 1869 '1868'‡**

SRI LANKA: AMNH A-23825*. Western Province: Sinharajah: AMNH A-77467–A-77473. Warakapola: AMNH A-74238.

***Nanorana parkeri* (Steneger, 1927)**

TIBET: AMNH A-53178, A-53179*. Tsang Po River at Shigatse: AMNH A-62939–A-62943, A-102782.

***Natalobatrachus bonebergi* Hewitt & Methuen, 1913‡**

SOUTH AFRICA: TMSA 21467, PEMA 4769*, 4848*. Kwa-Zulu Natal: NMSA 3279, 6939. Eshowe Dist, Eshowe: TMSA 22206. Kranskop: TMSA 49971.Vernon Crookes Nature Reserve: TMSA 51798–51800, 51803, ES 546*, 547*, 548, 549. Hillcrest: NMSA 3290, 3291. Ngoye Forest: NMSA 989. Oribi: NMSA 5896, 5900. Eastern Cape: Port St John's: TMSA 21466, NMSA 3292, 3294, 5854*, 5856, 5860, 5861, 5862, 5865, 5866, 5868, 5869.

***Nothophryne broadleyi* Poynton, 1963‡**

MALAWI: AMNH A-95098; Dzole Peak: BMNH 1965.817. Likambula-Chambe: CAS 156126, NMBZ 25273, 25274, 25277, 25278, 25279. Madzeka Basin: NMBZ 25175*, 25176,

25177, 25182, 25183, 25189, 25190, 25195, 25302, CAS 156122*, 156123*, 156124, 156125. Sombani Basin: NMBZ 25143. Tuchila Basin: AMNH A-95099, NMBZ 25286, 25287, 25291, 25293, 25294, CAS 156127. MOZAMBIQUE: Ribaue Mountain: NMBZ 19360, 25179.

***Nyctibates corrugatus* Boulenger, 1904**[‡]

CAMEROON: CAS 155901, 155902, 152526*. Bakaka, Forest Reserve: MNHG 1525.26*, CAS 153797. Nguti: TMSA 84312*.

***Pantherana pipiens* (Schreber, 1782)**[‡]

AMNH A-114359*, A-114360*. CANADA: Dauphin, 11 mi E on Rte 20: AMNH A-125965. Lake Manitoba: AMNH A-96579–A-96582. Ninette: AMNH A-18807–A-18810. Winnepeg: AMNH A-2983, A-5723–A-5733. USA: New York: Cayuga, ca. 1 mi. S of Port Byron: AMNH A-103207. Seneca, N of Waterloo: AMNH A-100505, A-100504, A-114452.

***Petropedetes cameronensis* Reichenow, 1874**[‡]

CAMEROON: Nguti: LM 24. Southwest Province: UTACV A-44398. Kumba, Barombi Mbo Lake: BMNH 1984.377, 1984.38. Manja: UTACV A-35341. Mt. Entali nr Nfainchang: UTACV A-35324, A-35325. Mt. Yuhan: UTACV A-35335. Mundemba, Ikenge Research Camp: UTACV A-35329. Western Region: Victoria, 4 mi E of: BMNH 1969.496*.

***Petropedetes natator* Boulenger, 1905**

LIBERIA: Mount Nimba: AMNH A-83319, A-83320. SIERRA LEONE: Freetown: AMNH A-84615, A-84604–A-84614. Kortright Stream: BMNH 1964.179[†]. Mt. Aureol: BMNH 1961.1248*.

***Petropedetes newtoni* (Bocage, 1895)**

CAMEROON: Lolodorf, 20 mi N of: CAS 103349. Akok, nr Kribi: AMNH A-3138. Bamenda: CAS 125582–125585. Kribi: AMNH A-6687. Kumba, Lake Barombi: CAS 103325, 103326*, 103327. Sak-bayeme: AMNH A-14369. Southwest Province: Mana Bridge control post, Mundemba: UTACV A-35348, A-35350. Mundemba: UTACV A-35352, A-35358, A-35360, A-35362.

***Petropedetes parkeri* Amiet, 1983**

CAMEROON: Eshobi: BMNH 1936.3.4.112 [misidentified as *johnstoni* in cat]. Tinta: BMNH 1936.3.4.126 [misidentified as *johnstoni* in cat]. Nguti: LM [6[†]]. Northwest Province: Anjake Village: UTACV A-44739, A-44740, A-44749, A-44751. Southwest Province: Nyasaso, Mt. Koupé: BMNH 1984.395*. Manafe Division: Eshobi: BMNH 1936.3.4.113 [misidentified as *johnstoni* in cat].

***Phrynoglossus laevis* (Günther, 1858)**

PHILIPPINE ISLANDS: San Juan, Tag-ibo: CAS-SU 16392*, 16395. Iloilo Province: Buaya: CAS 124059–124076. Negros Oriental Province: Ocoy River Valley, 3 km W of Palimpinon: CAS-SU 16275*.

***Philautus surdus* (Peters, 1863)**

PHILIPPINE ISLANDS: CAS 210012. Buena Suerte, 22 Km SE of: CAS-SU 20339, 20342–20343. Kasinganan: CAS 133163, 133199, 133200. Mount Hilonghilong: CAS 182568, 183204. Bohol Province: Cantaub, Sierra bullones: CAS-SU 23343–23345, 23347, 23348, CAS 136862*.

***Phrynobatrachus acridoides* (Cope, 1867)**

SOMALIA: Lower Juba River, nr Mareri: CAS 148377*, 148384*. TANZANIA: Ngorogoro: AMNH A-12667, A-126670, A-12671, A-12673, A-12687, A-12691, A-12696.

***Phrynobatrachus dendrobates* (Boulenger, 1919)**

CAS 180634. DEMOCRATIC REPUBLIC OF CONGO: Ituri Province: Manguerets Hipa: CAS 145294*. UGANDA: CAS 202132–202136. Munyanga Falls Trail: CAS 204736. Ruhizha, Institute for Tropical Research: CAS 202233, 202234, 202236.

***Phrynobatrachus krefftii* Boulenger, 1909**

TANZANIA: Tanga Region: East Usambara Mountains, vicinity of Amani: CAS 168512, 168514*, 168530, 168538*, 168547, 168549, 168550. West Usambara Mountains, Muzambai Forest Reserve: CAS 169380, TMSA 84038, ES 701, 731, 732, 733*, 727, 728*, 729, 730, BMNH 1974.80*.

***Phrynobatrachus natalensis* (Smith, 1849)**[‡]

EVD [2*]. KENYA: Kakamega Forest Station: CAS 141564*. NAMIBIA: Bagani, nr Popa Falls: AC 515. Caprivi Strip, Katima Mulilo: CAS 160639*, 160640*. SOUTH AFRICA:

Winston Park: EVD 13176*. Eastern Cape: Port St. John's: ES 113–115. Kwa-Zulu Natal: Pietermaritzburg: ES 139, 282, 283*, 284, 285, 286–288*, 289.

***Phrynobatrachus plicatus* Günther, 1858**‡

CAMEROON: Nguti: TMSA 84101. GHANA: Eastern Region: Kade, agricultural station: CAS 104017, 104020, 126443–126448, 126451–126454, 136292, 136293, 136294*, 136295–136297, 136298*, 136299–136305. Tafo, Cocoa Research Institute: CAS 141769.

***Phrynobatrachus versicolor* Ahl, 1924**

DEMOCRATIC REPUBLIC OF CONGO: Kivu Province: Kundhuru-ya-Tshuwe: CAS-SU 13008*. UGANDA: Buhoma Rd, 1 km S of forest reserve boundary: CAS 180634. Kasiru North, upper E fork Ntengere River: CAS 202262, 202264, 202266. Munyanga Falls Trail: CAS 204737. Ruhizha, Wolfram Mine: CAS 180612–180627.

***Phrynodon sandersoni* Parker, 1935**‡

CAMEROON: Mt Kala, Yaounde: CAS 153804, 153805. Southwest Province: Dikome Balue between village and Rata Mount: UTACV A-35103, A-35105. Mt. Entali nr Nfainchang: UTACV A-35065, A-35066, A-35068. Mt. Yuhan: UTACV A-35069, A-35071, A-35074, A-35079, A-35080*, A-35085, A-35076. Rumpi Hills trail to Dikone Balue: UTACV A-35125, A-35132, A-35127, A-35129.

***Phrynomantis bifasciatus* (Smith, 1847)**‡

NAMIBIA: Klein Hamakari: AC 554, 555. SOUTH AFRICA: Limpopo Province: Ben Lavin Nature Reserve: ES 668*.

***Platymantis corrugatus* (A. Duméril, 1853)**

PHILIPPINE ISLANDS: CAS 21999*. Cana-as, 27 km NW Bondo, Siaton: CAS-SU 19523. Bohol Province: Sierra Bullones: CAS-SU 21992, 21999–22001, 22022, 22032, 22033, 22136*. Camiguin Province: slopes of Mount Mamajao, 5.5 km NE Catarman Town: CAS-SU 24060.

***Poyntonia paludicola* Channing & Boycott, 1989**‡

SOUTH AFRICA: Western Cape: EVD*. Franschoek: CNC 6605–6608, 6610. Grabouw: CNC 6612, 6636*, 6637, 6643, 6644, 6613, 6635, 6638–6641, 6642*, 6645*, 6646. Stanford: CNC 6622, 6623, 6624, 6625*, 6628–6630, 6677–6683. Steenbras: MB 1253*.

***Ptychadena anchietae* (Bocage, 1867)**‡

SOMALIA: Lower Juba River, nr Mareri: CAS 148187*. SOUTH AFRICA: Wilhaushöhe, Tvl: TMSA 6434. Mpumalanga Province: Skukuza: JPB 140*. Makutswi River: TMSA 6449. Waterfal Onder: TMSA 6476. Limpopo Province: Ben Lavin Nature Reserve: ES 662, 663, 681–686. Broederstroom: TMSA 6811. Leeupoort: TMSA 26049. Nylstroom: TMSA 6468.

***Ptychadena mascarieniensis* (Duméril & Bibron, 1841)**‡

CAMEROON: Nyabessan: Ebolowa, 157 km SW of: CAS 153558–153562. KENYA: Malindi-Mombasa Rd, 3 km S of Watamu junction, 1 km W on dirt rd: CAS 165129. MALAWI: AC 611*, 621*. SOUTH AFRICA: Kwa-Zulu Natal: Ndumu Game Reserve: TMSA 37247. Kosi Bay Estuary: TMSA 67751. Lake Sibaya Research Station: TMSA 46056, 46057. SUDAN: Ilemi Triangle, ca. 1 mi. E of Lokomarinyang: CAS 131481*. ZIMBABWE: Nkuku, Zambezi: JPB 163*, 164*.

***Pyxicephalus adspersus* Tschudi, 1838**‡

CAS [2*]. NAMIBIA: AMNH A-23621. SOUTH AFRICA: Gauteng: Pretoria: TMSA 14981, 83676. Eastern Cape: Aliwal North, 12 km S of: AC 1484.

***Scotobleps gabonicus* Boulenger, 1900**‡

MHNG 1524.78*, 1324.73*. CAMEROON: Yaounde, Otoma, Forest Reserve: CAS 153796. Bipindi: CAS 153579. Kribi: CAS 103918. Nguti: TMSA 84313*.

***Sooglossus sechellensis* (Boettger, 1896)**‡

SEYCHELLES ISLANDS: Morne Seychellois trail: CAS 160084, 160085, BMNH 1906.8.15.6, 1906.8.15.7.

***Staurois natator* (Günther, 1859 1858)**‡

PHILIPPINE ISLANDS: Zamboange: CAS 61901–61935. Bohol Province: Sierra Bullones, 10 km SE: CAS-SU 23364*, 23368*.

***Strongylopus grayii* (Smith, 1849)**

SOUTH AFRICA: Eastern Cape: Hogsback: ES 109*. Weza: ES 125*. Kwa-Zulu Natal: Boston: ES 321, 322. Pietermaritzburg: ES 350. Western Cape: AC*, ES 698.

***Tomopterna marmorata* (Peters, 1854)**

BOTSWANA: Francistown: AMNH A-95118, 95119. KENYA: CAS 130900, 130901, 130904, 130905, 131559. Vicinity of El Wak, nr Manyatta W of fort: CAS 130580. MALAWI: RAS 73/A.5.1.73*. MOCAMBIQUE: Magasso: AMNH A-95116, A-95117.

***Tomopterna tandyi* Channing & Bogart 1996**

NAMIBIA: Grootfontein: AC 1553–1555, 1557–1560, 1561*, 1562, 1563. Hardap irrigation scheme: AC 1171, 1181*, 1568, 1569, 1570*, 1571–1574. SOUTH AFRICA: Eastern Cape: S of Jamestown: ES 182*.

***Trichobatrachus robustus* Boulenger, 1900**‡

CAMEROON: Kribi: CAS 54740. Lolodorf: CAS 38843*, 38844, 38845. Mamfe-Bamende Rd, W or SW of Widekum: CAS 152596.

Appendix 2. Expanded morphological character list, indicating references to previous usage, explanations, where necessary, and optimizations onto the equally-weighted topology. For an abbreviated list of characters and states only, see Table 3. Due to uncertainty surrounding the rank of certain ranoid clades, naming conventions that avoid implications of rank are often used. Primary outgroup = *Heleophryne*; Arthroleptidae = (astylosternids + arthroleptids); arthroleptids = (*Arthroleptis*, *Cardioglossa*); astylosternids = (*Nyctibates*, *Astylosternus*, *Scotobleps*, *Leptodactylon*, *Trichobatrachus*); dendrobatids = (*Dendrobates*, *Colostethus*, *Mannophryne*); hyperoliids = (*Kassina*, *Hyperolius*); microhylids = (*Phrynomantis*, Brevicipitinae); phrynobatrachids = (*Phrynobatrachus*, *Phrynodon*, *Dimophognathus*, *Natalobatrachus*); cacosternids = (*Cacosternum*, *Microbatrachella*, *Nothophryne*, *Ericabatrachus*, *Poyntonia*, *Arthroleptella*, *Anhydrophryne*); petropedetids = (*Petropedetes*, *Arthroleptides*); Ptychadeninae = (*Ptychadena*, *Hildebrandtia*); Tomopterninae = (*Tomopterna*); mantellids = (*Mantella*, *Mantidactylus*); rhacophorids = (*Philautus*, *Chiromantis*).

Spine and pelvis:

0. Atlantal intercotylar distance: (0) widely separated, at least one cotyl width apart (Lynch's type I); (1) juxtaposed but distinct, very narrowly separated by a notch (Lynch's type II).

Previously used by Lynch (1973) 5*, Heyer (1975) 29, Heyer & Liem (1976) 10*, Lynch (1978) 11*, Clarke (1981) 15*, Drewes (1984) 29*, Ford (1990) 10*, Blommers-Schlösser (1993) 23*, Wu (1994) 125*, Glaw, Vences & Böhme (1998) 1, Vences (1999) 5. Recognized as a useful higher level character, commonly used since Lynch (1971). Heyer (1975) suggested that juxtaposed cotyls were primitive. Ford (1990) did not polarise this character. Wu (1994) considered widely separated cotyls to be derived, following Lynch's (1973) arrangement. Trueb (1973) notes that widely separated cotyls characterise many archaic families and primitive members of more modern groups, suggesting that this condition is plesiomorphic. No taxa were seen in this study to exhibit Lynch's type III cervical cotyls (fully confluent without a small gap), in concordance with Trueb's (1973) assertion that type III cotyls are only found in Ceratophryninae leptodactylids and ascaphids. Clarke's (1981) observations of Type III cotyls as the adult state in *Hoplobatrachus occipitalis* were not verified. The one subadult and one adult specimen examined were found to have type II cotyls, in common with the majority of the large Raninae. However, Drewes (1984) observed type III cotyls (although type ii condyles) in two subadults of *Lithobates palmipes* (Spix, 1824), a species not examined here. This suggests that there may be a degree of ontological variation in some ranids. Juxtaposed cotyls are synapomorphic for the clade containing most Raninae (node 55), but reverse sporadically therein, notably synapomorphically for (*Phrynoglossus* (*Discodeles* + *Platymantis*)). Juxtaposition of the cotyls also originates independently in Brevicipitinae, *Astylosternus* and *Scotobleps*.

1. Atlas, neural arches: (0) fused; (1) failing to completely unite, dorsal gap present.

Duellman & Trueb (1986) note that in poorly ossified species (e.g. *Notaden* Günther, 1873) the halves of the neural arch may fail to unite on the anterior vertebrae. D. E. van Dijk (personal

communication), in his work on African anuran fossils from the rich Langebaanweg fossil site near Cape Town, has noticed that many ranid frogs have a furrow on the dorsal surface of the cervical vertebra through which, in extant frogs, a large nuchal ligament passes. State 1 is particularly obvious in *Amnirana*, illustrated in Fig. 1. This feature is coded as state 1 only in taxa in which it is not ossified in the adult, since the possibility exists that some ranid taxa exhibit failure of neural arch fusion as subadults, and that it subsequently fuses upon full maturity. This character is coded as unknown in taxa with fused first and second vertebrae. Fusion of neural arches is seen in *Heleophryne*, thus the unfused condition is considered derived, originating at node 5. It reverses to absent independently in *Mantella*, *Tomopterna marmorata*, *Batrachylodes*, *Natalobatrachus*, *Phrynobatrachus krefftii*, *Amolops*, *Hildebrandtia* and *Ptychadena mascareniensis*, as well as synapomorphically at node 43 for most cacosternids, and at node 38 for (*Phrynobatrachus cricogaster* + *P. plicatus*).

2. First and second presacral vertebrae: (0) normally ossified and separate; (1) neural spine of the first vertebra appears flattened and extends posteriorly, overlapping the anterior portion of the second vertebra to which it is fused, forming a dorsal bone bridge centrally between the first and second vertebrae; (2) neural spine strongly overlaps the second vertebra from the first, but no fusion of the first to the second vertebra occurs.

No taxa were observed to have a separate neural spine and the bridge of state 1, suggesting that it is the neural spine. However, it is also possible that this bridge is composed of the ossified nuchal ligament, and that neural spines are absent in the examined taxa exhibiting the bridge. This character is ambiguous in the outgroup, and was thus not polarized by this analysis. A bone bridge (state 1) is illustrated in Fig. 2, and is synapomorphic at node 52 for the petropedetids excluding *Petropedetes natator*, and again at node 23 for the (rhacophorids + *Staurois*). State 1 also originates independently in *Platymantis*, *Natalobatrachus*, *Arthroleptis variabilis* and *Leptopelis*, and occurs in *Leptodactylus* and some dendrobatids. Overlapping neural spines without fusion (state 2) is a unique synapomorphy for the Tomopterninae, and may be related to strengthening the vertebral column for burrowing.

3. Vertebral column, eighth vertebra, length of transverse processes: (0) much shorter than those of the fourth vertebra; (1) roughly equal in length to those of the fourth vertebra.
Previously used by Lynch (1973) 9*, Heyer (1975) 33*, Heyer & Liem (1976) 11*. Drewes (1984) mentions this in his character 7, and in personal communication. Analogous to Ford (1990) 71. Although Trueb (1977) noted variability in transverse process length in *Hyla lanciformis* (Cope, 1870), Drewes (1984) did not find this variability in the hyperoliids. This character was found to be consistent intraspecifically in the present study. Lynch (1973) and Heyer (1975) considered shorter transverse processes to be plesiomorphic, based on their

distribution amongst primitive families. Drewes (1984) considered equally long transverse processes to be plesiomorphic, based on outgroup comparison with the ranids. In this analysis, the outgroup *Heleophryne purcelli* was noted to have shorter transverse processes (although *H. natalensis* has them equally long) and this state was thus treated as plesiomorphic, with equally long transverse processes originating at the basal node. A reversal to shorter transverse processes occurs in *Hemisus* and the Brevicipitinae, and is synapomorphic for the cacosternids, wherein it reverses synapomorphically for (*Poyntonia* + *Ericabatrachus*) and in *Nothophryne*.

4. Vertebral column, eighth vertebra, orientation of transverse processes in frontal plane: (0) orientated laterally, perpendicular to spine; (1) slight anterolateral orientation, approximately 20° – 30°; (2) acute anterolateral orientation, approximately 45° or more.

Previously used by Drewes (1984) 8, and mentioned by Lynch (1973). Lynch (1973) and Trueb (1973) note that the transverse processes are short and directed strongly anteriorly in most archaic frogs and many transitional frogs. Drewes (1984) considered angled transverse processes to be derived for the hyperoliids, based on outgroup comparison with the ranids. Lynch (1973) did not consider this character discrete from that of the length of the transverse processes, but the distribution of this and the current characters in the cacosternids and petropedetids indicate that they vary independently. Drewes (1984) notes that the condition of the transverse processes is not related to size, but rather to the degree of lateral movement of the spine required by the frog's habit. Slightly anteriorly orientated processes (state 1) are synapomorphic for (*Hyperolius* + *Kassina*), for the Ptychadeninae and for the (cacosternids + phrynobatrachids), and occur sporadically in some other individual taxa. Acutely anterolaterally orientated transverse processes (state 2) occur in *Cacosternum* and *Microbatrachella*, and in some microhylids.

5. Vertebral column, shape in dorsal view of posterior four vertebrae: (0) square, minimal space between vertebrae; (1) rectangular, gap between vertebrae greater than half their width.

Previously used by Lynch (1973) 10*, Lynch (1978) 12 *, Drewes (1984) 6*, Ford (1990) 72*, Wu (1994) 136*. Lynch (1973, 1978) considered the similar character of imbricate vs. non-imbricate vertebrae to largely reflect the degree of ossification, and was sceptical of its usefulness. Trueb (1973) noted that most archaic frogs have imbricate neural arches, suggesting that this is the plesiomorphic condition, which is how Drewes (1984) also interpreted this. Rectangular vertebrae (state 1) are synapomorphic for the Ptychadeninae and under Deltran optimization for the cacosternids, wherein a reversal to square (state 0) is synapomorphic for the species of *Cacosternum*. Rectangular vertebrae also occur independently in many taxa.

Figure 1. Dorsal aspect of skull of *Amnirana albolabris* (CAS 141603) indicating the failure of neural arches to completely unite, leading to a dorsal gap in the atlas (c1:1), and a long cartilaginous process extending off the crista parotica towards the scapula (c72:0 and c73:1). Scale bar = 1 mm

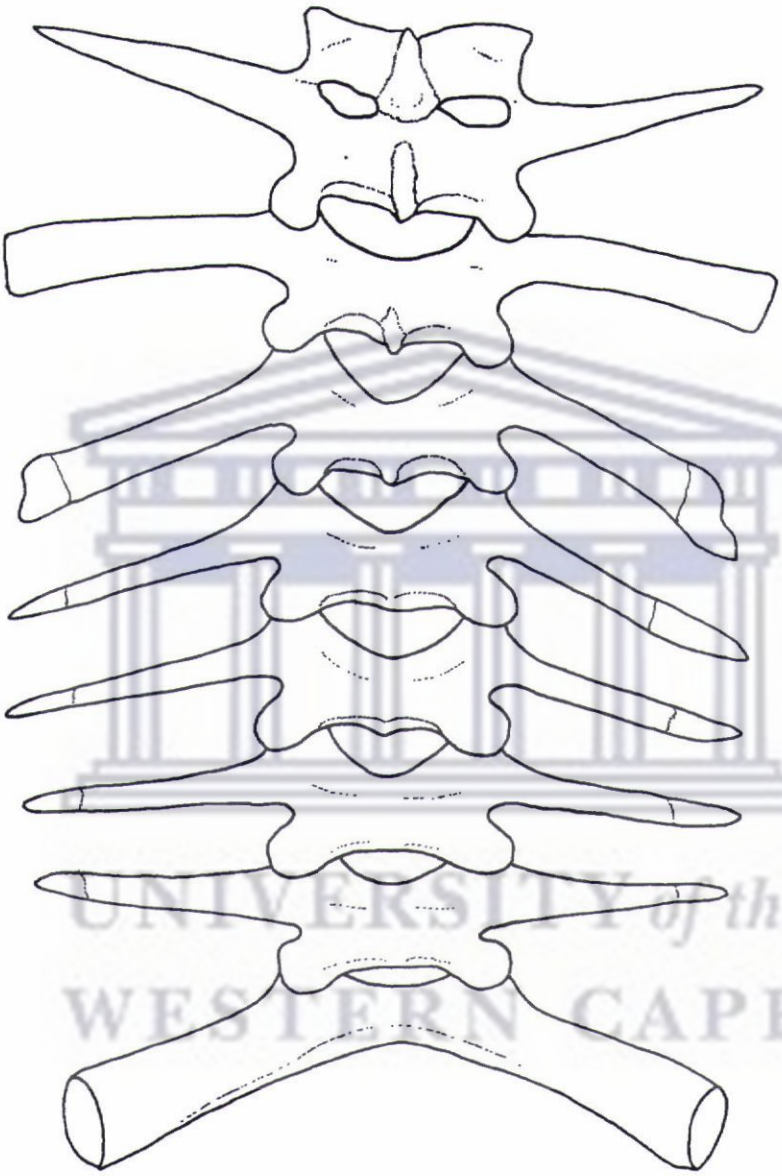

Figure 2. Dorsal view of the vertebral column of *Petropedetes parkeri* (BMNH 1936.3.4.113) showing the bone bridge between the first and second vertebrae (c2:1). Scale bar = 1 mm.

6. Vertebral column, dorsal view of posterior four vertebrae, margins: (0) very strong V-shaped indent in anterior margin, reaching approximately half of the vertebral width; (1) anterior and posterior margins parallel, no large indent.

This character could not be determined for many of the larger Raninae due to insufficient clearing of the connective tissue associated with the spine (fascia dorsalis of Gaupp 1896). Parallel margins occur in the dendrobatids, cacosternids, phrynobatrachids, petropedetids and most ranines, whereas V-shaped indents occur in the microhylids, arthroleptids and hyperoliids.

7. Neural spines on vertebrae two to four: (0) absent; (1) present; (2) extreme dorsal and posterior development of neural spines which may be totally fused in up to the first four vertebrae.

Previously used by Wu (1994) 133. The separation of the characteristics of imbricate versus non-imbricate vertebrae and the features of the neural spine is here similar to that implemented by Wu (1994). If these characters are combined, it obscures the state determination. The presence of neural spines occurs in most arthroleptids, hyperoliids and ranids, whereas absence of neural spines occurs in most cacosternids, phrynobatrachids and microhylids. Extreme dorsal and posterior development of the neural spines (state 2) is here uniquely synapomorphic for the included species of *Dendrobates*.

8. Fusion of eighth presacral and sacral vertebrae: (0) not fused; (1) fused.

Previously used by Lynch (1973) 3, Heyer & Liem (1976) 9, Clarke (1981) 20, Wu (1994) 139*. The fused condition is considered derived, since the Neobatrachian taxa in this study have a plesiomorphic number of eight presacral vertebrae (Trueb 1973). Fusion is a unique synapomorphy for the Ptychadeninae at node 67, occurring only in *Ptychadena* and *Hildebrandtia*, and according to the original description (Clarke 1982) in *Lanzarana* as well. It is consistent in this group according to Clarke (1981). Two large stained and cleared adult *Pyxicephalus adspersus* (CAS no accession numbers) exhibited what appeared to be fusion, but due to the size of the specimens, clearing of the surrounding tissue was incomplete and visibility was poor. Two smaller subadult individuals of EVD, and the two specimens examined by Clarke (1981) exhibited the unfused condition, as did those examined by Sheil (1999). Single aberrant specimens exhibiting fusion were also seen in *Staurois natator*, *Ericabatrachus baleensis* and *Dendrobates speciosus*. Noble (1922) and Laurent (1940) note that the eighth presacral and sacral vertebrae are reportedly fused in *Cardioglossa elegans* Boulenger, 1905, but this was not seen in any arthroleptids examined.

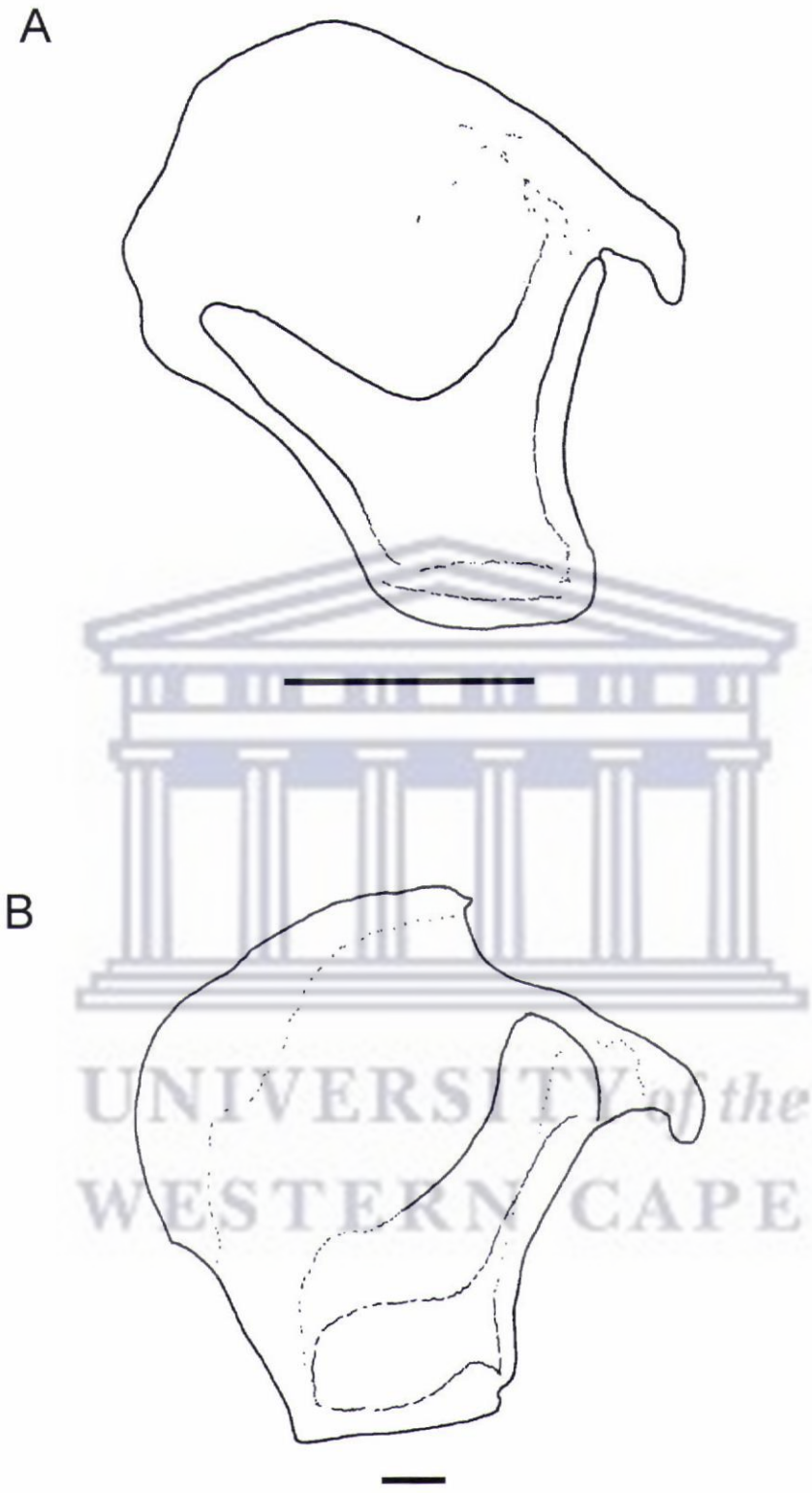

Figure 3. Mineralisation of the suprascapulae. **A.** Y-shaped bony flange (c10:0) of *Cacosternum nanum* (ES 95). **B.** Single rounded, rectangular or triangular bony flange (c10:1) of *Phrynobatrachus krefftii* (CAS 168514). Scale bar = 1 mm.

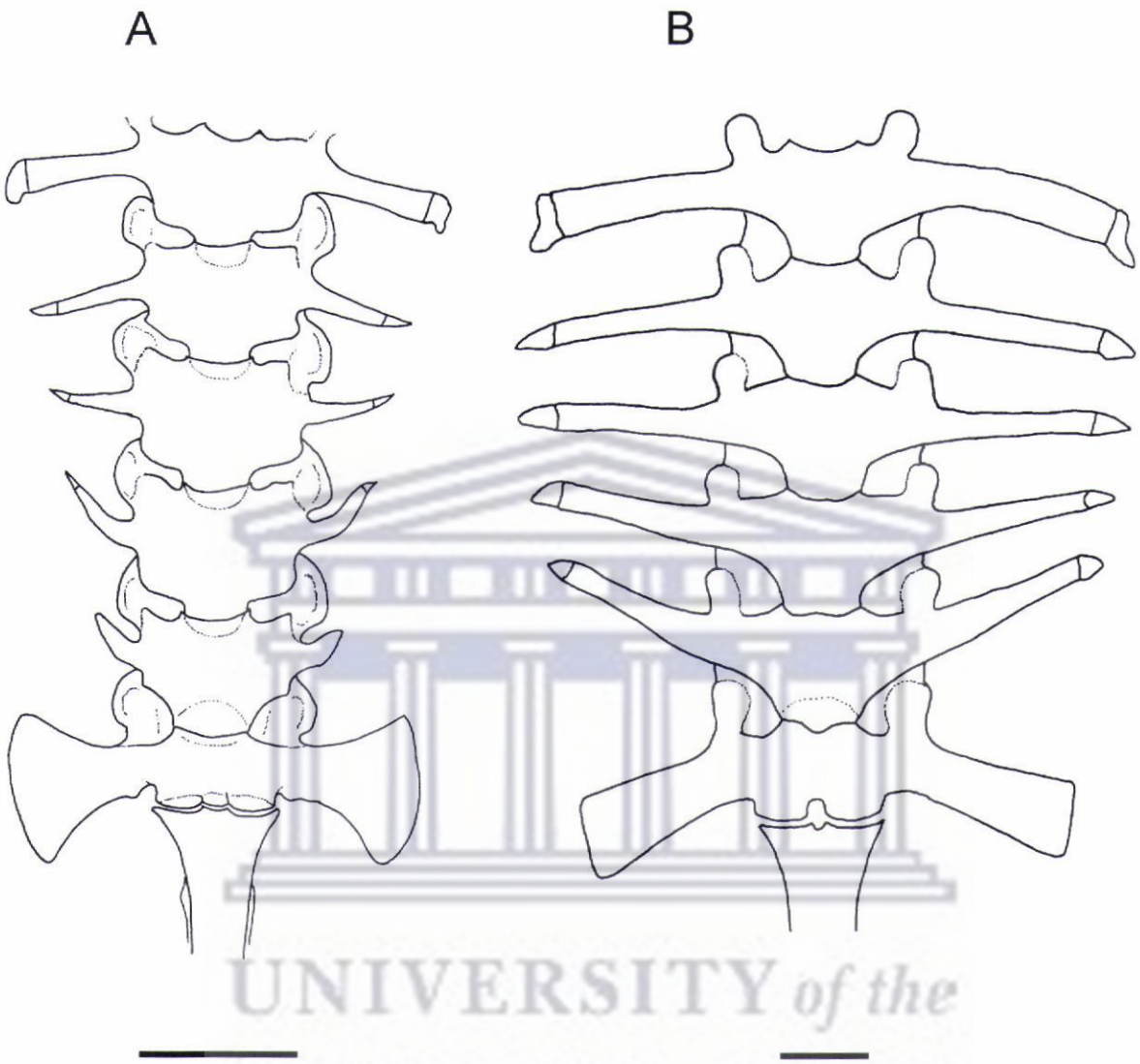

Figure 4. Ventral view of vertebral columns. **A.** Rectangular centra (c11:1) of *Cacosternum boettgeri* (ES 152). **B.** Diamond-shaped centra (c11:2) of *Phrynobatrachus krefftii* (ES 733). Scale bar = 1 mm.

9. Fusion of first (atlas) and second presacral vertebrae: (0) fused; (1) unfused.

Previously used by Lynch (1973) 2, Heyer & Liem (1976) 9, Ford (1990) 66, Wu (1994) 137. Fusion was assessed by the presence of transverse processes on the first presacral vertebra, which, according to Trueb (1973), indicates fusion, since the first vertebra (atlas) does not bear transverse processes. Drewes (in preparation) noted this condition in the Arthroleptidae. Lynch (1971) notes that fusion also occurs in three pipid genera, pelodytids, rhinodermatids, myobatrachids, most cycloranids and in several bufonid genera. Fusion of the first and second vertebrae is considered by Lynch (1973) and Trueb (1973) to be derived. The outgroup *Heleophryne purcelli* was found to exhibit fusion, although Lynch (1971) found the unfused condition uniformly in this genus, and it is thus treated here as plesiomorphic, rendering this character nearly uninformative. A single specimen of *Ericabatrachus baleensis* exhibits fused first and second vertebrae, and it is coded as polymorphic for this taxon. Most species of *Schoutedenella* Witte, 1921 and *Cardioglossa* of the Arthroleptidae are reported to exhibit this fusion, but it is absent in *Arthroleptis* (Drewes, in preparation), although none of the exemplars of *Cardioglossa* examined here showed state 0. The brevicipitid microhylids (except *Spelaeophryne* Ahl, 1924) and *Hemisus* also exhibit fusion of vertebrae one and two (Wu 1994). Various states of fusion of the first three vertebrae occur in the dendrobatids. Vertebrae two and three were found to be fused in some *Dendrobates* specimens examined.

10. Ossification of suprascapular cartilage: (0) limited, so that only the proximal section is ossified and forms a Y-shaped flange of mineralisation with the cleithrum, with the fork facing dorsally; (1) heavily ossified, 1/3 to 2/3 of blade, forming one rounded, rectangular or triangular flange with the cleithrum.

Ford (1990) 99 alludes to variation in the degree of calcification of the suprascapula. Both states are illustrated in Duellman & Trueb (1986:347) Fig. 13.36, with state 1 in B and state 0 in D, F and G, and are illustrated here in Fig. 3. This character needs to be assessed from adult specimens. Under Acctran optimization, state 1 arises at node 9 in the Ranoidea, but a reversal to state 0 unites the petropedetids, and independently (*Cacosternum* + *Nothophryne*).

11. Vertebrae five to eight, ventral view; shape of centrum and base of transverse processes: (0) centra cylindrical or sub-cylindrical, bases of the transverse processes not laterally expanded; (1) centra rectangular-shaped, with a small gap between the bases of the transverse processes; (2) centra diamond-shaped, well developed lateral expansion of the bases of the transverse processes.

Not previously used, but Liem (1970) 17 and Lynch (1978) 21* recognise some of the variation described in the states of this character. States 1 and 2 are illustrated in Fig. 4A and 4B respectively. Rectangular-shaped vertebrae (state 1) are synapomorphic for the dendrobatids,

and independently for the genus *Cacosternum*, but also occur independently in *Mantella*. Diamond-shaped vertebrae (state 2) are synapomorphic for the two species of *Arthroleptis* included, and for the (cacosternids + phrynobatrachids) but also occur in a few other taxa.

12. Vertebrae five to eight, attachment of zygapophyses: (0) on lateral (mid) portion of centrum, which thus gives the curvature of the centrum (and the initiation of the base of the transverse processes) an evenly graded appearance in ventral view; (1) on dorsolateral surface of centrum, thus giving the centrum's curvature a sharply cylindrical appearance in ventral view, and leading to a sharp distinction between the bases of the transverse processes and the centrum.

Previously used by Ford (1990) 73. State 0 is illustrated in Liem (1970:32) Fig. 20, whilst state 1 is illustrated in Liem's Figs 21 and 22. Dorsolateral attachment (state 1) is synapomorphic for the large ranid clade wherein it reverses three times, and elsewhere in the tree in the mantellid-rhacophorid clade.

13. Vertebra eight, centrum: (0) procoelous; (1) diplasiocoelous.

Previously used by Inger (1967), Liem (1970) 16, Lynch (1973) 4, Heyer & Liem (1976) 8*, Drewes (1984) 5, Ford (1990) 65*, Wu (1994) 140*, Vences (1999) 11. Noble (1922, 1931) was the first worker to use this character in the classification of frogs. Trueb (1973) provides good definitions of this widely used character, although its use here only distinguishes the state of vertebra eight. Procoely is generally considered to be plesiomorphic with respect to diplasiocoely, although Trueb (1973) considered amphicoely to be the ancestral anuran condition, although she noted that its presence in Neobatrachia could be paedomorphic. Heyer & Liem (1976) considered amphicoely as derived relative to procoely in the leptodactylids. Heyer & Liem (1976) found *Heleophryne* to be amphicoelous, but in this analysis *Heleophryne* is considered procoelous. The examined specimens of *Leptopelis vermiculatus* displayed the procoelous condition, which is anomalous given that all other examined species of *Leptopelis* are diplasiocoelous (Liem 1970; Drewes 1984). Diplasiocoely is synapomorphic at node 6 for the Ranoidea, although unambiguously optimised from node 12 in the arthroleptid-hyperoliid lineage. Within the Ranidae, only *Ericabatrachus* displays the procoelous condition. This was clearly evident in two specimens, obscured by fusion in another and equivocal from the last, assessed using X-ray photography. Fusion of the eighth presacral and sacral vertebrae also obscures the determination of this character in the Ptychadeninae, which were coded as not applicable.

18. Ilium, dorsal protuberance: (0) oval and inconspicuous; (1) projected laterally and tending to be spike-like, can be small, sharp and triangular or slightly rounded; (2) large spike- or flange-like, not oval or adpressed to shaft.

Previously used by Clarke (1981) 21*, Cannatella (1985) 109, Ford (1990) 101*, Wu (1994) 166*, Glaw, Vences & Böhme (1998) 13*. Large crests obscure the coding of differences in the dorsal protuberance whilst taxa with reduced or absent crests appear to have very well-developed protuberances which sometimes protrude laterally. Laterally projecting well-defined processes (state 1) occur in most cacosternids, petropedetids and various taxa in the base of the tree, but do not optimise unambiguously to the root. Large spike- or flange-like protuberances (state 2) are a unique synapomorphy for the genus *Tomopterna*.

19. Ilium, height of crest along dorsal surface measured centrally: (0) absent; (1) 0.5 to 1 times height of ilium; (2) 1 to 2.5 times height of ilium, very well developed and squared off posteriorly.

Previously used by Heyer (1975) 36*, Heyer & Liem (1976) 14*, Clarke (1981) 21*, Cannatella (1985) 104, Ford (1990) 102*, Wu (1994) 165. The presence of the crest is noted as derived by Trueb (1973) and Heyer (1975). State 1 arises at the basal node but the crest is lost synapomorphically for (*Cacosternum* + *Nothophryne*) and occurs in some microhylids. A large ilial crest (state 2) is synapomorphic for the Arthroleptidae (reversing in *Leptopelis*), and is the common state in the Raninae, petropedetids and phrynobatrachids.

20. Sacral diapophyses, expansion: (0) ratio of distal end to proximal region (base) is greater than two (strongly dilated); (1) ratio of distal end to proximal region is greater than one but less than two (slightly dilated); (2) ratio of distal end to proximal region is equal to one (undilated).

Previously used by Lynch (1973) 6, Heyer (1975) 34*, Lynch (1978) 22*, Heyer & Liem (1976) 12*, Ford (1990) 75, Wu (1994) 143. Parker (1934) and Lynch (1973) note that dilated sacral diapophyses characterise the archaic and transitional frog families, and are only present in a few advanced families. Dilated diapophyses are considered to be the plesiomorphic condition by Trueb (1973), Heyer (1975) and Wu (1994). Undilated diapophyses (state 2) arise at the base of the Ranoidea and independently in the dendrobatids. Sight dilation (state 1) arises in the basal cacosternids, and a reversal to strongly dilated diapophyses occurs in the more distal genera *Microbatrachella* and *Cacosternum*. Elsewhere, strongly dilated diapophyses occur only in *Nannophrys*, and slightly dilated diapophyses occur in (*Hyperolius* + *Kassina*), *Hemisus*, *Leptodactylus*, *Chiromantis*, *Mantella* and *Euphlyctis*.

21. Sacral diapophyses, distal ends: (0) distinctly flattened (dorsoventrally compressed); (1) cylindrical or nearly so in lateral view.

If the diapophyses are dilated, then the distal ends are always distinctly flattened. Undilated diapophyses can be cylindrical or flattened. This character does not optimise unambiguously through the spine of the tree. Cylindrical diapophyses (state 1) occur in most Raninae and phrynobatrachids, whilst distinctly flattened diapophyses characterise the cacosternids, mantellids and rhacophorids and most petropedetids.

22. Sacral diapophyses, anterior margin: (0) angled posteriorly; (1) angled transversely (perpendicular to the spine), even if due to dilation; (2) directed anteriorly, due to rounded (axe-shaped) type of sacral diapophysis dilation.

Previously used by Heyer & Liem (1976) 12*, Wu (1994) 142*. Taxa with expanded diapophyses can have them pointing forward or laterally. In *Nannophrys*, the diapophyses have straight lateral edges, and point posteriorly, unlike those in *Cacosternum*, where the lateral margin is crescent-shaped and points laterally. This character thus makes the distinction between these types of diapophyses, since if the diapophyses are straight edged, they are never directed anteriorly. Taxa with unexpanded diapophyses generally have them pointing backwards or laterally. Transversely angled diapophyses (state 1) occur in some arthroleptids and *Mantella*, but are synapomorphic for the included species of *Dendrobates*, independently for the microhylids, and for the cacosternids, wherein a transition to anteriorly directed diapophyses (state 2) is synapomorphic for (*Cacosternum boettgeri* + *C. nanum parvum*). Anteriorly directed diapophyses (state 2) also occur in the Brevicipitinae and the sooglossids.

Sternum

23. Clavicles, width: (0) slightly tapering along whole length, meeting the procoracoid cartilage medially; (1) narrowing sharply, half the length of the coracoids; (2) slight ossified expansion medially.

Previously used by Wu (1994) 151. Clavicles narrowing sharply and becoming unossified medially (state 1) is a unique synapomorphy for the cacosternids, wherein many taxa lose the clavicles and are thus coded as inapplicable for this character. A slight expansion at the medial edge of the clavicle (state 2) is synapomorphic for (Brevicipitinae + *Hemisus*), but also occurs in *Nyctibates*.

24. Clavicles, nature: (0) stout and thick; (1) reduced and thin; (2) absent.

Previously used by Lynch (1973) 14, Ford (1990) 83*, Trueb & Cloutier (1991) 46*, Blommers-Schlösser (1993) 24*. State 1 is based on disproportionately thin but ossified clavicles, as noted by Laurent (1940). In state 2, usually only the cartilaginous procoracoid, or

vestiges thereof, occur (Fig. 5). The loss of clavicles is considered derived (Lynch 1973), and has been noted to have occurred many times in the microhylids (Parker 1934; Griffiths 1963), as in *Phrynomantis*. Under Acctran optimization, considerably reduced and thin clavicles (state 1) are synapomorphic for the (cacosternids + phrynobatrachids), and independently for (*Colostethus* + *Mannophryne*). State 1 occurs elsewhere on the tree in *Nannophrys*, *Petropedetes natator* and *Philautus*. In the later case, and in *Colostethus* lineage, this reduction is associated with strong contact with the expanded anterior end of the coracoids, which buttress the entire girdle (c26:1).

25. Clavicle orientation: (0) strongly or slightly bowed, pointing distinctly anteromedially and contacting only the procoracoid cartilage; (1) bowed slightly but roughly at right angles to the main to body axis; (2) straight and perpendicular to body axis.

Previously used by Clarke (1981) 17*, Cannatella (1985) 93, Ford (1990) 84*, Wu (1994) 152*. The bowed anteriorly pointing condition (state 0) is seen in arciferal frogs, with the clavicles becoming straight (state 2) in more advanced firmisternal frogs. Straight perpendicular clavicles (state 2) arise at node 6, and independently in the dendrobatids. Bowed perpendicular clavicles (state 1) are synapomorphic for the Ptychadeninae, but also occur independently in *Aubria*. Although this state could be assumed as intermediate between states 0 and 2, the distribution on the cladogram does not support this. Bowing in the larger frogs, such as *Aubria*, may be related to structural reinforcement, since it was observed in some exceptionally large *Afrana* females, although not in smaller male individuals of the same species.

26. Clavicle-coracoid, contact: (0) clavicle not touching coracoid, separated by long procoracoid cartilage; (1) procoracoid cartilage ossified and indistinguishably fused to the coracoid, which expands strongly towards the clavicle medially: coracoid appears fused to clavicle in this manner for about 1/5 to 1/4 of the latter's length; (2) clavicle descends medially and is fused to coracoid for approximately the medial 1/3 of is length; (3) only point contact anteromedially via short procoracoid cartilage.

State 1 is illustrated in Deckert (1938) Figs 8, 17, 18 and 23. This character is similar to Ford (1990) 32, but is concerned more with the hyperossification of the procoracoids, with states 1 and 2 occurring only in firmisternal frogs. This character must be coded from adult frogs. The clavicles are often reduced or relatively thin (c24:1) in taxa where these are ossified to the coracoids (state 1), e.g. *Philautus*. State 1 is synapomorphic for the dendrobatids, but alternates sporadically amongst the clades of the Ranidae together with state 3. State 2 is the unambiguously defined derived state of Clarke (1981) 17, and is uniquely synapomorphic for the Ptychadeninae.

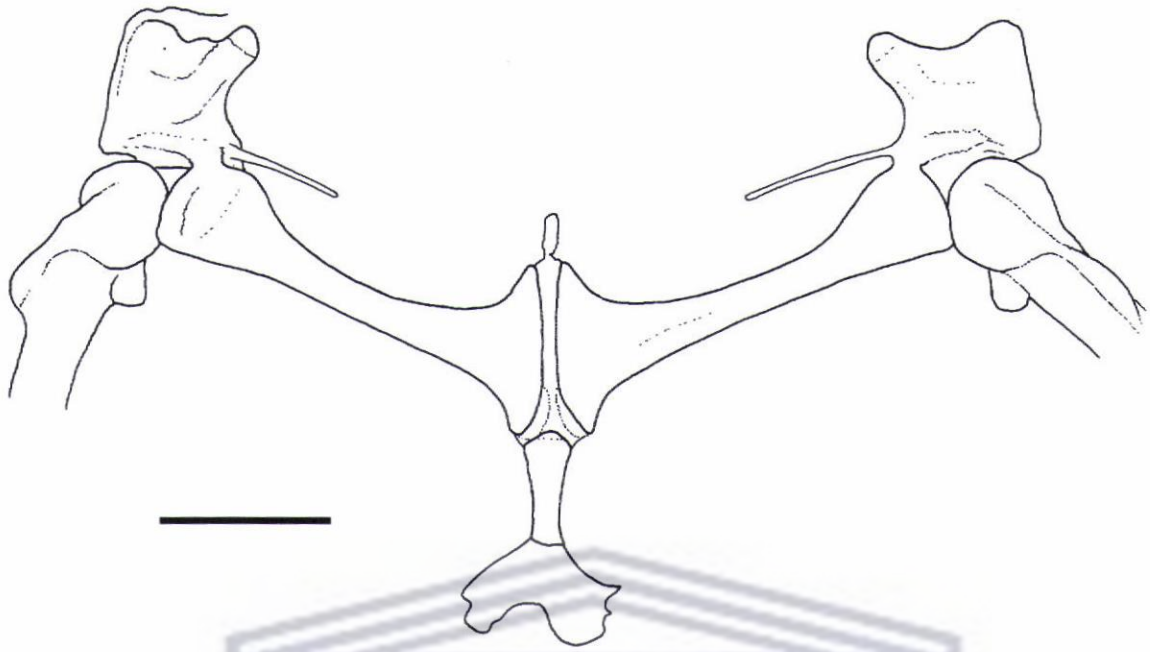

Figure 5. Ventral view of the pectoral girdle of *Cacosternum boettgeri* (ES 152), showing absence of clavicles (c24:2), T-shaped medial edges of the coracoids (c28:1) and the omosternum a minute cartilaginous peg (c32:0). Scale bar = 1 mm.

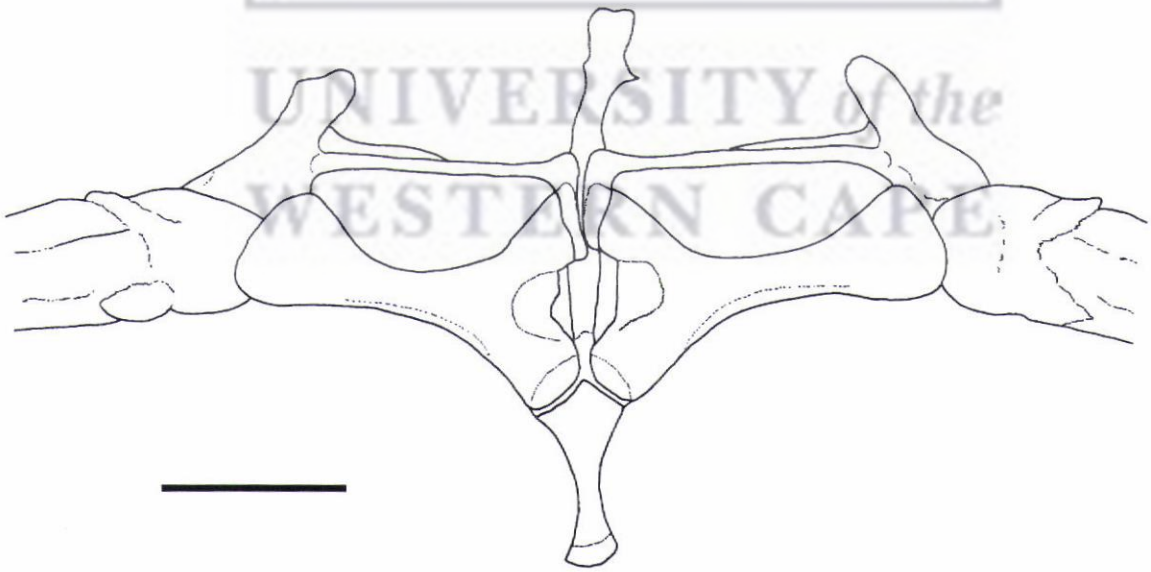

Figure 6. Ventral view of the pectoral girdle of *Microbatrachella capensis* (ES 32), showing the slight trumpet-shaped medial edges of the coracoids (c28:2) and medial bifurcation of the coracoids (c31:1). Scale bar = 1 mm.

27. Overlap of the medial borders of the coracoids: (0) epicoracoids elaborated into posterior epicoracoid horns which overlap medially, usually fused in the interclavicle region (arciferal condition); (1) epicoracoid cartilages fused medially, coracoids slightly angled ventrally and one side of coracoid overlapping the other medially, overlapping coracoid usually fenestrated at its medial edge (modified firmisternal condition, or pseudoarciferal condition); (2) epicoracoid cartilage fused medially (firmisternal condition); (3) firmisternal, with fused epicoracoid cartilages and extremely long procoracoid cartilages.

Previously used by Inger (1967), Lynch (1973) 11*, Clarke (1981) 18*, Duellman & Trueb (1986) C, Ford (1990) 88*, Wu (1994) 158*, Emerson *et al.* (2000a) 1*. State 1 illustrated in Deckert (1938) Figs 1 and 2, Trueb (1973) Fig. 2.9 F, and in Duellman & Trueb (1986) Fig. 13.36 G, and discussed in Noble (1926a), Clarke (1981) and in considerable detail for some of the large Raninae by Kaplan (2000). State 3 is figured in Deckert (1938) Fig. 11. Arciferal girdle architecture is widely considered plesiomorphic. According to Griffiths (1959b) *Sooglossus* exhibits pseudoarcifery, but Wu (1994) and Kaplan (2000) considered sooglossids as arciferal, which is followed here. Pseudoarcifery (state 1) was found to be synapomorphic for (*Phrynoglossus* (*Discodeles* + *Platymantis*)), for the Pyxicephalinae and at node 70 leading to *Hoplobatrachus* and *Nanorana* (reversing to state 2 in *Euphlyctis*), and thus occurs in most fanged ranids. Clarke's (1981) observations of this state in *Tomopterna* were not confirmed from a large number of specimens, but a similar state was seen in some *Hildebrandtia* specimens, suggesting that this state sometimes, but not commonly, occurs in large burrowing forms, and is thus possibly related to structural strength or size. An aberrant state, long pseudoarciferal (state 3), was discerned late in the course of this study (when many specimens were unavailable for re-examination) in *Scotobleps* and *Nyctibates*, and may have been overlooked in other taxa. This should be further investigated.

28. Coracoid, shape: (0) evenly constricted from medial edge to centre, trumpet-shaped; (1) strong constriction just after medial edge, T-shaped; (2) weaker constriction just after medial edge, broader medially than state 1.

Evenly constricted coracoids occur in most taxa. T-shaped coracoids (state 1, Fig. 5) are uniquely synapomorphic for (*Cacosternum boettgeri* + *C. nanum parvum*), but an intermediate modification (state 2, Fig. 6) is an autapomorphy for *Microbatrachella*.

29. Dilation of coracoid: (0) lateral and medial edges of coracoid about the same width, medial edge less than 1.3 times width of lateral edge; (1) medial edge of coracoid dilated and distinctly wider than lateral edge, more than 1.4 times its width.

Previously used by Tyson (1988) 48, Ford (1990) 80, Wu (1994) 149. Coracoids in which the lateral edge is wider than the medial edge were considered plesiomorphic by Ford (1990),

but this state was not found in this taxon set. Dilated medial edges of the coracoids (state 1) are synapomorphic for the dendrobatids and independently for the Ranidae (except *Ericabatrachus*), but optimise ambiguously in the arthroleptid-hyperoliid lineage.

30. Coracoid, posterior margin (excluding extreme medial section): (0) straight; (1) curved; (2) sigmoid.

Previously used by Wu (1994) 147. Most ranids display a curved posterior margin of the coracoid, but it is straight in some phrynobatrachids, some cacosternids, *Petropedetes natator* and *Staurois natator*. A sigmoid-shaped posterior margin (state 2) is autapomorphic for the Brevicipitinae.

31. Medial edges of both coracoids: (0) always single; (1) often bifurcated or nicked.

Previously used by Drewes (1984) 15, Wu (1994) 146. Oxnard (1971) suggests that net tension on flat bones can lead to fenestra and replacement of bone by fibrous material. This character is thus not of great taxonomic importance, but is included here since it occurs in many cacosternids and may be relevant to their relationships. The tendency towards bifurcation is marked in many small species. Single-sided fenestration, as is often associated with pseudoarciferal condition in large ranids (c27:1), was not coded as state 1 for this character. Bifurcation (state 1, Fig. 6) occurs in some microhylids, some Arthroleptinae, various cacosternids and *Tomopterna tandyi*, and was reported in the hyperoliids *Tornierella* Ahl, 1924 and *Kassinula* Laurent, 1940 by Drewes (1984).

32. Omosternum style: (0) minute cartilaginous peg, occasionally absent; (1) present and cartilaginous, large; (2) present and well ossified; (3) always absent.

Previously used by Lynch (1973) 12, Lynch (1978) 14*, Cannatella (1985) 85, Tyson (1988) 61, Ford (1990) 89, Blommers-Schlösser (1993) 24*, Wu (1994) 159–161. Trueb (1973) notes that the omosternum is myocommatous in origin and thus extremely labile in its distribution among taxa. Whether or not it was forked was found to be hypervariable, as illustrated in Deckert (1938) Fig. 3 for *Tomopterna delalandii*, and was not coded in this study, although this has been commonly used by previous authors. Trueb (1973) notes that the status of the omosternum as primitive or derived is debatable, but that it is absent in several arciferal families. Lynch (1973) coded the presence of prezonal elements as plesiomorphic and the absence as apomorphic, and he states that the osseous omosternum is apparently derived from the cartilaginous state. A well ossified omosternum (state 2) occurs in most taxa, but reverses to the plesiomorphic condition of a minute peg (state 0) in Brevicipitinae, and also synapomorphically for species of the genus *Cacosternum* (Fig. 5). A cartilaginous metasternum (state 1) occurs in the cacosternids *Anhydrophryne*, *Ericabatrachus* and *Microbatrachella*, and

independently in *Nannophrys*. The absence of an omosternum (state 3) is autapomorphic for *Phrynomantis*.

33. Metasternum: (0) cartilaginous and broad, sometimes with slight calcification; (1) narrow bony stylus; (2) absent.

Previously used by Liem (1970) 25, Lynch (1973) 13*, Heyer (1975) 32*, Drewes (1984) 25, Cannatella (1985) 91*, Tyson (1988) 62–64, Ford (1990) 92, Blommers-Schlösser (1993) 7*, Wu (1994) 162*, Emerson *et al.* (2000a) 6*. Laurent (1979, 1986) proposed a bony metasternum as a synapomorphy for the family Ranidae. This state is found to be synapomorphic at node 20 leading to the Ranidae, but also arises independently in *Leptodactylus*. Within the Ranidae, a reversal to a cartilaginous metasternum (state 0) occurs only in *Ericabatrachus*. The metasternum is heavily mineralised in *Leptopelis*, but still considered sufficiently different from the ranid condition to be coded as cartilaginous. The loss of the metasternum (state 2) is autapomorphic for *Hemisus*.

34. If metasternum ossified, shape: (0) short, hourglass-shaped plate, expanded at both ends; (1) long, narrow and tapering markedly anteriorly to posteriorly, length up to 3.5 times maximum width; (2) long, narrow and tapering markedly anteriorly to posteriorly, length more than 4 times maximum width.

Previously used by Lynch (1978) 15*, Clarke (1981) 19*, Ford (1990) 93*. This character is variable between genera, and its usage is therefore simplified from that of previous authors. It is unpolarised here due to its inapplicability in the outgroup *Heleophryne*, but unambiguously optimised to the base of this cladogram as state 1. An hourglass-shaped metasternum (state 0) occurs in the petropedetids, the phrynobatrachids and the cacosternids *Nothophryne* and *Poyntonia*. In the Raninae, state 0 arises at node 50, and transforms to state 1 sporadically five times therein. A metasternum longer that 4 times its width (state 2) is uniquely synapomorphic for the rhacophorids.

35. Xiphisternum, shape: (0) large, rounded; (1) small peg, usually triangular; (2) large triangular with distinctly serrated distal edge; (3) roughly X-shaped, two expansions of cartilage attached to a short inflated mineralised section; (4) large inverted U-shaped plate; (5) rectangular with a smooth distal end; (6) large anchor shape; (7) narrow and rectangular, divided with two long projections with distal expansions; (8) rectangular with strongly serrated distal end.

Previously used by Heyer (1975) 32*. Tyson (1988) 26 refers to the shape of the posterior margin of the xiphisternal plate as pointed, expanded slightly or expanded greatly, as used by Wu (1994) 164. Heyer (1975) notes that the posterior sternum has traditionally been given great

weight in the classification of leptodactylid genera, and here it is shown to be useful in ranid systematics. A rounded xiphisternum (state 0) is autapomorphic to *Heleophryne*. A small triangular peg (state 1) is found in *Mantella*, *Philautus* and *Phrynodon*. A large triangular xiphisternum with a serrated posterior edge (state 2, Fig. 7A) is uniquely synapomorphic for the petropedetids. An X-shaped xiphisternum (state 3, Fig. 7B) is uniquely synapomorphic for the phrynobatrachids excluding *Natalobatrachus*. A large inverted U-shaped plate (state 4, Fig. 7C) occurs in most Raninae from node 55 onwards, but optimises ambiguously due to its presence at the base of the tree in the microhylids, *Leptodactylon* and *Leptodactylus*. State 5 is autapomorphic for the sooglossids, whilst state 6 occurs in the vast majority of ranids. A narrow rectangular xiphisternum divided into two projections with distal expansions (state 7, Fig. 7D) is autapomorphic for *Leptopelis*, whilst state 8 is autapomorphic for *Staurois*.

36. Xiphisternum, posterior fenestra: (0) absent; (1) present on posterior periphery; (2) present centrally on plate, cartilage fusion posterior to fenestra.

The presence of the recess was mentioned by Heyer (1975) 32 and by Wu (1994) 163. This character varies considerably, but is fairly consistent within clades. Fusion behind the fenestra (state 2) is autapomorphic for *Leptopelis*.

Skull

37. Sphenethmoid, ventral portion: (0) fused, single; (1) paired.

Previously used by Liem (1970) 21*, Heyer & Liem (1976) 5, Drewes (1984) 2*, Cannatella (1985) 17, Ford (1990) 7, Wu (1994) 63*. Trueb (1973) notes that state 1 reflects reduced ossification, and is often seen in small frogs. Paired sphenethmoids are considered to be derived by Heyer & Liem (1976). In the taxa examined here, paired sphenethmoids occur only in *Microbatrachella*, *Hyperolius* and *Phrynomantis*. Paired sphenethmoids are noted in the literature for some *Leptopelis*, but this state was not evident in specimens of the species examined here. Griffiths (1959b) lists state 1 for *Sooglossus*, but Wu (1994) gives them as fused. Ford (1990) found *Mantella* to have paired sphenethmoids, but this was also not evident in the single specimen examined here. This character appears to be more variable within species and genera than previously thought, and may depend on the age of the specimen. The ventral sphenethmoid appears unossified in adult *Amnirana* and *Hydrophylax* (not coded as such).

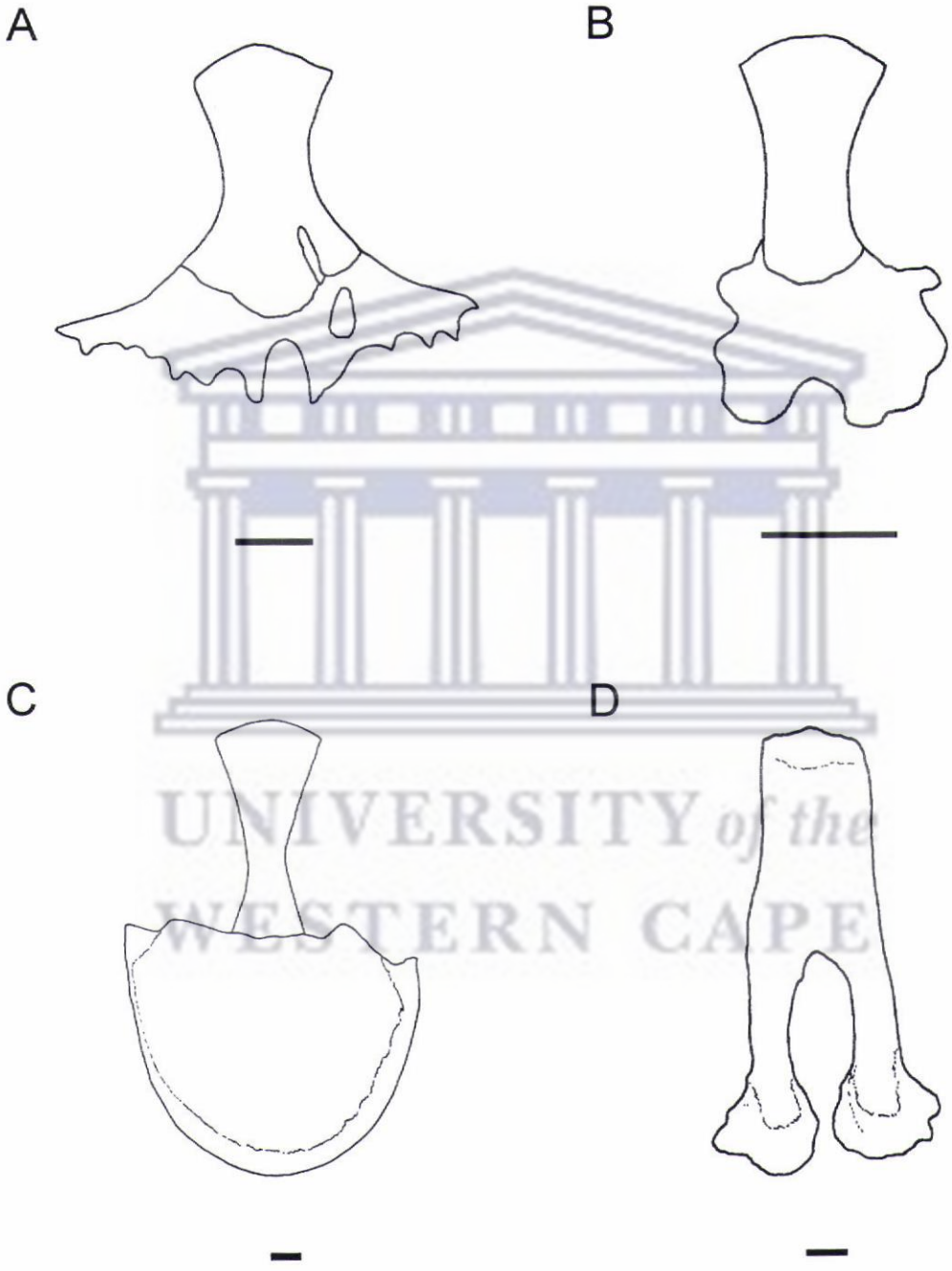

Figure 7. Shapes of xiphisterna. **A.** Large triangular with distinctly serrated distal edge (c35:2) of *Petropedetes palmipes* (BMNH 1906.5.28.28). **B.** X-shaped xiphisternum (c35:3) of *Phrynobatrachus krefftii* (ES 728). **C.** Large inverted U-shaped plate (c35:4) of *Aubria subsigillata* (CAS 144214). **D.** Narrow and divided with expanded distal portions (c35:7) of *Leptopelis vermiculatus* (ES 717). Scale bar = 1 mm.

olfactoria): (0) reduced and narrow, adpressed to braincase; (1) covering about 1/2 of the

38. Ventral sphenethmoid, extension of ossified anterior portion (antrum pro lobo olfactoria): (0) reduced and narrow, adpressed to braincase; (1) covering about 1/2 of the distance from the palatines (or anterior edge of orbit) to the premaxilla; (2) covering 2/3 or more of the distance from the palatines (or anterior edge of orbit) to the premaxilla.

Previously used by Liem (1970) 20*, Glaw, Vences & Böhme (1998) 3. Drewes (1984) 1* coded the dorsal extent of the sphenethmoid, but here it is coded ventrally, as a variation of Ford (1990) 6*. Both derived states occur sporadically throughout the cladogram and are synapomorphic for various sister terminals or triplet terminals.

39. Ethmoid cartilage, septum nasi: (0) thin, nasal capsules close together; (1) thick, nasal capsules medially separate.

Previously used by Cannatella (1985) 14, Ford (1990) 48*. State 1 is illustrated in Myers & Ford (1986) Fig. 3. Medially separated nasal capsules occur in the dendrobatids, the mantellids, some phrynobatrachids and some cacosternids.

40. Palatines: (0) present and well developed; (1) reduced, thin sliver of bone only; (2) absent.

Previously used by Lynch (1973) 22*, Clarke (1981) 11*, Cannatella (1985) 12, Duellman & Trueb (1986) E, Ford (1990) 35*, Trueb & Cloutier (1991) 7*, Wu (1994) 95*. Loss of palatines in the Anura is considered to be derived (Lynch 1973), since palatines are present in salamanders and all extinct orders of amphibians (Duellman & Trueb 1986). If the palatine is absent, its loss is usually compensated for (Parker 1934; Trueb 1993). In the taxa examined here, compensation is either by the anterior ramus of the pterygoid being long and curving medially over the planum antorbitale (as in the Ptychadeninae), or by the anterior portion of the sphenethmoid expanding laterally over the planum antorbitale (as in the dendrobatids). Reduced palatines (state 1) are synapomorphic for *Cacosternum* (reversing to well-developed in *C. capense*), and occur independently in *Anhydrophryne* and two species of *Phrynobatrachus*. Absence of palatines is synapomorphic for (dendrobatids + sooglossids) but a transformation to the reduced state is synapomorphic for (*Colostethus* + *Mannophryne*). Absence of palatines is independently synapomorphic for the microhylids including *Hemisus*, and independently for the Ptychadeninae.

41. Palatines: (0) present, touching the sphenethmoid but not nearly meeting medially; (1) present, nearly meeting at the midline over the sphenethmoid, medial portion can be slightly expanded.

Previously used by Duellman & Trueb (1986) E, Ford (1990) 35*, Wu (1994) 95*. Palatines ossify late in the developmental series, and are thus prone to reduced ossification in small or poorly ossified taxa (Trueb 1993). Palatines nearly meeting medially (state 1) are

synapomorphic for the astylosternids including *Leptopelis*, but occur in most of the (petropedetids + Raninae) lineage and the Tomopterninae.

42. Vomer, anterior process: (0) absent; (1) present.

Previously used by Ford (1990) 37, Wu (1994) 89. The interpretation of presence of the process applied here appears to differ slightly from that of Ford (1990). If an anteriorly directed point could be discerned here, the process was considered to be present. Presence of the anterior process is the more common state, evolving at the base of the tree and occurring in most included taxa. A reversal absence (state 0) is synapomorphic for (Brevicipitinae + *Hemisus*), and independently for (*Arthroleptella landdrosia* + *A. lightfooti*), and occurs in a few other taxa.

43. Vomers, position and reduction: (0) not reduced, centre of vomer not lateral to articulation of the maxilla and premaxilla; (1) reduced, vomers placed laterally, with centre of vomer lateral to articulation of premaxilla and maxilla.

Lynch (1971) noted that the vomers can be widely spaced in some leptodactylids, and were noted to be reduced in all these cases. Presence of reduced lateral vomers interferes with the coding of the extent of the anterior process of the vomer and overlap with the articulation of the premaxilla and maxilla (c44). Often the reduced condition is correlated with the absence of the posterior (dentigerous) process of the vomer (c46), but this is considered to be an independent character. Reduced lateral vomers (state 1) are synapomorphic for the Arthroleptinae, independently for the dendrobatids and the mantellids. State 1 occurs in all phrynobatrachids and some cacosternids.

44. Vomer, anterior process: (0) short or absent, separated by a small or large gap from articulation of premaxilla and maxilla; (1) long, passing dorsally to articulation of premaxilla and maxilla; (2) long, but curving anteriorly and laterally and passing dorsally to the anterior end of the maxilla.

Previously used by Clarke (1981) 10*, Ford (1990) 37*, Wu (1994) 89*. Coded as not applicable if vomers are lateral (c43:1). Long anterior processes of the vomers (state 1) are synapomorphic for the Tomopterninae and occur in many of the fanged ranids, as well as *Nannophrys* and *Amolops*. Long, anteriorly and laterally curving processes (state 2) are autapomorphic for *Hildebrandtia*.

45. Vomer, postchoanal process: (0) horizontal; (1) vertical; (2) oblique; (3) fused to hyperossified sphenethmoid.

Alternate version of Ford (1990) 36*. This character refers to whether post- and prechoanal processes, not the whole vomer as in Ford (1990) 36, are in same plane or not. It gives a

measure of the complexity and degree of development of the postchoanal process of the vomers, which usually reflects that of the vomers in general. The process is usually vertical in taxa where it is well developed, and horizontal when the vomer is reduced and uncomplicated. The depth of the head and requirement of support for the choana may be indicated to some extent by this character. Vertical postchoanal processes (state 1) are synapomorphic for the astylosternid lineage including *Leptopelis* and for the Tomopterninae. Oblique postchoanal processes (state 2) are synapomorphic for the two species of *Ptychadena*, the two species of *Afrana* and occur in some other Raninae. Postchoanal processes fused to the hyperossified sphenethmoid (state 3) occur only in some fanged ranids, *viz. Conraua crassipes*, *Hoplobatrachus* and *Aubria*.

46. Vomer, posterior (dentigerous) process: (0) present; (1) absent.

Previously used by Ford (1990) 32, Wu (1994) 92*. The posterior process of the vomer being absent (state 1) is synapomorphic for the microhylids including *Hemisus*, and independently for the two species of *Arthroleptis*, for (dendrobatids + sooglossids) and for the cacosternids plus phrynobatrachids, wherein it reverses to present in some cacosternids and synapomorphically in (*Phrynobatrachus dendrobates* + *P. versicolor*). Absence of the process also occurs in *Mantella* and *Staurois*.

47. Vomer, posterior (dentigerous) process, if present: (0) connected to main body of vomer; (1) separate from main body of vomer.

Du Toit (1943) first noted that the vomers of *Petropedetes* were divided, with the posterior process fused to the planum antorbitale, and noted this state elsewhere only in *Crinia georgiana* and certain Malagasy and Indo-Malayan Microhylidae. Divided vomers (state 1) occur uniquely in three species of *Petropedetes*, but optimise ambiguously due to state 0 being exhibited by *Arthroleptides*.

48. Vomerine teeth: (0) present; (1) absent.

Previously used by Liem (1970) 22, Heyer (1975) 26*, Heyer & Liem (1976) 7*, Drewes (1984) 4*, Ford (1990) 43, Wu (1994) 94, Vences (1999) 7*. The presence of vomerine teeth was considered plesiomorphic by Heyer (1975). The loss of vomerine teeth appears to occur readily. The presence of an odontophore is thought to be independent of the presence of the teeth, but here the coding was found to be identical, with the exception of *Kassina*, *Conraua crassipes* and *Tomopterna marmorata*, which have the odontophore but no vomerine teeth. Absence of vomerine teeth (state 1) arises near the base and occurs throughout most of the base of the tree. A reversal to presence of vomerine teeth (state 0) is synapomorphic for the astylosternids including *Leptopelis*, and again at node 50 for the petropedetids plus Raninae.

49. Maxillary and premaxillary teeth: (0) present; (1) absent.

Previously used by Lynch (1973) 21, Heyer & Liem (1976) 1, Cannatella (1985) 64*, Ford (1990) 20*, Wu (1994) 21*, Glaw, Vences & Böhme (1998) 5, Vences (1999) 8. Absence of maxillary teeth is generally considered derived within the Neobatrachia (Lynch 1973), and may be correlated to microphagy (Vences *et al.* 1998). Absence of maxillary teeth (state 1) is synapomorphic for the microhylids including *Hemisus*, and for the two species of *Dendrobates*. This state also occurs in *Cardioglossa* and *Mantella*. Teeth may be reduced in *Cacosternum namaquense* but are never absent.

50. Premaxilla, shape of pars palatina: (0) medial edge greater than lateral edge; (1) medial edge equal to lateral edge; (2) medial edge less than lateral edge; (3) lateral edge slanting outwards therefore longer, and lateral section of pars palatina usually thicker than medial section.

Previously used by Cannatella (1985) 52 and 53*, Ford (1990) 14, Wu (1994) 73. May vary slightly intraspecifically (e.g. in *Phrynobatrachus krefftii*, where 5 specimens were examined). The medial edge equal to the lateral edge (state 1) is synapomorphic for the (dendrobatids + sooglossids), and evolves independently at node 9 leading to the arthroleptid-hyperoliid and ranid lineages. The medial edge less than the lateral edge (state 2) is synapomorphic for most of the phrynobatrachids. The lateral edge slanting outwards (state 3, Fig. 10) is synapomorphic for the rhacophorids and independently for the cacosternids, wherein a reversal to state 1 occurs synapomorphically for (*Cacosternum* + *Nothophryne*) and in *Ericabatrachus*.

51. Maxilla, expansion of the pars palatina (not including the anteromedial flange): (0) expansion of anterior 1/4 of pars palatina equals the expansion of posterior 1/4 in width; (1) anterior 1/4 more expanded than posterior 1/4.

Previously used by Lynch (1978) 7*, Ford (1990) 18*. Compared from two points 1/4 of the distance along maxilla from the anterior and posterior ends of the maxilla, and not including the anterior expansion associated with the presence of the flange. The length of the anterior flanges was noted to vary, but not coded for this analysis, since an objective method of assessing this was not apparent. The anterior of the flange being more expanded than the posterior (state 1) arises at the basal node and reverses sporadically in many single terminals. A reversal to equally expanded anterior and posterior parts (state 0) is synapomorphic for the phrynobatrachids, and occurs again in the petropedetids and Raninae, wherein state 1 reappears.

52. Maxilla, anteromedial flange of pars palatina: (0) absent; (1) present; (2) present and large, veering medially, creating a strongly concave anterior margin of the maxilla which creates a large fenestra between the maxilla and premaxilla.

Previously used by Clarke (1981) 8*, Cannatella (1985) 55*, Ford (1990) 17*, Vences (1999) 5*. Clarke's (1981) character 8 referred to whether the anterior edge of the maxilla was concave, convex or straight. Whether or not the edge is concave or not depends on the presence of the flange (Ford 1990). The presence of the flange (state 1) arises near the base of the tree. This character is prone to frequent transformations, but a loss of this flange is synapomorphic for the astylosternids, and again for (*Amnirana* + *Hydrophylax*). Large medially-directed flanges leaving a fenestra (state 2) occur in *Nannophrys*, *Batrachylodes*, (*Hoplobatrachus* + *Euphlyctis*) and *Aubria*.

53. Pterygoid, anterior ramus: (0) in contact with or fused to the maxilla; (1) separated slightly from the maxilla by cartilage.

Previously used by Clarke (1981) 9*, Ford (1990) 32, Wu (1994) 86. This is character ignores expansion of the pterygoid process. Ford (1990), in discussing characters 19 and 32, indicates some of the difficulty in quantifying this character. It was coded from the inside of the oral cavity, facing dorso-laterally at the point of junction of the anterior ramus of the pterygoid and the maxilla. Care was taken to code a fully ossified adult, since the state determined for this character seems to be correlated with ossification. The anterior ramus separated slightly from the maxilla by cartilage (state 1) is synapomorphic for the two species of *Dendrobates*, and occurs sporadically in a few taxa in the basal regions of the tree. The major evolutions of state 1 occur at node 50 for the petropedetids and Raninae, and in the basal half of the cacosternids. Reversals to state 0 occur in many of the fanged ranids.

54. Mandibular odontids: (0) absent; (1) present as large thickened processes of the anterior edge of angulosplenial, more developed in males but also present in a reduced state in females; (2) small, fine, tooth- or tusk-like projections of the dentary, angled posteriorly, in adult males only; (3) irregularly-shaped jagged fang-like odontids present for the entire length of lower jaw (false teeth).

Previously used by Emerson & Berrigan (1993) 7*. Noble (1931) reports that the teeth in *Dimorphognathus* (state 2) are the hypertrophied margins of the prearticular bone, which is figured in Noble (1922) p. I. Tusk-like odontids (state 2) occur only in males of *Phrynodon*, *Dimorphognathus* and *Petropedetes natator*, but are not synapomorphic for these taxa, as assumed by Parker (1935) when he united the subfamily Petropedetinae on the basis of this character. Large thickened processes of the anterior edge of the angulosplenial (state 1) occur in the large fanged ranids, which the equally-weighted topology indicates to have evolved three times. False teeth (state 3) are autapomorphic in this taxon set for *Nannophrys*. *Sooglossus* is also reported to have false teeth (Wu 1994), but these were not detected on the whole specimens examined.

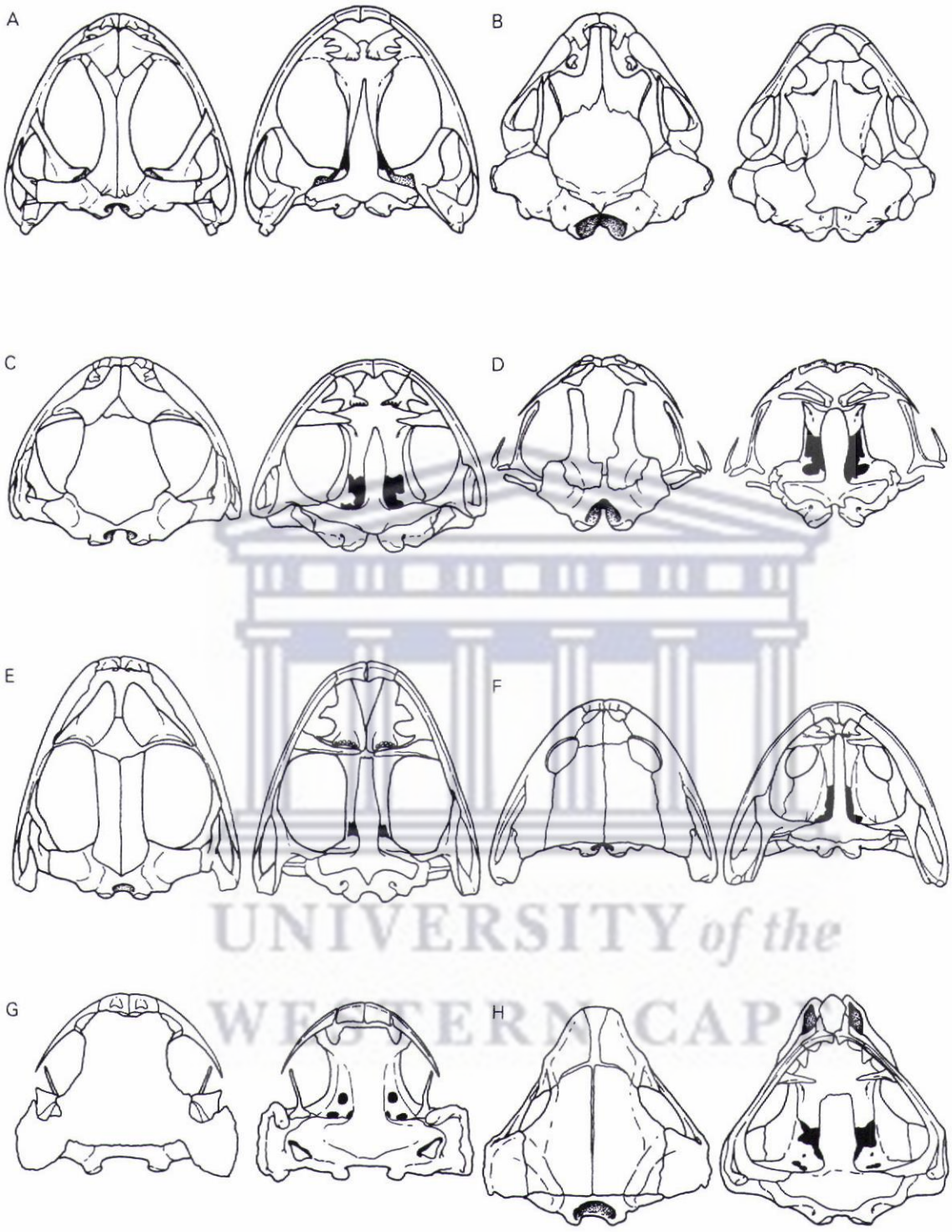

Figure 8. Dorsal (left) and ventral (right) views of anuran skulls, unmodified Figure 13.17 of Duellman & Trueb (1986:314), reproduced with permission. **A.** *Barbourula busuquanensis* (Discoglossidae). **B.** *Rhinophrynus dorsalis* (Rhinophrynidae). **C.** *Pelobates fuscus* (Pelobatidae). **D.** *Notaden nichollsi* (Myobatrachidae). **E.** *Leptodactylus bolivianus* (Leptodactylidae). **F.** *Caudiverba caudiverba* (Leptodactylidae). **G.** *Brachycephalus epihippium* (Brachycephalidae). **H.** *Rhamphophryne festae* (Bufonidae).

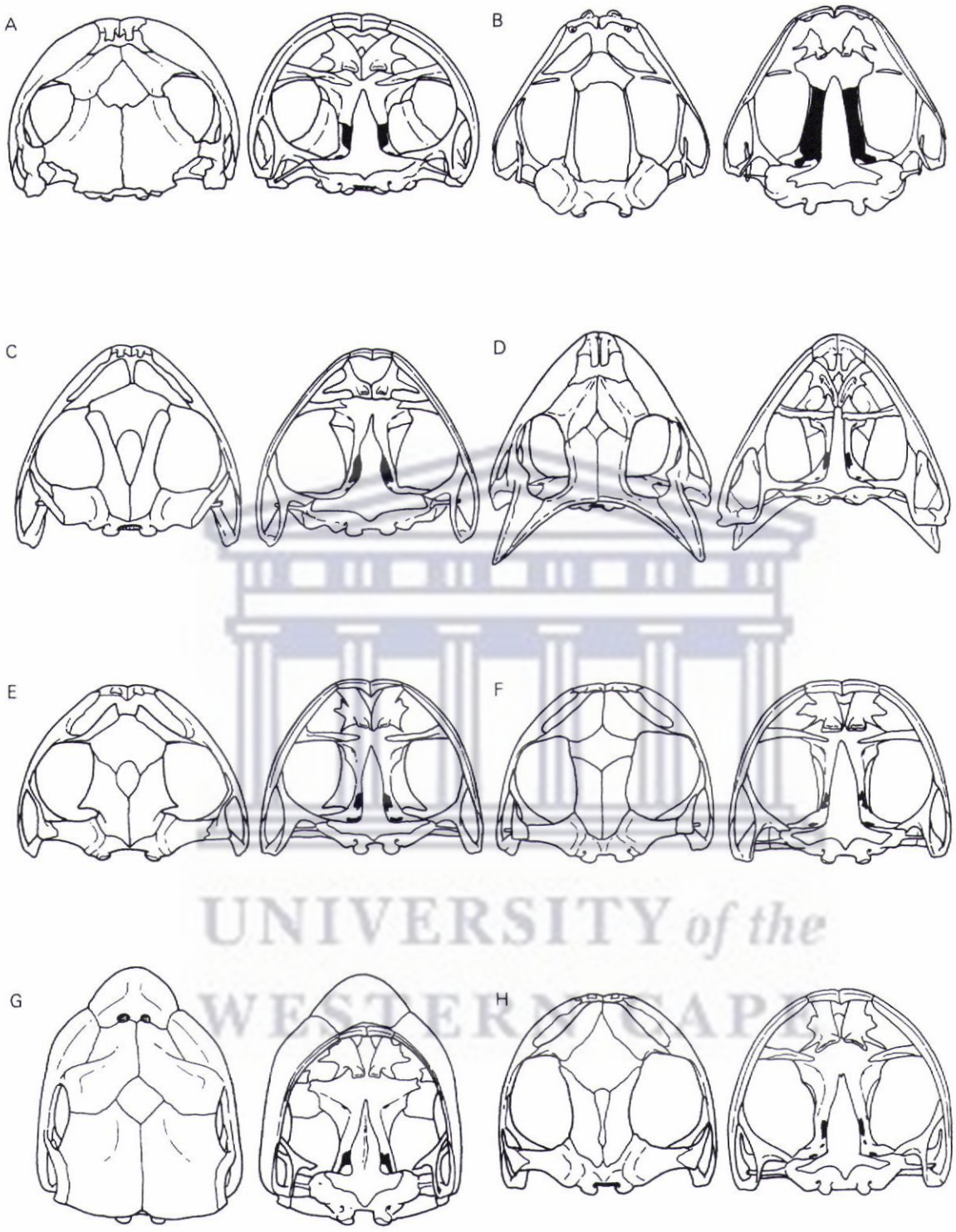

Figure 9. Dorsal (left) and ventral (right) views of skulls of hylid frogs, unmodified Figure 13.18 of Duellman & Trueb (1986:315), reproduced with permission. **A.** *Gastrotheca ovifera*. **B.** *Pseudacris clarkii*. **C.** *Phyllomedusa venusta*. **D.** *Hemiphractus proboscideus*. **E.** *Smilisca baudinii*. **F.** *Phrynohyas venulosa*. **G.** *Triprion petasatus*. **H.** *Osteocephalus leprieurii*.

55. Mentomeckelian bone, relative height on medial versus lateral edges: (0) height of medial edge is equal to height of lateral edge; (1) height of medial edge is less that height of lateral edge; (2) mentomeckelian long and fused with the angulosplenial.

Previously used by Ford (1990) 52, Wu (1994) 103. The height of the medial edge of the mentomeckelian bone being less than that of the lateral edge (state 1) is synapomorphic for the two species of *Arthroleptis*, the (Pyxicephalinae + *Conraua*), the petropedetids and for (*Discodeles* + *Platymantis*). This state also occurs in various phrynobatrachids, but optimises ambiguously to the base of this clade. A long fused mentomeckelian bone (state 2) is autapomorphic for *Phrynoglossus*. This character is coded as inapplicable in the sooglossids, which lack the mentomeckelian bones (Wu 1994).

56. Mentomeckelian bone, lateral processes: (0) absent; (1) shorter than or equal in length to mentomeckelian bones; (2) much longer than mentomeckelian bones.

Previously used by Wu (1994) 105. De Vos (1935) suggested that large plates on the mentomeckelian bones (state 2) are synapomorphic for the microhylids, but Wu (1994) found this not to be so. In the smaller taxon set examined here, this state was found to be a unique synapomorphy for the microhylids including *Hemisus*. A short lateral process (state 1) arises at the basal node and occurs in most taxa. Many of the Raninae from node 57 onwards display a reversal to no lateral process. This character is not applicable to the sooglossids and *Phrynoglossus*, where the mentomeckelian bones are absent and fused respectively.

57. Angulosplenial: (0) terminates at jaw articulation; (1) extends posteriorly to jaw articulation due to retroarticular process.

Previously used by Ford (1990) 53. The presence of a retroarticular process is an unambiguous synapomorphy for the family Dendrobatidae (Ford 1990; Ford & Cannatella 1993). Posterior extension of the lower jaw was evident in *Phrynoglossus*, (coded as 1), and to a much lesser extent in *Leptodactylus* and some *Arthroleptis variabilis* (coded as 0).

58. Parasphenoid, shape of tip of cultriform process: (0) rounded or serrated; (1) sharply pointed.

Previously used by Clarke (1981) 12*, separated into two characters since many permutations of this and character 59 were evident. State 0 is illustrated in Duellman & Trueb (1986) Fig. 13.17 (reproduced in Fig. 8) where D, E and H represent state 0, whilst A and B represent state 1. Sporadic single-taxon transformations to a pointed tip of the cultriform process (state 1, Fig. 10) occur in a few taxa of the arthroleptid-hyperoliid clade, but this state is synapomorphic for (*Arthroleptella landdrosia* + *A. lightfooti*) and for (*Cacosternum capense* + *C. namaquense*), and finally under Acctran optimization for the (Pyxicephalinae + *Conraua*).

Figure 10. Ventral view of skull of *Poyntonia paludicola* (MB 1254), showing lateral edge of pars palatina of premaxilla slanting outwards (c50:3), and a pointed tip (c58:1) to a biconcave (c59:1) cultriform process of the parasphenoid. Scale bar = 1 mm.

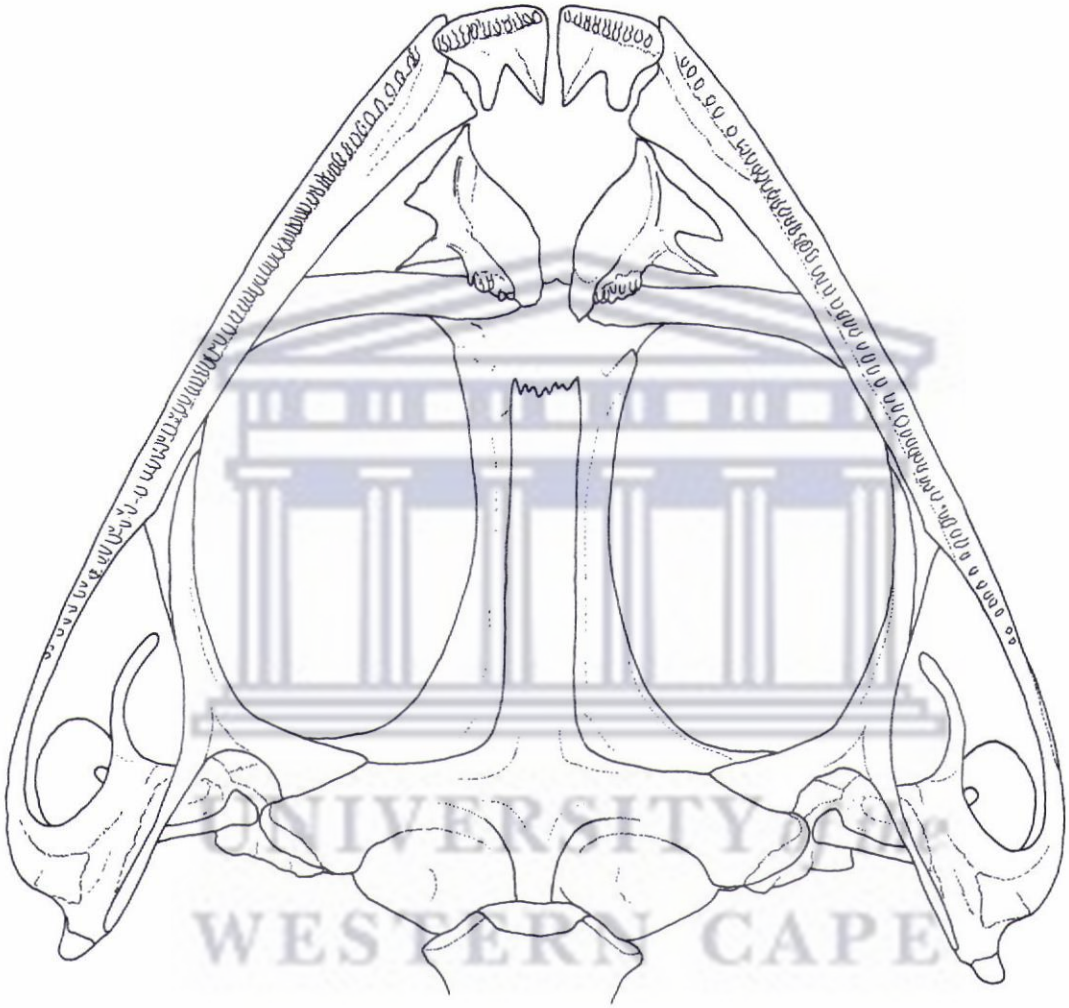

Figure 11. Ventral view of skull of *Discodeles bufoniformis* (CAS 109895), showing a serrated tip (c58:0) to a straight bordered (c59:0) cultriform process of the parasphenoid. Scale bar = 1 mm.

59. Parasphenoid, shape of cultriform process: (0) borders straight, process relatively wide; (1) borders biconcave, i.e. slight expansion in middle with narrower posterior section; (2) borders not straight but slightly tapering, can be very thin; (3) borders strongly converging, strongly triangular-shaped cultriform process.

Previously used by Clarke (1981) 12*, Ford (1990) 45*. Variation is illustrated by Duellman & Trueb (1986) Fig. 13.17 (reproduced in Fig. 8) where H corresponds to state 0, D and E correspond to state 1 and F corresponds to state 2. In their Fig. 13.18 (reproduced in Fig. 9), B and F correspond to state 3. State 1 is also illustrated in Fig. 10, whilst state 0 is illustrated in Fig. 11. Biconcave cultriform processes occur in some dendrobatids, the arthroleptid-hyperoliid lineage, the rhacophorids, *Tomopterna*, most cacosternids, petropedetids and the (Pyxicephalinae + *Conraua*). Thin tapering cultriform processes (state 2) are synapomorphic for (*Arthroleptella landdrosia* + *A. lightfooti*), and also occur in *Microbatrachella* and *Kassina*. Strongly triangular-shaped cultriform processes are synapomorphic for the species of *Cacosternum*, and occur independently in *Phrynoglossus* and *Phrynomantis*.

60. Parasphenoid, length of cultriform process: (0) reaching the anterior 1/5 of the orbit, but falling just short of the level of the palatines and planum antorbitale; (1) shorter, reaching only to about 2/3 length of orbit; (2) long, reaching the level of the palatines and planum antorbitale.

Previously used by Lynch (1978) 10*, Cannatella (1985) 30*, Ford (1990) 46, Wu (1994) 99*, Vences (1999) 9*. Short cultriform processes (state 1, Fig. 12) are synapomorphic for (*Colostethus* + *Mannophryne*) but also occur in *Cardioglossa*, the cacosternids *Cacosternum nanum parvum* and *Ericabatrachus*, and in the phrynobatrachids *Phrynobatrachus versicolor* and *P. krefftii*. Longer cultriform processes (state 2) are synapomorphic for three astylosternids, and independently at node 20, whereafter a reversal to state 0 is synapomorphic for the petropedetids excluding *Petropedetes natator*, and independently for (*Batrachylodes* + cacosternids + phrynobatrachids).

61. Anterior ramus of pterygoid in relation to the palatines and planum antorbitale in the dorsoventral plane: (0) falling far short of palatines, extending to approximately mid-orbital level; (1) short gap or slight overlap; (2) long, curving medially away from the maxilla towards an enlarged, wider planum antorbitale, separated from the lateral border of planum antorbitale by wide gap, palatines absent.

Previously used by Lynch (1978) 8*, Clarke (1981) 13*, Cannatella (1985) 35*, Ford (1990) 32*. A short gap or slight overlap (state 1) arises at node 6 for the (microhylids + ranoids). Reversals to falling far short (state 0) are synapomorphic for the Arthroleptinae, for (*Arthroleptella landdrosia* + *A. lightfooti*) and for (*Amolops* + *Nannophrys*). Medially curving

anterior rami of the pterygoid (state 2) are a unique synapomorphy for the Ptychadeninae, reportedly also occurring in *Lanzarana* (Clarke 1981, 1982).

62. Pterygoid, length of medial ramus: (0) present and long; (1) reduced, short but longer than its width, or rudimentary bumps; (2) extra long and thin.

Previously used by Cannatella (1985) 37, Ford (1990) 33*. Reduced rami (state 1, Fig. 12) are synapomorphic for the dendrobatids and independently for (Brevicipitinae + *Hemisus*). This state also occurs individually in *Mantella* and the cacosternids *Poyntonia*, *Microbatrachella* and *Cacosternum nanum parvum*. Extra long thin pterygoid rami (state 2) are uniquely synapomorphic for the Astylosterninae including *Leptopelis*.

63. Pterygoid, articulation of medial ramus: (0) anteroventral surface of otoccipital, may be a large gap; (1) ventrolateral edge of otic capsule; (2) anterior to and adpressed to parasphenoid ala along at least 1/2 its length.

Previously used by Lynch (1978) 9*, Ford (1990) 34, Wu (1994) 87*. Lynch (1978) considered state 1 as primitive whilst Ford (1990) considered state 0 as primitive. Pterygoids articulating with the ventro-lateral edge of the otic capsule (state 1) occurs unambiguously from node 9 for the ranoids, but optimise ambiguously to node 6 for the (microhyloids + ranoids). A reversal to articulation on the antero-ventral surface (state 0, Fig. 13) is synapomorphic in the cacosternids for (*Nothophryne* + *Cacosternum*). Medial rami of the pterygoid anterior to and adpressed strongly to the parasphenoid alae (state 2) are uniquely synapomorphic for the Pyxicephalinae. The state of this character was obscured by uncleared tissue in (*Hoplobatrachus* + *Euphlyctis*).

64. Overlap of the anterior border of the parasphenoid ala and medial ramus of pterygoid in the anterior to posterior plane: (0) point overlap (approximately 1/5) to moderately overlapping (approximately 1/4) along the length of the anterior edge of the ala, abutting; (1) close together but no contact (distinct gap), since medial ramus is more anterior; (2) strong overlap, approximately 1/2 length of anterior edge of the ala, abutting.

Previously used by Clarke (1981) 14*. This character is influenced by the length of both the alae and the median rami of the pterygoid, their separation and any curvature of the median rami (Lynch 1971). Optimization of this character is ambiguous down the spine of the tree until the Ranidae (node 20). State 1 occurs in the dendrobatids, and most hyperoliids and arthroleptids, although it reverses in *Leptopelis*, and synapomorphically so in (*Astylosternus* (*Nyctibates* + *Trichobatrachus*)). State 1 is synapomorphic for (cacosternids + phrynobatrachids). State 2 is a unique synapomorphy for the Pyxicephalinae.

Figure 12. Ventral view of skull of *Cacosternum nanum* (ES 342), showing a short cultriform process of the parasphenoid (c60:1), and reduced medial ramus of the pterygoid (c62:1). Scale bar = 1 mm.

Figure 13. Ventral view of skull of *Cacosternum boettgeri* (ES299), showing articulation of the medial ramus of the pterygoid on the anteroventral surface of the otoccipital (c63:0), and reduced parasphenoid ala (c66:1). Scale bar = 1 mm.

65. Parasphenoid alae, in frontal plane: (0) perpendicular to body axis; (1) pointing slightly anteriorly; (2) pointing distinctly posteriorly.

State 1 is illustrated in Figs 8C and 9G, whilst state 2 is illustrated in Fig. 8A. Anteriorly directed alae (state 1) are autapomorphic for Brevicipitinae. Posteriorly directed alae (state 2) are synapomorphic for the phrynobatrachids excluding *Natalobatrachus*, and for (*Amnirana* + *Hydrophylax*). This state also occurs in most species of *Cacosternum* and in sporadic single taxa throughout the tree.

66. Parasphenoid alae: (0) moderately long; (1) reduced or short.

Lynch (1971) notes the occurrence of this variation in the leptodactylids, where the parasphenoid alae may be short or long, orientated at right angles to the anterior rami or deflected posteriorly, and overlapped or not by the median rami of the pterygoids. Salamanders lack parasphenoid alae, but frogs generally have them (Lynch 1973). At the level of the Anura, their presence is considered plesiomorphic, and reduction derived. Reduced alae (state 1, Fig. 13) are synapomorphic for the microhylids including *Hemisus*, and also for (*Hyperolius* + *Kassina*). Reduced alae also occur in *Mantella* and three cacosternids.

67. Cranial exostosis: (0) absent, or slightly on sphenethmoid and/ or otoccipitals only, occasionally on the nasals; (1) present, extensive on sphenethmoid, nasals and other skull bones.

Previously used by Clarke (1981) 2, Cannatella (1985) 3*, Ford (1990) 4*, Wu (1994) 62. Trueb (1973) notes that exostosis is correlated with large size and with burrowing habits. Ford (1990) considered the presence of exostosis to be derived. The presence of cranial exostosis (state 1) is synapomorphic for the Pyxicephalinae but also occurs independently in *Nannophrys*. The latter genus and *Pyxicephalus* also exhibit co-ossification of the skin to the skull bones.

68. Nasals, contact with sphenethmoid: (0) overlapping the sphenethmoid; (1) not overlapping the sphenethmoid.

Previously used by Heyer & Liem (1976) 2, Wu (1994) 54. Also used as touching the frontoparietals (in modified form) by Heyer (1975) 23*, who suggested that nasals not in contact with the frontoparietal were primitive. Nasals are late ossifying elements, so this character is likely to be influenced by the stage of development of the specimens examined, which must therefore be adults. This character does not optimise unambiguously down the spine of the tree. Nasals not overlapping the sphenethmoid (state 1) occur in the microhylids including *Hemisus*, in the hyperoliids and one astylosternid, in most cacosternids and petropedetids, and are synapomorphic for (*Amnirana* + *Hydrophylax*).

69. Nasals, median contact: (0) separate, not in contact; (1) contact extensively on medial margin.

Previously used by Lynch (1978) 2*, Clarke (1981) 1*, Ford (1990) 1, Wu (1994) 51, Vences (1999) 1*. Ford (1990) found that the extent of contact of the nasals was correlated with size of the nasals, but was a less subjective measure than the relative size of the nasals. Nasals in contact on the medial margin (state 1) are synapomorphic for the Pyxicephalinae and occur in most fanged ranids. This state is also present in some phrynobatrachids and astylosternids, and in sporadic single taxa.

70. Nasals, shape: (0) large, triangular; (1) rectangular to round; (2) small, triangular or club-shaped.

Previously used by Liem (1970) 20, Clarke (1981) 1, Cannatella (1985) 4*, Ford (1990) 2*, Wu (1994) 52. This character has traditionally been difficult to assess. A more conservative coding strategy than that employed by Ford (1990) was used here, whereby orientation was not considered. Rectangular or round nasals (state 1) are synapomorphic for the (dendrobatids + sooglossids), for the arthroleptid-hyperoliid lineage, and for the (phrynobatrachids + cacosternids). Small, triangular or club-shaped nasals (state 2) are synapomorphic for the microhylids including *Hemisus*, (*Staurois* + rhacophorids), the Tomopterninae, (*Microbatrachella* (*Nothophryne* + *Cacosternum*)), two species of *Arthroleptella*, the Ptychadeninae and for (*Amnirana* + *Hydrophylax*), and occur in some petropedetids.

71. Degree of development of the otic plate of the squamosal and its relationship with the otoccipital: (0) otic plate present, overlapping the crista parotica, even posteriorly only or the lateral border of the otoccipital; (1) overlapping most or all of crista parotica and 1/4 to 1/2 of the otoccipital; (2) otic plate rudimentary or absent, only a thin rib of bone overlaps the outside of the crista parotica; (3) otic plate rudimentary, otic ramus extends posteriorly for only about 1/2 width of lateral border of the otoccipital in an arc, otic plate overlaps the crista parotica only in this region.

Previously used by Lynch (1978) 5*, Clarke (1981) 5*, Ford (1990) 29*. The otic plate overlapping most or all of the crista parotica and 1/4 to 1/2 of the otoccipital (state 1) is synapomorphic for the (Pyxicephalinae + *Conraua*), but also occurs in *Limnonectes*. Rudimentary otic plates (state 2) are synapomorphic for the cacosternids and independently for the Ptychadeninae, where a change to a rudimentary arc-shaped plate (state 3) is autapomorphic for *Hildebrandtia*.

72. Otic capsule, crista parotica, cartilaginous process extending towards the suprascapula: (0) present; (1) absent; (2) present, but part of the dorsal section of an extra large tympanum.

Absence of a cartilaginous spike of the crista parotica (state 1) arises at the basal node of the tree. Reversals to state 0 (Fig. 1) are synapomorphic for the Raninae, wherein a reversal to absence of the spike (state 1) occurs in four taxa. Independent reversals from state 1 to 0 also occur in *Leptodactylus* and *Mantidactylus*. Cartilage from the crista parotica that is integrated into the dorsal section of an extra large tympanum (state 2) is uniquely synapomorphic for (*Petropedetes newtoni* + *Arthroleptides*).

73. Otic capsule, crista parotica, cartilaginous process extending towards the suprascapula, if present: (0) short, cartilaginous; (1) very long, cartilaginous; (2) long and ossified, as is the crista parotica.

Most taxa in the basal portion of the tree code as inapplicable for this character. Processes being long and spike-like (state 1, Fig.1) are synapomorphic for the Ptychadeninae, and independently for (*Amnirana* + *Hydrophylax*). Processes being long and ossified (state 2) were identified for *Aubria* and *Limnonectes*.

74. Otic capsule, crista parotica, nature: (0) cartilaginous; (1) mostly ossified.

Previously used by Ford (1990) 49*, in a simplified form. Ossified crista parotica (state 1) are synapomorphic for (Pyxicephalinae + *Conraua*), and for (*Nanorana* (*Euphlyctis* + *Hoplobatrachus*)). Ossified crista parotica also occur independently in *Hildebrandtia* and *Leptodactylus*.

75. Otic capsule, crista parotica, angle: (0) perpendicular to body axis in frontal plane; (1) angled forward in the frontal plane, assessed from the position of the anterior margin of the crista parotica.

In state 1 (Fig. 14), the crista parotica is distinctly displaced forward, and much narrower distally than proximally. The otic capsules in some taxa displaying state 1 are extremely rounded, which may be partly responsible for this unique geometry. Rounded versus transversely elongated otic capsules were used by Laurent (1973) as a character in the arthroleptids. In *Cacosternum*, the crista parotica are also very reduced. The crista parotica being angled forward (state 1) is synapomorphic for the microhylids including *Hemisus*, and for the species of *Cacosternum*. State 1 also occurs independently in *Nanorana* and *Phrynoglossus*.

Figure 14. Dorsal view of the skull of *Cacosternum nanum* (ES 342), showing the crista parotica angled forward in the frontal plane (c75:1), and a small frontoparietal fontanelle not more than about 1/3 width of frontoparietal and gap (c76:1). Scale bar = 1 mm.

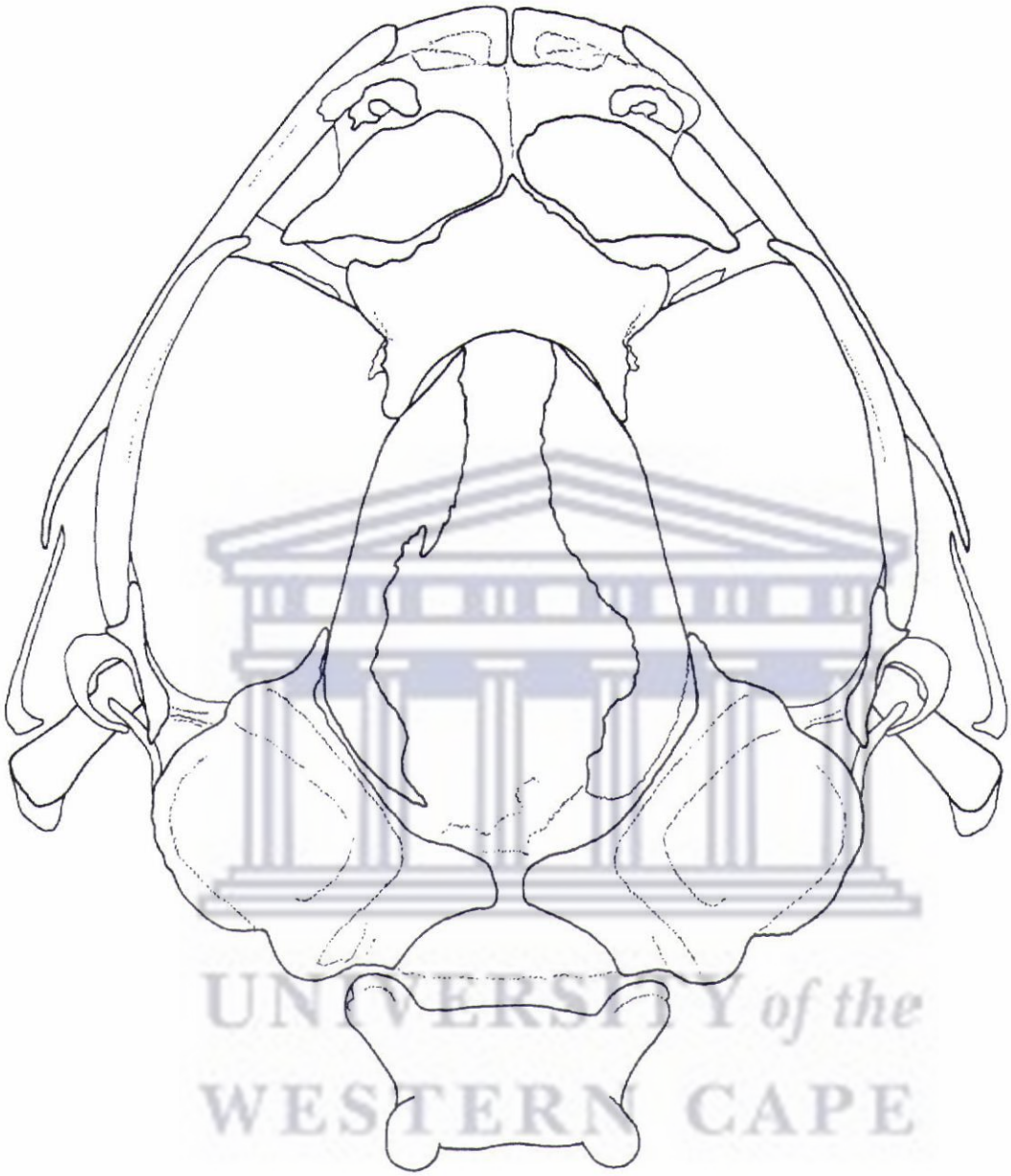

Figure 15. Dorsal view of the skull of *Cacosternum boettgeri* (ES 299), showing a large frontoparietal fontanelle more than about 1/3 width of frontoparietal and gap (c76:0), and an incomplete tympanic annulus (c87:1). Scale bar = 1 mm.

and at node 43 in the cacosternids. Diamond-shaped frontoparietals (state 3) are autapomorphic for *Pyxicephalus*.

79. Squamosal, thickness of zygomatic versus otic ramus: (0) otic ramus noticeably thicker, since distinct angular bend as it turns over the crista parotica not evident; (1) approximately equally thick, distinct angular bend onto the surface of the crista parotica evident; (2) zygomatic ramus notably expanded and exostosed.

Equal length otic and zygomatic rami with a distinct bend (state 1) are synapomorphic for the astylosternids including *Leptopelis*, and independently at node 20 for the Ranidae, wherein a reversal to state 0 unites the phrynobatrachids, cacosternids and *Tomopterna*. Zygomatic rami notably expanded and exostosed (state 2) are uniquely synapomorphic for the Pyxicephalinae.

80. Squamosal, length of the zygomatic ramus in comparison with that of the otic ramus: (0) zygomatic ramus longer than the otic ramus; (1) zygomatic ramus approximately equal in length to the otic ramus; (2) zygomatic ramus shorter than the otic ramus.

Previously used by Heyer (1975) 25*, Heyer & Liem (1976) 6*, Clarke (1981) 6*, Cannatella (1985) 42*, Ford (1990) 30*, Glaw, Vences & Böhme (1998) 7*, Vences (1999) 2. Heyer (1975) considered equal length rami, or a slightly greater zygomatic ramus, to be primitive in the leptodactylids. Zygomatic rami shorter than otic rami (state 2) arise at the basal node on this cladogram. Zygomatic rami approximately equal in length to otic rami (state 1) are synapomorphic for the (phrynobatrachids + cacosternids), and independently in the petropedetids excluding *Petropedetes natator*. This character state varies in the astylosternids and a reversal to zygomatic rami longer than otic rami (state 0) is synapomorphic for the (Raninae + petropedetids) clade.

81. Maxilla, shape of pars fascialis (lateral view): (0) well developed and rectangular; (1) reduced anteriorly, strong and triangular; (2) reduced to absent, may be rectangular and short.

Previously used by Clarke (1981) 7*, Ford (1990) 16*, Wu (1994) 76*, Glaw, Vences & Böhme (1998) 6, Vences (1999) 3* and 4*. The processus palatinus (= p. frontalis) was not included in the assessment of this character state, since it appears to be consistently present in the taxa examined. Rather, variation in the flange extending anterior to this is assessed. An anteriorly reduced triangular pars fascialis (state 1) is synapomorphic for the (dendrobatids + sooglossids), for the Arthroleptinae, for the cacosternids, for the two species of *Conraua* and independently for (*Nanorana* (*Euphlyctis* + *Hoplobatrachus*)). Reduced or absent pars fasciata (state 2) are synapomorphic for the microhylids including *Hemisus*, and for (*Cacosternum nanum* + *C. nanum parvum*), and occur sporadically elsewhere on the tree only in *Staurois* and *Arthroleptella*.

82. Quadratojugal, overlap with maxilla: (0) continuous, articulating with maxilla, slanting over each other or strongly overlapped, no reduction in quadratojugal; (1) anterior process of the quadratojugal reduced or absent, not touching the maxilla.

Previously used by Heyer (1975) 21*, Drewes (1984) 3*, Ford (1990) 21 and 22*, Wu (1994) 75*. Heyer (1975) considered continuous, articulating quadratojugals (state 0) to be plesiomorphic. Reduction in the anterior process is correlated with a general decrease in ossification that is often evident in smaller frogs (Trueb 1973). Reduction of the anterior process (state 1) is synapomorphic for (Brevicipitinae + *Hemisus)*, and independently for the species of *Cacosternum* (reversing in *C. capense*) and (*Arthroleptella landdrosia* + *A. lightfooti*).

83. Quadratojugal: (0) present; (1) absent.

Similar to Lynch (1978) 1*, Ford (1990) 21*, Wu (1994) 78*. The quadratojugal is one of the most frequently lost anuran skull bone (Lynch 1973; Trueb 1973). The quadratojugal was considered absent if the descending ramus of squamosal can be seen to be separated from descending ramus of the palatine by cartilage, and if the articular is predominantly cartilaginous. De Villiers (1931a, 1931b) first noted that the quadrate cartilage is entirely unossified in *Cacosternum*. The quadratojugal being absent (state 1) is synapomorphic at node 43 in the cacosternids, and independently for the hyperoliids, occurring also in *Leptopelis*.

84. Pars externa plectri of breeding males: (0) large, present, rounded, covering 1/3 to 2/3 of the area inside the tympanic annulus; (1) small and rod-like, or absent; (2) extremely large, covering more than 2/3 of area inside tympanic annulus.

Specimens in which it may have been torn during preparation were not used for coding. Sexual dimorphism in tympanum size has been noted in the Ranidae by various authors since Noble (1931). Small pars externa plectri (state 1) arise at the basal node on this cladogram, and occur in most ranids. A reversal to large plectri (state 0) is synapomorphic for the microhylids, (changing to state 1 in *Hemisus*) and independently for the hyperoliids and for (*Poyntonia* + *Ericabatrachus*). Extremely large pars externa plectri (state 2) are uniquely synapomorphic for the dendrobatids in this study.

85. Premaxilla, projection of pars fascialis (alary process): (0) vertical (dorsal); (1) backwards (posterodorsally); (2) forwards (anterodorsally).

Previously used by Ford (1990) 12, Wu (1994) 68. This character appears to be uncorrelated with the extent of forward projection of the snout tip, as it is vertical in *Phrynobatrachus* where the snout is wedge-shaped and considerably overshot. In combination with state 1 of character 86, state 2 was thought to be one of a suite of diagnostic characters for the dendrobatids (Ford 1990), but this state also occurs independently in *Mantella*, possibly an adaptation to

myrmecophagy. Backwardly projecting alary processes (state 1) are synapomorphic under Acctran for the arthroleptids (including *Leptopelis*), at node 28 for (*Batrachylodes* + phrynobatrachids + cacosternids), wherein a reversal to vertical processes (state 0) is synapomorphic for the genus *Cacosternum* and independently for (*Poyntonia* + *Ericabatrachus*). Under Acctran, state 1 optimises as synapomorphic for the Raninae, but reverses many times therein.

86. Premaxilla, angle of pars fascialis (alary process): (0) dorsally, perpendicular to pars dentalis; (1) inclined laterally outwards away from midline.

Previously used by Wu (1994) 72. Laterally inclined alary processes (state 1) are synapomorphic for (dendrobatids + sooglossids), the two species of *Arthroleptis*, the mantellids + rhacophorids (reversing in the rhacophorids), the phrynobatrachids, for (*Anhydrophryne* + *Arthroleptella hewitti*), and at node 73 in the Raninae for ((*Amnirana* + *Hydrophylax*)(*Amolops* + *Nannophrys*)).

87. Tympanic annulus: (0) complete; (1) incomplete, rounded; (2) absent; (3) incomplete, pear-shaped, involving the squamosal as its dorsal limit, with the dorsal section of cartilage fused onto squamosal.

Previously used by Wu (1994) 66*. Care was taken to code this from well-prepared specimens or to consider any potential damage to the tympanic annulus. The tympanic annulus is incomplete (state 1, Fig. 15) independently in *Leptodactylus*, *Phrynomantis* and *Cacosternum boettgeri*. It is absent (state 2) in *Hemisus*, *Cacosternum namaquense* and the sooglossids. Pear-shaped tympanic annuli (state 3) are synapomorphic for the dendrobatids examined here, independently for the two species of *Arthroleptis*, and for the astylosternids. Elsewhere, a pear-shaped tympanic annulus occurs only in *Hyperolius* and *Ericabatrachus*.

88. Stapes (columella): (0) present; (1) reduced; (2) absent.

Previously used by Lynch (1973) 22, Lynch (1978) 20*, Cannatella (1985) 45, Ford (1990) 11*, Wu (1994) 67*. Lynch (1973) noted that this character was limited in usefulness to discussing the distinctions between and relationships of species within a genus, which was also found to be the case within the present taxon set. A reduced stapes (state 1) occurs in some species of *Cacosternum*. Absence of the stapes (state 2) occurs in the sooglossids, *Hemisus* and *Cacosternum namaquense* are postulated to be independent transformations.

Hyobranchial Skeleton

89. Hyoid, hyale, width from start of anteromedial process: (0) narrow, without a flange extending to half the length of hyale; (1) wide, flange extending to half the length of hyale.

Drewes (1984:12) states, 'in the microhylids, this structure (whole anterior horn) can be interpreted as either present as a thick strip or flange contiguous with the ceratohyal, or absent'. Here it is interpreted as absent for the microhylid exemplars examined. However, in many of the taxa given state 1 for this character, a separate medial branch was also observed, accordingly they are treated as two characters. A flange to half the length of the hyale (state 1, Figs 16A, C, D and F) is synapomorphic for (*Colostethus* + *Mannophryne*), independently for (*Hyperolius* + *Kassina*), and under Acctran optimization for the Tomopterninae. State 1 also arises at node 41 in the cacosternids, wherein it reverses four times.

90. Hyoid, hyale, free flange towards jaw just anterior to its angle: (0) absent; (1) present.

A free flange (state 1, Fig. 16C) is uniquely synapomorphic for the Tomopterninae.

91. Medial branch of anterior process of hyale: (0) long, straight, thin; (1) short and usually curled, relatively thick; (2) small nipple-like knob only, (3) slightly elongated, but not more than three times its width; (4) absent.

Previously used by Heyer (1975) 30 part, Heyer & Liem (1976) 19*, Drewes (1984) 11 part, Ford (1990) 55, Wu (1994) 110*. Heyer (1975) suggested that the presence of the anterior process is primitive. The plesiomorphic condition is illustrated in Fig. 16B. A short, thick and usually curved anterior process (state 1, Fig. 16E) is synapomorphic for (*Cacosternum capense* + *C. namaquense*), and independently for (*Arthroleptides* + *Petropedetes parkeri*). A small nipple-like knob (state 2, Fig. 16C) arises at node 25 and is the common state in the Ranidae, reversing to state 0 in *Petropedetes* and independently at node 72 in the Raninae. Slightly elongated anterior processes (state 3, Fig. 16D) are uniquely synapomorphic for (*Cacosternum boettgeri* + *C. nanum parvum*). The medial branch being absent (state 4), is uniquely synapomorphic for the microhylids including *Hemisus*.

92. Hyoid, shape of the stalk of the alary processes: (0) narrow and pinched, blade-like; (1) thick and rounded, slightly less than or as expanded as the thick distal portion.

The shape of the alary processes was used by Liem (1970) 12*, Heyer (1975) 31*, Heyer & Liem (1976) 18*, Ford (1990) 59*, Wu (1994) 112*. Heyer & Liem (1976) considered 'broad and wing like' alary processes (equivalent of state 1 here) to be primitive. Thick rounded alary processes (state 1, Figs 16A, D and F) are synapomorphic for (dendrobatids + sooglossids), reversing in *Dendrobates*, for the Arthroleptinae, at node 26 in the Ranidae (reversing synapomorphically in some cacosternids). State 1 occurs in most of the large fanged Raninae.

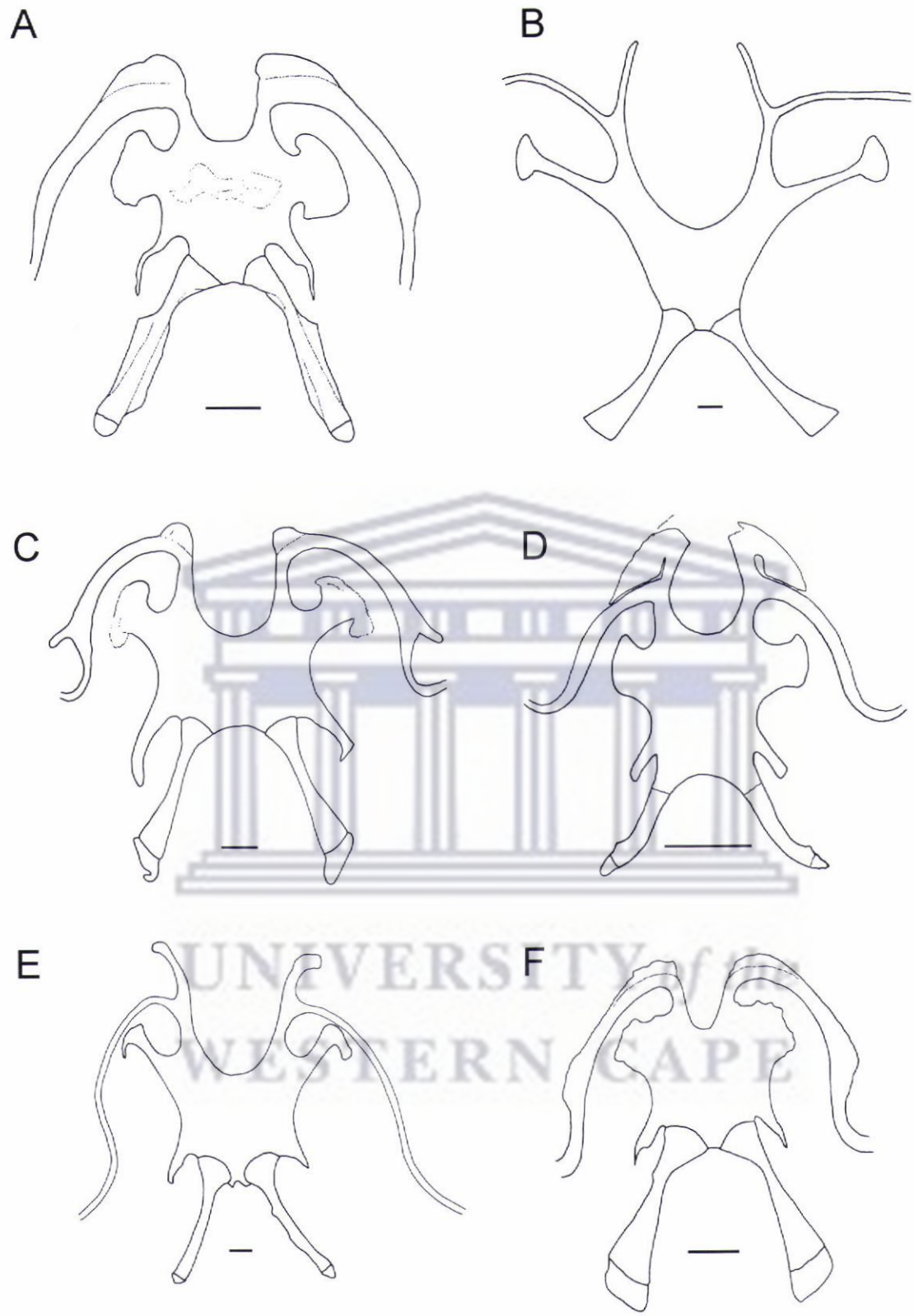

Figure 16. Hyoid apparatus of **A.** *Phrynobatrachus natalensis* (ES 288) showing c96:1, c101:2, c104:2, c105:2. **B.** *Leptopelis vermiculatus* (ES 717) showing c91:0, c92:0, c93:0, c96:0, c102:1. **C.** *Tomopterna tandyi* (AC 1561) showing c89:1, c90:1, c91:2, c97:0. **D.** *Cacosternum boettgeri* (ES 152) showing c91:3, c92:1, c101:1. **E.** *Arthroleptides martiensseni* (ES 770) showing c89:0, c91:1, c97:0. **F.** *Poyntonia paludicola* (MB 1254) showing c89:1, c92:1, c96:1, c97:0. Scale bar = 1 mm.

93. Hyoid, alary process, width of base: (0) equal to the stalk; (1) broader than stalk.

The base of the alary process being broader than the stalk (state 1) is synapomorphic at node 9 for the (arthroleptid-hyperoliids + Ranidae), and under Acctran optimization for the dendrobatids. Within the Ranidae, reversals to state 1 are synapomorphic for the rhacophorids and the Ptychadeninae.

94. Hyoid, distal expansion of alary process: (0) absent; (1) present.

An expansion at the end of the alary process arises at the basal node, and most ranids have some form of it. Reversals to absence of the distal expansion (state 0) are synapomorphic for (Brevicipitinae + *Hemisus*), and independently for (*Staurois* + rhacophorids).

95. Hyoid, shape of the distal expansion of the alary process: (0) large rounded to trumpet-shaped or slightly triangular expansions; (1) oval, slanted posteriorly at a 45° angle to the body axis; (2) extremely small, rounded, edges can be ragged; (3) small, narrow, blade-like, slanting posteriorly at a 45° angle.

Many taxa were coded as unknown for this character due to insufficient staining of cartilages leading to poor visibility. Oval, slanted distal expansions (state 1) are uniquely synapomorphic for the astylosternids. Extremely small, rounded and ragged expansions (state 2) optimize to the base of the arthroleptid-hyperoliid lineage, reversing therein to state 0 in the Arthroleptinae. Small, narrow, downwardly slanting processes (state 3) are synapomorphic for the Ptychadeninae, for (*Amnirana* + *Hydrophylax*) and the petropedetids, wherein a reversal to state 0 is synapomorphic for (*Arthroleptides* + *Petropedetes parkeri*).

96. Hyoid, angle of alary processes: (0) angled anteriorly; (1) angled laterally.

Many taxa were coded as unknown for this character due to insufficient staining of cartilages leading to poor visibility. Laterally angled alary processes (state 1, Figs 16A, C, D and F) are synapomorphic for the (dendrobatids + sooglossids), the microhylids including *Hemisus*, and at node 26 for (Tomopterninae + *Batrachylodes* + cacosternids + phrynobatrachids), and independently for the Ptychadeninae.

97. Hyoid, hyoglossal sinus: (0) deeper than anterior border of base of alary processes; (1) shallow, less than or just reaching anterior border of base of alary processes; (2) shallow, but fibrous line of a deep sinus visible.

Previously used by Ford (1990) 57, Wu (1994) 111. State 0 is illustrated in Figs 16B, C and E. A shallow sinus (state 1, Figs 16A, D and F) is synapomorphic for (dendrobatids + sooglossids), for the hyperoliids, most astylosternids, the (mantellids + rhacophorids), the

(cacosternids + phrynobatrachids), and three times for smaller clades in the Raninae. A hyoid plate with a line of a deep sinus present (state 2) is autapomorphic in *Hemisus*.

98. Hyoid plate, calcification: (0) not or only slightly calcified centrally, but not calcified between the thyrohyals; (1) well calcified, with large proximal expansions at the bases of the thyrohyals, resulting in the thyrohyals appearing almost fused at the posterior end of the plate.

Previously used by Emerson & Berrigan (1993) 36*. Parahyoid bones do not occur in the taxa studied here, although parahyoid calcification is common. The calcification referred to in this character is only that between the thyrohyals. Calcification between the thyrohyals (state 1) is synapomorphic for (Brevicipitinae + *Hemisus*), and for (*Phrynoglossus* (*Platymantis* + *Discodeles*)) but is independently present in *Leptodactylus*.

99. Hyoid, fibrous uncalcified suture on hyoid plate: (0) absent; (1) present centrally, running transversely; (2) present centrally, running longitudinally and not present at extreme anterior and posterior edges of the plate.

Previously used by Wu (1994) 118. An uncalcified transverse suture anterior to the thyrohyals (state 1) is synapomorphic for (Brevicipitinae + *Hemisus*), and for (*Phrynoglossus* (*Platymantis* + *Discodeles*)). An uncalcified longitudinal suture (state 2) is synapomorphic for (*Amnirana* + *Hydrophylax*), and occurs independently in *Conraua crassipes*.

100. Hyoid plate, shape: (0) wide, width greater than or equal to length; (1) narrow, longer than wide.

Previously used by Emerson & Berrigan (1993) 37*, Wu (1994) 108. Measured from the medial point between the thyrohyals to the antero-medial edge of the hyolaryngeal sinus, and across from underneath the alary processes. Narrow hyoids (state 1) are synapomorphic for the two species of *Dendrobates*, for the hyperoliid–arthroleptid clade (wherein a reversal to wide hyoids is synapomorphic for the astylosternids), for (*Arthroleptella landdrosia* + *A. lightfooti*), for (*Cacosternum boettgeri* + *C. nanum parvum*) and for (*Amnirana* + *Hydrophylax*).

101. Hyoid, posteromedial process (thyrohyal): (0) cartilaginous stalk absent; (1) cartilaginous stalk present; (2) hyoid plate pinched above thyrohyals, posterior lateral processes originating close to base of alary processes.

Previously used by Liem (1970) 10, Heyer & Liem (1976), Drewes (1984) 10, Ford (1990) 62, Blommers-Schlösser (1993) 9, Wu (1994) 114, Emerson *et al.* (2000a) 5*. Trewavas (1933) noted that absence of the stalk is the common condition. Laurent (1978) discusses the importance of cartilaginous stalks in hyperoliid–arthroleptid relationships.

A cartilaginous stalk at the base of the thyrohyal is reportedly present in most microhylid taxa (Parker 1881; Ramaswami 1939) but is absent in brevicipitids and a few other taxa (Wu 1994), including the choice of microhylids examined here. Presence of a cartilaginous stalk (state 1, Fig. 16D) is synapomorphic for the hyperoliid–arthroleptid lineage, reversing to state 0 in *Leptopelis*. The state is coded as indeterminate for *Cardioglossa*, for which Blommers-Schlösser (1993) reported stalks absent, since stalks were not apparent on the specimens examined. Stalks also appeared to be present in a single specimen of *Amnirana* examined, which was slightly immature. Stalks present (state 1) are also synapomorphic for node 45 in the cacosternids (transforming to state 2 in *Nothophryne*).

The hyoid plate pinched above thyrohyals (state 2) represents a condition whereby the thyrohyals are close together, but attached to a cartilaginous base which is formed by a narrowing of the posterior portion of the hyoid plate. This narrow section could conceivably be the fused vestiges of the stalks, or a pre-stalked condition. State 2 is illustrated in Fig. 16A, and for *Colostethus* in Ford's (1990) Fig. 19. State 2 is synapomorphic for the dendrobatids, independently in the phrynobatrachids for (*Phrynobatrachus acridoides* + *P. natalensis*), and again for (*Anhydrophryne* + *Arthroleptella hewitti*). State 1 was not detected in *Arthroleptella* (*cf.* Blommers-Schlösser 1993), although the presence of state 2 in this group may explain past observations.

102. Hyoid, posterolateral process: (0) present; (1) absent; (2) extremely reduced, small bumps only.

Previously used by Liem (1970) 15, Drewes (1984) 9, Ford (1990) 60, Wu (1994) 113*, Vences (1999) 21*. Laurent (1978) used this character to support his proposed relationship between the hyperoliids and arthroleptids (Laurent 1951). Absence of posterolateral processes (state 1, Fig. 16B) is uniquely synapomorphic for the hyperoliid–arthroleptid lineage, with a reversal in the Astylosterninae, where *Scotobleps*, *Trichobatrachus* and *Leptodactylon* have the processes present. Laurent (1978) illustrates *Astylosternus* as also having posterolateral processes. Reduced processes (state 2) occur independently in *Nyctibates* and *Staurois*.

103. Hyoid, posterolateral processes, length: (0) long; (1) short, less than 1/3 length of posteromedial process (thyrohyal); (2) rudimentary bumps or stumps.

Previously used by Liem (1970) 15 part, Ford (1990) 61. Since this character is assessed by comparison to the thyrohyals, its coding is dependent on the length of the thyrohyals: long thyrohyals make the processes appear short. This was nevertheless considered to be the most objective method of quantifying the length of the posterolateral processes. Short posterolateral processes (state 1) optimize to node 9 for the Ranoidea, but reverse to state 0 at node 25. Thereafter, short processes (state 1) are synapomorphic for the two species of *Ptychadena*, and

for the (cacosternids + phrynobatrachids), reversing to state 0 for most cacosternids. Rudimentary bumps (state 2) are synapomorphic for some phrynobatrachids and also occur in *Staurois* and *Nyctibates*.

104. Hyoid, posteromedial process (thyrohyals), expanded flange on medial side: (0) absent; (1) present, small; (2) present, widening of thyrohyals due to distal medial expansion towards larynx, which has a concave inside edge.

Wu (1994) 116 mentions flanges on the inner surfaces of the thyrohyals in the microhylids. Small medial flanges (state 1) are synapomorphic for the two species of *Ptychadena*, but also for the species of *Arthroleptella* and for (*Anhydrophryne* + *Arthroleptella hewitti*) but occur individually in *Cardioglossa*, *Philautus*, *Platymantis* and *Staurois*. Large medial flanges with a concave inside edge (state 2) are uniquely synapomorphic for the phrynobatrachids excluding *Natalobatrachus*.

105. Hyoid, posteromedial process (thyrohyals), expanded flange on lateral side: (0) absent; (1) present distally, small; (2) present medially, with curved edge.

Wu (1994) 117 mentions flanges on the outer surfaces of the thyrohyals in the microhylids. Under Acctran optimization, this flange (state 1) is synapomorphic for (*Cacosternum* + *Nothophryne*). Medial flanges with curved edges (state 2) are uniquely synapomorphic for the phrynobatrachids excluding *Natalobatrachus*, wherein a reversal to state 0 is synapomorphic for (*Phrynobatrachus dendrobates* + *P. versicolor*) and also occurs in *Dimorphognathus*.

106. Hyoid, posteromedial process (thyrohyals): (0) expanded at proximal ends only; (1) equal width, not expanded at either end; (2) expanded at both ends.

State 1 is similar to that used by Wu (1994) 115. Unexpanded thyrohyals (state 1) are synapomorphic for the dendrobatids, for the arthroleptid-hyperoliid lineage, for (*Amnirana* + *Hydrophylax*), and under Acctran optimization for node 45 in the cacosternids. Thyrohyals expanded at both ends (state 2) arises at the basal node, and reversals to state 0 are synapomorphic for the (microhylids + *Hemisus*), rhacophorids, petropedetids, node 62 in the Ranidae, and (*Batrachylodes* + cacosternids + phrynobatrachids).

107. Hyoid, distance between posteromedial processes (thyrohyals): (0) close together, less than one times the width of the proximal expansion of the thyrohyal apart; (1) about once the width of the proximal expansion of the thyrohyal apart; (2) more than 1.5 times the width of the proximal expansion of the thyrohyal apart.

Previously used by Liem (1970) 10*, Ford (1990) 63. Stalked thyrohyals are naturally further apart, and taxa having these mostly display state 2. One width separation (state 1) arises

at node 25 in the Ranidae. Wide thyrohyals (state 2) are synapomorphic for the hyperoliid–arthroleptid lineage, and for (*Microbatrachella* (*Nothophryne* + *Cacosternum*)). Reversals to state 0 are synapomorphic at node 58 in the Ranidae, and node 35 in the phrynobatrachids.

108. Cricoid ring, oesophageal process: (0) present; (1) absent.

Previously used by Wu (1994) 120. Trewavas (1933) suggested that a mediodorsal oesophageal process occurs only in and is diagnostic for the Ranidae and rhacophorids, but this process occurs widely in the leptodactylids (Lynch 1971) and was found in some microhylids, dendrobatids and sooglossids by Wu (1994). Lynch (1971) expressed doubt as to the value of this character. Where it was observed it is coded as present, but absence recorded for some taxa could be an artefact of preparation, staining or indeed genuine. In some of these cases, it was coded as unknown. Length of the process was found to vary in the ranids. Absence of the process (state 1) is synapomorphic for the microhylids including *Hemisus*, for (*Hyperolius* + *Kassina*) and for the two species of *Ptychadena*. It was recorded as individually absent in many individual taxa.

109. Cricoid, bronchial processes: (0) present, short, not branched or latticed; (1) present, long, ending in an extensive lattice of cartilage surrounding or ramifying through the lungs.

Previously used by Blommers-Schlösser (1993) 8*, Wu (1994) 115. Long latticed bronchial processes (state 1) are uniquely synapomorphic for the microhylids including *Hemisus*.

110. Larynx, arytenoid cartilages of breeding male: (0) rounded; (1) disproportionately long and oval-shaped, relative to the width of the entire larynx.

A distinct lengthening of the arytenoid cartilages (state 1) is postulated to be synapomorphic for the (dendrobatids + sooglossids), for the hyperoliids, for the two species of *Ptychadena*, and for node 26 in the Ranidae, whereafter reversals to state 0 are synapomorphic for (*Anhydrophryne* + *Arthroleptella hewitti*). State 1 occurs sporadically in a few other taxa throughout the tree.

Limb Osteology

111. Tarsal one (not naviculare): (0) absent as independent element; (1) present.

Previously used by Lynch (1973) 18, Drewes (1984) 27*, Ford (1990) 120, Blommers-Schlösser (1993) 25*, Wu (1994) 180, Vences (1999) 16. Terminology of Ford (1990) used here. This character was not assessed for many of the fanged ranids, due to insufficient clearing. Under Acctran optimization, a free tarsal 1 (state 1) is synapomorphic for the arthroleptids, again at nodes 32 and 36 in the phrynobatrachids, for the mantellid-rhacophorid lineage

(reversing in the rhacophorids), at node 73 in the Raninae for ((*Amnirana* + *Hydrophylax*)(*Amolops* + *Nannophrys*)), and for (*Pyxicephalus* + *Aubria*).

112. Tarsal two: (0) free, not fused to tarsal three; (1) fused to tarsal three.

Previously used by Ford (1990) 119, whose terminology is adopted. Duellman & Trueb (1986) note that salamanders have up to four elements, suggesting that the greater number of free elements in the Anura is plesiomorphic. A fused second tarsal (state 1) is synapomorphic for the (mantellids + rhacophorids), the Tomopterninae, the genus *Phrynobatrachus* (including *Dimorphognathus* and *Phrynodon*), and at nodes 58 and 72 in the Raninae. Fused tarsalia also occur independently in *Hemisus* and *Ericabatrachus*.

113. Carpal state *sensu* Laurent & Fabrezi (1989): (0) A; (1) B; (2) C; (3) D; (4) E; (5) F.

These six states recognized by Laurent & Fabrezi (1989), were coded from the original work, and extrapolated to other taxa with the similar carpal structure. This coding is deemed the best way of extracting the phylogenetic signal from the carpi, since, as noted by Ford (1990), there are three factors complicating the determination of the number of carpal elements. The first of these is disagreement concerning the homology of the different elements forming during ontogeny. Secondly, different patterns of fusion may lead to the same reduced numbers. Thirdly, there is taxonomic variation in the individual elements involved in the fusion (Holmgren 1933; Jarosovà 1973; de Saint-Aubain 1981; Ford 1990). State 1 (B) is synapomorphic for the two species of *Arthroleptis*. State 2 (C) is not found in any taxa included here, but is reported to occur in *Schoutedenella*, amongst ranoid taxa. State 3 (D) arises at node 20 leading to the Ranidae, and is the common state therein. State 4 (E) is synapomorphic for the dendrobatids, and independently for the microhylids, wherein it transforms to state 5 (F) in *Hemisus*. State 4 (E) is also synapomorphic for (*Discodeles* + *Platymantis*), and independently for the Pyxicephalinae, and occurs independently in *Staurois* and *Nanorana*. State 5 (F) is also synapomorphic at node 35 in the phrynobatrachids, and occurs independently in *Ericabatrachus*.

114. Distal intercalary elements: (0) absent; (1) present, thick concave discs; (2) present, wedge-shaped, rounded anteriorly and slightly concave posteriorly.

Previously used by Lynch (1973) 16, Drewes (1984) 24, Duellman & Trueb (1986) J, Tyson (1988) 26, Ford (1990) 116, Blommers-Schlösser (1993) 6*, Wu (1994) 178–9, Glaw, Vences & Böhme (1998) 8*, Vences (1999) 15*, Emerson *et al.* (2000a) 2*. The presence of intercalary elements is considered an adaptation to an arboreal habit (Laurent 1964) and is considered to be derived (Lynch 1973). Drewes (1984) states that the intercalary elements in hyperoliids are probably homologous, but notes that the shape is different in other groups of Anura which

possess them. Following this, the thick concave discs in *Phrynomantis* are given a separate autapomorphic state. Wedge-shaped intercalary elements (state 2) are synapomorphic for the hyperoliids and occur independently in *Leptopelis*. State 2 is independently synapomorphic for the (mantellids + rhacophorids).

115. Digital subarticular sesamoids: (0) absent; (1) present.

Previously used by Drewes (1984) 13, Ford (1990) 113, Blommers-Schlösser (1993) 16. Also referred to in the literature by Laurent (1940, 1941a, 1941b, 1942), Vences (1999) and Vences *et al.* (2000a). Drewes (1984) reported the presence of digital subarticular sesamoids in *Ptychadena oxyrhynchus* (Smith, 1849). Within the Ptychadeninae examined in this study, they were only found in *Ptychadena* [*mascareniensis*]. Digital subarticular sesamoids are rare and occur only sporadically in the ranids. Drewes (1984) considered the absence of sesamoids as plesiomorphic, which is how this character is treated in this analysis. Subarticular sesamoids (state 1) are synapomorphic for the arthroleptid-hyperoliid lineage, and for (*Phrynoglossus* (*Discodeles* + *Platymantis*)). State 1 also occurs independently in *Colostethus*, *Leptodactylus*, *Hemisus*, *Phrynobatrachus plicatus*, *Ptychadena* [*mascareniensis*] and *Cacosternum boettgeri*.

116. Sesamoid(s) on ventromedian surface of tarso-metatarsal joint: (0) absent; (1) present.

Previously used by Ford (1990) 123 in part, Wu (1994) 183. Ford (1990) did not distinguish between ventro-medial sesamoids and ventro-lateral sesamoids, but in this study, the placement as well as the number of elements were found to be variable. Accordingly, the character was separated into two. Sesamoids on the ventro-median surface of the tarso-metatarsal joint (state 1) are synapomorphic for the two species of *Dendrobates*, and independently for (Brevicipitinae + *Hemisus*). State 1 occurs elsewhere only in *Natalobatrachus*, *Cacosternum boettgeri* and *C. namaquense*.

117. Sesamoid(s) on ventrolateral surface of tarso-metatarsal joint: (0) absent; (1) one present; (2) two present; (3) three present.

Previously used by Ford (1990) 123 part, Wu (1994) 174. A single sesamoid (state 1) is synapomorphic for (*Cacosternum capense* + *C. namaquense*). Two sesamoids (state 2) optimises between the basal node and node 6, but transforms to state 1 in the sooglossids. This state is synapomorphic in the cacosternids for (*Arthroleptella landdrosia* + *A. lightfooti*), and occurs independently in *Mantella* and *Natalobatrachus*. The presence of three sesamoids (state 3) is autapomorphic for *Cacosternum boettgeri*.

118. Sesamoid in the aponeuris palmaris: (0) none; (1) one.

Previously used by Tyson (1988) 32, Ford (1990) 108 and Wu (1994) 168. The latter author refers to a dorsal carpal sesamoid, not the ventral sesamoid referred to here. The presence of this sesamoid is synapomorphic for the dendrobatids, and for (*Cacosternum* + *Nothophryne*).

119. Os sesamoides tarsale: (0) absent; (1) present.

Previously used by Wu (1994) 179. Nussbaum (1982) discusses this character in detail, and notes that among the Anura, it occurs only in some petropedetine ranids, the Sooglossidae and the Pipidae. In the ranids, this element generally occurs only in small taxa, and probably has a protective function over the Achilles tendon. The presence of the os sesamoides tarsale is synapomorphic for (*Arthroleptella landdrosia* + *A. lightfooti*) and independently for species of the genus *Cacosternum*, but also occurs in the enigmatic cacosternine *Ericabatrachus*. Elsewhere on the tree, state 1 occurs only in *Natalobatrachus* and the sooglossids.

120. Cartilagio sesamoides: (0) present; (1) absent.

Nussbaum (1982) discusses this character, which is far more common in the ranids than the os sesamoides tarsale. *Natalobatrachus* lacks the cartilagio sesamoides, which is present in all other species of *Phrynobatrachus* and allied genera, but has only a single element at the joint, which has the superficial appearance of the os sesamoides tarsale. Here, it is coded as such although the possibility exists that this element is actually the cartilagio sesamoides. Under Acctran optimization, the absence of the cartilagio sesamoides (state 1) is shown to arise at node 6, whereafter a reversal to state 0 is synapomorphic for the arthroleptid-hyperoliid lineage, node 22 in the mantellid-rhacophorid lineage, the phrynobatrachids excluding *Natalobatrachus*, node 43 in the cacosternids, and nodes 64 and 69 in the Raninae.

121. Prehallux: (0) small, usually cartilaginous; (1) large, either ossified or cartilaginous.

Previously used by Wu (1994) 182*. Large prehalli (state 1) arise at node 5. Reversals to small (state 0) are synapomorphic for (*Staurois* + rhacophorids), the cacosternids, the petropedetids, the two species of *Ptychadena*, and (*Amolops* + *Nannophrys*).

122. Prepollex, length versus length of first metacarpal in mature male: (0) approximately 1/4 to 1/3 in length; (1) greater than 1/2; (2) short, ossified and tear-drop shaped, may be fused to base of metacarpal in species where this is reinforced into a fighting spike; (3) almost full length of metacarpal, curved; (4) rectangular, flat.

Length variation in the prepollex was used by Wu (1994) 172, but assessed differently here. A long prepollex (state 1) is synapomorphic at node 66 in the Raninae (reversing synapomorphically at node 70 for (*Nanorana* (*Euphlyctis* + *Hoplobatrachus*)), although this

state occurs individually in a few taxa. Short, tear-drop shaped prepolli (state 2) are uniquely synapomorphic for the petropedetids excluding *Petropedetes natator*. Amongst the taxa examined here, long curved prepolli (state 3) occur only in *Amolops*, but are undoubtedly more common in other Asian ranids, e.g. the *Paa* clade, which also display the corresponding spiny nuptial pads. Rectangular flat prepolli (state 4) are autapomorphic for *Staurois*, although those of *Chiromantis* are also somewhat rectangular (coded here as state 1, since not identical).

123. Flange (crista lateralis) on dorsolateral surface of humerus of mature male: (0) absent; (1) present proximally, large; (2) present distally, small.

Previously used by Lynch (1978) 23*. Lynch (1971) notes that the greatly enlarged arms of males of some species of *Leptodactylus* have frequently been commented on in the literature. The skeletal basis for this is the presence of enlarged flanges on the humeri of mature males, which are sexually dimorphic, being absent in females, and are illustrated in Lynch's (1971:64) Fig. 41B for *Leptodactylus pentadactylus* (Laurenti, 1768). A large flange (state 1, Fig. 17) is synapomorphic for the petropedetids excluding *P. natator*, ascertained from X-rays of mature males, since the single stained and cleared specimen examined was subadult. A small distal flange (state 2) is a much more reduced form of the flange, and is synapomorphic at node 45 in the cacosternids.

124. Flange (crista ventralis) on ventral surface of humerus: (0) long, about 1/2 of length, grading into bone; (1) small, about 1/4 to a 1/3 of length, abruptly ending; (2) long, about 1/2 of length, but squared off and ending abruptly.

Variation in this feature across the Ranoidea was noted by D. E. van Dijk (personal communication). A small flange (state 1) optimises to the basal node. A reversal to a long flange (state 0) is synapomorphic for (Brevicipitinae + *Hemisus*), for the Tomopterninae, some cacosternids, and at node 55 for the Raninae, whereafter reversal to small flanges (state 1) is synapomorphic for nodes 63, 73 and the Ptychadeninae. A long but squared off flange (state 2) occurs independently in four taxa.

125. Metacarpal of the third finger of breeding male, distal tuberosity: (0) absent; (1) present.

Previously used by Liem (1970) 26, who notes that this knob is the insertion point of the third slip of the musculus humerodorsalis. A small distal knob (state 1) is synapomorphic for the hyperoliids and independently for the rhacophorids.

Figure 17. X-ray photographs of **A.** Male of *Arthroleptides martiensenii* (CAS 168627). **B.** Male of *Petropedetes newtoni* (UTACV 44446), illustrating the identical suite of sexually-dimorphic states, *viz*. the first metacarpal spike-like (c127:1) and expanded crista lateralis of humerous (c123:1).

126. Metacarpal of the first finger of breeding male: (0) no enlargement; (1) enlarged flange-like tuberosity distally, on the outer edge.

This knob was named the *tuberositas pro musculus abductor indicis longus* by Gaupp (1896), who illustrates this in his Figs 43 and 44 (later reproduced on frontispiece), and noted that it is the point of insertion for the musculus abductor indicus longus. Duellman & Trueb (1986) refer to this as the nuptial tuberosity. Presence of the knob (state 1) is synapomorphic for (*Cacosternum capense* + *C. namaquense*), but it occurs independently in *Amolops*, *Staurois*, *Natalobatrachus*, *Tomopterna tandyi* and *Nanorana*, and evidently also occurs in *Pelophylax esculenta* (Linnaeus, 1758), from figures of Gaupp (1896).

127. Metacarpal of first finger in breeding male: (0) uniformly thickened, noticeably more so than other metacarpals, not penetrating skin, not spike-like; (1) thick, enlarged into spike which may or may not penetrate skin, thus leaving the distal phalanges set off at an angle to the axis of the finger; (2) blade-like expansion at medial distal edge and on prepollex; (3) as other metacarpals.

The first metacarpal being as the other metacarpals (state 3) arises at the basal node, and is the common state. A reversal to a thickened first metacarpal (state 0) occur in *Leptodactylon*, *Trichobatrachus*, *Amolops* and *Nanorana*. Among taxa examined, state 2 is autapomorphic in *Leptodactylus*, and is illustrated in Lynch (1971:67) Fig. 46 B. The first metacarpal enlarged into a spike (state 1) is uniquely synapomorphic for the petropedetids excluding *P. natator*, which exhibits the common state 3. The spike does not penetrate the skin in *Arthroleptides* (illustrated in Fig. 17), but does penetrate the skin in *Petropedetes*. Parker (1936) observed that in *Petropedetes johnstoni* (Boulenger, 1887), males in their first breeding season often have a nuptial pad at the dislocation of the first metacarpal-phalangeal joint, and that the spine may not yet be protruding. In fully mature breeding males, the spine is always present and the nuptial pad is always absent. Parker's (1936) Fig. 1 illustrates the condition seen in *Arthroleptides*. It is thus possible that in *Arthroleptides*, the development of the spine arrests at this phase.

128. Shape of tips of terminal phalanx of third finger: (0) bifurcate, T- or Y-shaped; (1) knob-like, simple; (2) sharply pointed, slightly elongated.

Previously used by Liem (1970) 27, Heyer (1975) 35*, Lynch (1978) 16*, Drewes (1984) 14*, Tyson (1988) 27, Ford (1990) 117-8, Blommers-Schlösser (1993) 20* and 26*, Wu (1994) 177. This is a simplified version of this widely used character. Heyer (1975) considered simple phalanges as plesiomorphic, but the outgroup used here renders large T's as plesiomorphic. Knob-like terminal phalanges (state 1) are synapomorphic for the astylosternids including *Leptopelis*, (Brevicipitinae + *Hemisus*), the Tomopterninae, the cacosternids (although *Ericabatrachus* shows an extremely small T, coded as state 1), the (Pyxicephalinae + *Conraua*)

and (*Discodeles* + *Platymantis*). Sharply pointed, elongated phalanges (state 2) arise at node 55 for the Raninae, reversing to T-shaped at node 73 for ((*Amnirana* + *Hydrophylax*)(*Amolops* + *Nannophrys*)).

129. Shape of terminal phalanx of the fourth toe: (0) large T-shaped; (1) small T-shaped; (2) simple or only slightly dilated; (3) long, sharply pointed; (4) Y-shaped, arms bearing flattened oval-shaped flanges; (5) pointed, truncated (short), tip may be a very small globule; (6) long, sharply pointed, as in state 3 but tip separate from the body of the terminal phalanx and bent sharply downwards, which may or may not perforate the integument in life.

Previously used by Liem (1970), Heyer (1975) 35*, Drewes (1984) 14*, Blommers-Schlösser (1993) 20*, 26*. Glaw, Vences & Böhme (1998) 9*, Vences (1999) 19*. This character represents a much finer coding of c128, but is applied to the toes. *Phrynodon* was suggested to have large T-shaped tips by Blommers-Schlösser (1993), whilst only Y-shaped tips were observed here. This suggests either variability within this species, or demonstrates the inseparability of large T- vs. Y- shaped tips. Accordingly, these were not coded as separate states here, both being coded as state 1. This is distinctly different to the tips described in state 4, which have flanges. Small T's (state 1) are synapomorphic for the phrynobatrachids excluding *Natalobatrachus*, and for (*Amnirana* + *Hydrophylax*). Simple tips (state 2) unite (Brevicipitinae + *Hemisus*), the Arthroleptinae, the Tomopterninae, the cacosternids, and the (Pyxicephalinae + *Conraua*). State 3 is synapomorphic at node 55 for the Raninae, but commonly transforms therein. Y-shaped tips with expanded arms (state 4) are uniquely synapomorphic for the (mantellids + rhacophorids). Pointed truncated tips (state 5) occur in *Leptopelis* and *Hyperolius*, and are synapomorphic for (*Discodeles* + *Platymantis*). Long phalanges with a detached tip (state 6) was found to be uniquely synapomorphic for the astylosternids. Sanderson (1936) reported that this state seems to be retractile in the astylosternids. State 6 was not seen in species of *Ptychadena* examined, where the tip remains attached to terminal phalanx, and thus codes as state 3.

Tongue and Jaw

130. Medial lingual process: (0) absent; (1) type A, retractile upright cone-shaped process with alpha-type retraction; (2) type B, retractile upright rugose process with alpha-type retraction; (3) type C, elongate longitudinally reclining process with alpha-type retraction or non-retractile; (4) only a sublingual cartilaginous rudiment present.

The medial lingual process has frequently been noted in species descriptions in the older literature (e.g. Boulenger 1882; Noble 1924; Ramaswami 1934, 1935; Narayan Rao 1937; Inger 1954; Loveridge 1954; Poynton 1964; Poynton & Broadley 1985) but information concerning this character was only recently synthesised by Grant *et al.* (1997). In the present study, it is

coded as used by Grant *et al.* (1997), with some minor alterations. Grant *et al*'s. (1997) type D process was not seen, rather *Arthroleptis variabilis* was deemed to have a type C process (state 3), whilst a different species of *Discodeles* was here deemed to have a type A, cone-shaped process (state 1). *Arthroleptides martiensseni* was here deemed to have a type B (state 2) process, as in *Petropedetes*. In some cacosternine taxa, in which a large sample size of specimens were cleared, the occasional overstaining with alcian blue revealed the presence of a rudiment of a medial lingual process in some taxa, which takes up some of the excess alcian blue. A new state (state 4) was added to accommodate this. This rudiment does not protrude through the surface of the tongue in whole specimens, but they may exhibit a slight indent medially on the lingual surface, as noted by Poynton (1963) and Grant *et al.* (1997).

On the cladogram, upright cone-shaped processes (state 1) are synapomorphic for (*Discodeles* + *Platymantis*), and under Acctran optimization, for the mantellid-rhacophorid clade. Upright rugose processes (state 2) are a unique synapomorphy for the petropedetids excluding *Petropedetes natator*. Elongate longitudinally reclining processes (state 3) are synapomorphic for the phrynobatrachids excluding *Natalobatrachus*, and also occur independently in the cacosternids *Ericabatrachus* and *Nothophryne*, and in *Arthroleptis variabilis*. A cartilaginous sub-lingual rudiment (state 4) is synapomorphic for the cacosternids, with transitions to state 3 as mentioned above, and a reversal to absent (state 0) being synapomorphic for (*Cacosternum capense* + *C. namaquense*). State 4 was not detected in *Arthroleptella*.

131. If medial lingual process present, texture of surface: (0) smooth; (1) rugose.

Under Acctran optimization, rugose medial lingual processes (state 1) are synapomorphic at node 50 for the (petropedetids + Raninae), since they occur in the petropedetids excluding *Petropedetes natator*, and (*Discodeles* + *Platymantis*).

132. If medial lingual process present, shape: (0) short, bump-like; (1) elongated.

Under Acctran optimization, elongated medial lingual processes (state 1) optimise to the base of the arthroleptid-hyperoliid lineage, and to node 26 in the Ranidae for (*Tomopterna* + *Batrachylodes* + phrynobatrachids + cacosternids).

133. If medial lingual process present, shape of tip: (0) rounded and blunt; (1) sharply pointed.

Under Acctran optimization, pointed tips (state 1) are synapomorphic for (*Phrynobatrachus cricogaster* + *P. plicatus*), and independently for the cacosternids.

134. If medial lingual process present, orientation: (0) upright; (1) reclined posteriorly.

Under Acctran optimization, posteriorly reclined medial lingual processes (state 1) arise at node 26 in the Ranidae for (*Tomopterna* + *Batrachylodes* + phrynobatrachids + cacosternids).

135. Tongue, shape: (0) maximum width greater than or equal to length at centre; (1) length at centre greater than maximum width; (2) wide, but just short of being wider than long.

Perret (1987) demonstrated some of the variation observed in petropedetid and arthroleptid frogs in unpublished literature presented at the Sixth Symposium on African Amphibians. The variation appears to contain useful phylogenetic signal, but an entirely satisfactory quantification of this variation was not achieved in this study. Long narrow tongues (state 1) arise at the basal node. A reversal to state 0 is synapomorphic for the arthroleptid-hyperoliid lineage, and independently for the rhacophorids. A medium-wide tongue (state 2) is synapomorphic at node 50 for the (petropedetids + Raninae), whereafter reversals to state 1 are synapomorphic for the Ptychadeninae, and for the Pyxicephalinae

136. Tongue, distal margin: (0) not indented, entire; (1) indented in centre, lobed.

This feature is mentioned extensively in literature, (Boulenger 1882; Deckert 1938; Laurent 1950, 1986), but a notched tongue has only recently been suggested by Ford & Cannatella (1993) to be synapomorphic for the Ranidae. The entire tongue tip is plesiomorphic within the Ranoidea, with the indented tongue being synapomorphic at the node 5. A reversal to an entire tongue is synapomorphic for (Brevicipitinae + *Hemisus*). Independent reversals to entire tongues have occurred in *Poyntonia*, *Batrachylodes*, *Phrynoglossus* and in *Cacosternum leleupi* Laurent, 1951 (the latter species not included in this study, but mentioned here due to the rarity of this condition in the Ranidae).

137. Posterior palatial fold: (0) absent; (1) present.

Previously used by Blommers-Schlösser (1993) 11, Wu (1994) 8 and 9 combined, Emerson *et al.* (2000a) 10*. Presence of posterior palatial folds are synapomorphic for the microhylids including *Hemisus*, and are reportedly synapomorphic for all microhylids (Parker 1934, Wu 1994).

138. Snout profile: (0) rounded and overshot; (1) wedge-shaped.

This variation was also observed in the leptodactylids and is illustrated in Lynch (1971) Fig. 4C for state 1, and Fig. 4D for state 0. Inger (1954) mentions the shape of the snout extensively in his treatment of the Philippine Amphibia. Wedge-shaped snout profiles are synapomorphic for the dendrobatids, for the microhylids (reversing in Brevicipitinae), and for the phrynobatrachids, whereafter a reversal to state 0 occurs at node 35. Wedge-shaped snouts are

also synapomorphic for (*Discodeles* + *Platymantis*) and (*Anhydrophryne* + *Arthroleptella hewitti*), and many single-taxon state transitions occur elsewhere.

139. Callusing of dorsal snout of breeding males: (0) absent; (1) present.

Callusing of the tip of the snout was seen only in males of *Batrachylodes* and *Anhydrophryne*, and is presumably used in the construction of subterranean nest chambers (Noble 1931). In *Anhydrophryne*, the sphenethmoid is more highly ossified in the males than in the females.

Muscles

140. Musculus cutaneous pectoris (mcp): (0) absent; (1) present as thin slip; (2) present as thick slip.

Previously used in analyses by Drewes (1984) 28*, Tyson (1988) 65, Blommers-Schlösser (1993) 10*, Wu (1994) 38*, Emerson *et al.* (2000a) 3*. Tyler (1971) discusses the distribution of this muscle. Tyler (1971) and Ford & Cannatella (1993) suggested that the presence of the mcp could be synapomorphic for the Ranidae. The mcp is confirmed to be synapomorphic for node 20 leading to the Ranidae, including the mantellids and rhacophorids, but was not seen in the two rhacophorids examined here. However, Liem (1970:71) uses thin versus thick mcp (state 1 versus state 2) to distinguish between *Polypedates* and *Rhacophorus*. It is thus present at least in some rhacophorids. Under Acctran optimization, a thin slip of mcp (state 1) is synapomorphic at node 29 for (cacosternids + phrynobatrachids), whereafter a reversal to absent occurs in *Cacosternum namaquense*, and a transition to a thick slip occurs for the phrynobatrachids excluding *Natalobatrachus*. A reversal to absent occurs in *Phrynobatrachus natalensis* and possibly in its sister taxon, *Phrynobatrachus acridoides*, where the muscle was not seen.

Secondary Sexual Characteristics

141. Breeding males, colour of testes: (0) uniformly white to off-white, no black pigment present; (1) dark, pigment present throughout or on mesorchium or dorsal sections only.

Bhaduri & Basu (1957) first noted black pigment on the testes of *Cacosternum*, and to a lesser extent on those of *Ptychadena mascareniensis*. The arrangement of the vessels entering the kidney was used by Liem (1970) for the Hyperoliidae, and variation was noted within the Ranidae in this study. Bhaduri & Basu (1957) also noted variation in the configuration of the uterus in ranid frogs. These characters are mentioned since they may be useful in future studies. Testes with black pigment (state 1) are synapomorphic for the cacosternids (with a reversal to white testes in *Nothophryne*). Dark pigment occurs independently in *Ptychadena* and on the

mesenteric tissue above the testes in most dendrobatids examined. Slight pigment on the testes also occurs in *Phrynobatrachus natalensis*, a species which displays large amounts of pigment in many organs and mesenteries, even showing greying of the bones.

142. Breeding males, velvety nuptial pads: (0) absent; (1) on finger one only; (2) on fingers one and two; (3) on fingers one, two and three; (4) short spines on fingers one, two and three.

Previously used by Liem (1970) 35, Heyer (1975) 3*, Emerson & Berrigan (1993) 8*, Glaw, Vences & Böhme (1998) 15b, Vences (1999) 24*. Variation in African ranids was meticulously observed by Stewart (1967) for the amphibians of Malawi. Inger (1954) notes variation in this character in the Philippine ranids. Lynch (1971) and Heyer (1975) note various states of pads or spines in the leptodactylids. Parker (1940) suggested that spines and pads are an adaptation to amplexing in water, since he observed that frogs that amplex on land lack nuptial pads, but those that amplex in water have them. However, some aquatic African ranids, such as *Aubria*, have no spines or pads (Perret 1994). Heyer (1975) considered the presence of nuptial spines and pads to be plesiomorphic, with spines probably being a derived condition over pads. He also states that development of spines and loss of asperities has probably occurred several times in leptodactylids. States vary sporadically in various groups, but nuptial pads on fingers one, two and three (state 3) is a unique synapomorphy for the Ptychadeninae.

143. Breeding males, sub-terminal metacarpal spike: (0) absent or non-protruding; (1) present, protruding through skin.

Noble (1931) mentions this spike in *Petropedetes* and suggests that its function is to assist in grasping the female during amplexus. Species of *Petropedetes* in which the spike occurs and *Arthroleptides* also display the enlarged humeral flange for additional attachment of the hypertrophied muscles. Males are substantially larger than females in these frogs, and larger males often display substantial scarring, suggesting that the function of the metacarpal spike is a weapon used during male-male combat (Les Minter, personal communication). A protruding spike-like metacarpal (state 1) occurs in *Petropedetes parkeri* and *P. newtoni*. In *Arthroleptides*, where the metacarpal is thickened, the phalanges of the first finger do not displace laterally out of alignment with the phalanges (see Fig. 17), nor does the metacarpal protrude through the skin.

144. Breeding males, pad of spines at base of first finger: (0) absent; (1) few, large sharp black cones in a cluster; (2) pad of small white spines, covering the entire area where nuptial pads occur on the first finger in other ranids.

Lynch (1971) and Heyer (1975) note various states of pads or spines in the leptodactylids. Duellman & Trueb (1986:57) illustrate state 1 in Fig. 3.8 F. A cluster of sharp black cones at the

base of the first finger in breeding males occurs only in *Leptodactylon* and *Trichobatrachus*, and combined with their enlarged humeral flanges, represent a breeding condition seen elsewhere in the Leptodactylidae in *Leptodactylus pentadactylus* (Duellman & Trueb 1986:57). In this taxon sample, an extensive pad of small white spines (state 2) is autapomorphic for *Amolops*, but was also apparent in *Paa boulengeri* (Günther, 1889) and undoubtedly occurs more widely in Asian ranids.

145. Breeding male, length of third finger: (0) normal; (1) considerably longer than other fingers, dorsal or lateral surface of fingers two and three covered in dermal denticles.

Previously used by Blommers-Schlösser (1993) 19. Under Acctran optimization, a long third finger with associated denticles (state 1) is a unique synapomorphy for Arthroleptinae (illustrated in Duellman & Trueb (1986) Fig. 3.11B), occurring in many species of *Arthroleptis* and *Cardioglossa* (Laurent 1957).

146. Breeding males, ventral spinules: (0) absent; (1) present in the axilla and/or flanks and chest region only; (2) present over the whole ventral surface; (3) present on the inner surface of the upper arm.

Previously used by Lynch (1978) 19*. This character has to be assessed from males in full breeding condition, since temporal variation in spinules has been noted in the literature (Inger 1954). Spinules present in the axilla and/or flanks and chest region (state 1) occurs in *Leptodactylon*, *Trichobatrachus* and *Nannophrys*, and is synapomorphic for the petropedetids excluding *Petropedetes natator*. Spinules over the whole ventral surface (state 2) were seen only in a giant mature male of *Conraua goliath* from the CAS, and are undoubtedly seasonal in appearance, explaining their absence in taxa known to display this. Spinules on the inner surface of the upper arm (state 3) are autapomorphic in this taxon set for *Batrachylodes*, but also occur in *Limnonectes corrugatus* (Peters, 1863) and probably more widely in the Asian ranids.

147. Breeding males, hedonic glands: (0) glandular region on inside of forearm; (1) hemispherical disc-like glandular flaps near axilla; (2) absent; (3) raised cylindrical patch on dorsal surface of wrist near first finger; (4) large glandular region on inside of forearm and pectoral glands.

Glandular regions on the inside of the forearms (state 0) are well known from the hyperoliids, but appear to occur in *Heleophryne* as well. Inger (1954:314) notes that males of *Pulchrana signata* (Günther, 1872) have 'humeral glands'. Noble (1931) suggests that pectoral glands function in holding the female during amplexus. Drewes (1984) suggests that in the hyperoliids, these are hedonic in nature, and are probably related to their unusual mode of amplexus. Large glandular regions on inside of forearm in combination with pectoral glands

(state 4) is autapomorphic for *Leptopelis* here. Hemispherical disc-like glandular flaps near the axilla (state 1) occur widely in the genus *Amnirana* (Perret 1977), and are highly developed in *Hydrophylax*. It is noteworthy that Perret (1994:256) observed for *Aubria occidentalis* Perret, 1994 that, 'at the base of the upper arm, on its ventral surface, a small, indefinite pale yellowish glandular aggregation may be present in either sex'. From Perret's (1994) Fig. 1A and 1B, the gland appears well developed, and in comparison to *Amnirana* (illustrated in Duellman & Trueb (1986:59) Fig. 3.14, and Perret's (1977) Fig. 6, would appear homologous. These glands in *Aubria* appear to be better developed in the females, as with the femoral glands (Perret 1994), so would best be considered as a separate character state (not implemented here, since *A. subsigillata* was coded). Raised cylindrical disc-like swellings on the dorsal surfaces of the wrists (state 3) are autapomorphic for *Dimorphognathus*, a genus for which male-male combat is likely, given that it is reported for *Phrynodon* (Amiet 1981). Their function is not known, but may be hedonic in nature. Duellman & Trueb (1986:58) report a similar structure in *Hemisus*, but this was not seen in the specimens of *H. viridiflavus* examined here.

148. Gular gland in breeding males: (0) absent; (1) present.

Previously used by Liem (1970) 36*, Drewes (1984) 18*, Blommers-Schlösser (1993) 22. Illustrated in Duellman & Trueb (1986:58) Fig. 3.12A and discussed in Liem (1970). The gular gland is a complex character, but for the purpose of this analysis is coded simply as present or absent. The gular gland has been considered to be a unique synapomorphy for the Hyperoliidae excluding *Leptopelis* (Ford & Cannatella 1993).

149. Spicules around jaw line in breeding males: (0) present, well developed; (1) absent; (2) present, fine.

Well-developed spicules (state 0) occur only in the outgroup. At the basal node, the spicules are lost (state 1). Fine spicules (state 2) arise sporadically in the cacosternids and the Raninae (including the Ptychadeninae).

150. Vocal sac breeding male, nature: (0) single medial subgular sac or no vocal sac; (1) two lateral vocal sacs, internal or external.

Previously used by Emerson & Berrigan (1993) 4*. This character is difficult to code without dissection or if the muscles of the vocal sac are not evident in stained and cleared material. Many mistakes exist in the literature (Inger 1954), but existing literature was still used where possible, e.g. Clarke (1983) for *Nannophrys*. Both states of this character could effectively be split, rendering four states, and the coding implemented here is suboptimal. Undissected specimens of *Pantherana* appeared to have two lateral vocal sacs, but were coded

as unknown. Two lateral vocal sacs are synapomorphic for the petropedetids, and for node 66 in the Raninae.

151. Femoral glands in males: (0) absent; (1) present; (2) less developed than in females.

Previously used by Blommers-Schlösser (1993) 28*, Glaw, Vences & Böhme (1998) 17, Vences (1999) 22* and 23*. This character would be more informative within the ranids if types of glands were coded, as in Glaw *et al.* (2000), requiring dissection. These authors also coded the position of the gland, distinguishing between glands closer to the knee, the vent or centrally between these, but this was found to be difficult to quantify. The presence of femoral glands (state 1) is synapomorphic for the mantellids (reversing to absent in the rhacophorids), the phrynobatrachids excluding *Natalobatrachus*, the petropedetids, and is postulated to have arisen independently in many single taxa. Femoral glands that are more highly developed in females than in males (state 2) are autapomorphic for *Aubria* (Perret 1994).

152. Femoral bumps: (0) clear, granular and confined to a small region proximally, extending for less than 1/2 length of thigh; (1) absent or very faint, there may be slight ridges; (2) as 0, but extending 1/2 to 3/4 length of thigh.

The skin of the ventral surface of the thighs is roughly granular in many species, and the extent of these femoral bumps varies. They are here considered as an independent character to the presence of femoral glands, contrary to the treatment of them as homologous to femoral glands in Glaw *et al.* (2000). Both of these structures can be present in the same individuals at the same time (especially evident in the mantellids, as ascertained from figures in Glaw *et al.* (2000). Daly *et al.* (1996:5) also report that 'the purported [femoral] glands are coexistent with the patch of granular skin on the underside of the thigh' in *Mantella*. Femoral bumps and femoral glands thus fail a homology assessment test on the criterion of conjunction (Patterson 1982; de Pinna 1991). The intensity of the femoral bumps may be affected by breeding condition (although they do not appear to be sexually dimorphic) or the state of preservation of the specimen, as also noted by Daly *et al.* (1996). The state of the bumps varies among smaller clades, but they are absent or very faint in the microhylids, most phrynobatrachids, some cacosternids and the larger odontid-possessing fanged ranids.

153. Papilla in the centre of tympanum, breeding males: (0) absent; (1) present.

Parker (1936) discussed this feature extensively. Du Toit (1943) described it as an outgrowth of the tympanic membrane. Duellman & Trueb (1986) followed Noble (1931) in considering it an outgrowth of the columella, whereas Klemens (1998) restated Du Toit's original views. Recently, Narins *et al.* (2001) investigated the histology of this papillae, and found that it is secretory in nature. It has been suggested that this feature may regress out of the breeding

season (Parker 1936), but no adult specimens out of breeding condition that lack it have been examined. The presence of the papillae is a unique synapomorphy for the petropedetids excluding *Petropedetes natator*, and reversing in *P. cameronensis*.

External Morphology

154. Supratympanic ridge: (0) strong, may be glandular; (1) absent or weak; (2) strong, encircling the entire dorsal section of a large tympanum.

Previously used by Wu (1994) 6 as 'tympanic fold'. Mentioned in species descriptions for the Philippine ranids by Inger (1954). Absence of the ridge (state 1) optimises to the basal node, whereafter a reversal to a strong ridge (state 0) occurs in the astylosternids, the phrynobatrachids excluding *Natalobatrachus* and the Raninae. Most remaining ranids display state 0, except the Pyxicephalinae and Ptychadeninae. Strong supra-tympanic ridges encircling a large tympanum (state 2) are uniquely synapomorphic for the petropedetids excluding *Petropedetes natator*. Various other single-taxon transformations between states 0 and 1 occur throughout the tree.

155. Tympanic membrane: (0) indistinct, covered by skin as thick as that on rest of head; (1) distinct, as skin over tympanum is thinned; (2) half distinct, half-covered by muscle, only a crescent visible.

Previously used by Heyer (1975) 2*, Drewes (1984) 23*, Wu (1994) 4*, Emerson & Berrigan (1993) 1*. Indistinct tympani were considered to be plesiomorphic by Heyer (1975), as polarized here. Distinct tympani (state 1) are synapomorphic for (*Anhydrophryne* + *Arthroleptella hewitti*), and under Acctran optimization for the (petropedetids + Raninae). Various other single-taxon transformations between states 0 and 1 occur throughout the tree. The tympanic membrane being half-covered by muscle (state 2) is a unique synapomorphy for the dendrobatids, although there is some covering of the tympanum by muscle in *Afrixalus* Laurent, 1944 and *Ericabatrachus*. Since dissection of the jaw musculature in the ranids was not undertaken here, this state is retained at present as a unique synapomorphy for the dendrobatids.

156. Width of eye versus tympanum (adult male): (0) tympanum less than or equal to radius of eye; (1) tympanum greater than half but less than full width of eye; (2) tympanum greater than full width of the eye.

Previously used by Vences (1999) 38*. Although tympanum size is sexually dimorphic in some American taxa formerly included in the genus *Rana*, e.g. *Aquarana catesbeiana* (Shaw, 1802) and *A. clamitans* (Latreille, 1801). (Noble 1931), this is rare in African ranids. The tympanum being greater than half but less than the full width of the eye (state 1) is a

synapomorphy for the phrynobatrachids, but reverses therein to state 0 at node 34. State 1 is also synapomorphic for node 55 leading to the Raninae, wherein reversals to state 0 occur in some clades. The tympanum being greater than the full width of the eye (state 2) is uniquely synapomorphic for the petropedetids excluding *Petropedetes natator*, and reversing in *P. cameronensis*.

157. Shape of pupil: (0) vertical; (1) horizontal; (2) round.

Previously used by Lynch (1973) 24, Heyer (1975) 1*, Heyer & Liem (1976) 34*, Lynch (1978) 17*, Drewes (1984) 22*, Blommers-Schlösser (1993) 30, Wu (1994) 3. Laurent (1957, 1986) used this character extensively in discussions of his proposed relationship of the hyperoliids with the arthroleptids. This character was coded mainly from the literature or photographs since the shape distorts in preservation. A vertical pupil has been considered to be plesiomorphic, since it occurs in families of the Archeobatrachia (Lynch 1971, 1973; Heyer 1975). Drewes (1984) conferred with this polarization. However, Ford & Cannatella (1993) note that a horizontal pupil is plesiomorphic at the level of the Neobatrachia, therefore the vertical pupil may be secondarily derived. Shape of pupil in *Heleophryne* is coded as vertical, as indicated by Lynch (1973), not horizontal as indicated in Heyer (1975). Horizontal pupils optimise throughout most of the base of the tree, with a reversal to vertical being synapomorphic for the astylosternids including *Leptopelis*. Independent evolutions of vertical pupils are postulated to have occurred in *Hemisus*, *Kassina*, *Conraua* and *Nannophrys*. Round pupils are autapomorphic for *Phrynomantis* in this taxon set.

158. Webbing between toes: (0) extensive; (1) rudimentary, 1/4 to 1/2 of longest toe; (2) trace at base, or no web.

Previously used by Heyer (1975) 9*, Heyer & Liem (1976) 37*, Wu (1994) 19*, Vences (1999) 32*. This character is highly variable intragenerically, and reflects more an adaptation to contemporary environments (Laurent 1964) than historical relationships. It is nevertheless included here but is coded conservatively, since it does appear to contain some phylogenetic signal. Heyer (1975) considered webbed toes primitive, with no web being derived. Absence of web (state 2) arises at the basal node. Some astylosternids exhibit rudimentary webs (state 1). A change to extensively webbed feet occurs at node 20 leading to the Ranidae, wherein reversals to no web (state 2) are synapomorphic for the cacosternids, and independently in the single taxa *Batrachylodes*, *Platymantis*, *Mantella*, *Strongylopus* and *Nannophrys*. A reduction in web (state 1) is synapomorphic for the phrynobatrachids excluding *Natalobatrachus*, but also occurs in the burrowing forms *Tomopterna marmorata*, *Hildebrandtia* and *Pyxicephalus*.

159. Toes, if unwebbed: (0) not flanged entire length; (1) flanged entire length.

If the toes are unwebbed, they can nevertheless bear flanges on the lateral margins. These are not sexually dimorphic nor do they develop only in the breeding season. Flanged toes are synapomorphic for (*Cacosternum capense* + *C. namaquense*) and independently for the Tomopterninae. Flanged toes are also present in *Leptodactylus* and *Hemisus*.

160. Dorsal digital scutes on terminal phalanx of feet: (0) absent; (1) present.

Previously used by Heyer (1975) 5 state E. Digital scutes are mentioned by Du Toit (1943) and Lynch (1971). A good photograph of theses scutes is given in Myers & Donnelly (1997) Fig. 37B. The presence of digital scutes has been cited as a synapomorphy of the dendrobatids and the elosiine leptodactylids (Lynch 1971). Ford (1993) showed that these are equivocal as to the placement of the dendrobatids, since they occur in both the ranids and the leptodactylids. Heyer (1975) envisioned a transformation series from toe-tips with discs to those with discs and scutes. Digital scutes are rare in the ranids, but a condition which could be described as incipient scutes or weak scutes is sometimes seen (e.g. in both rhacophorid exemplars examined in this study), suggesting that there may be a basis for such a series. Dorsal digital scutes are synapomorphic for the dendrobatids, and independently for the petropedetids, but are also present independently in *Ericabatrachus*.

161. Relative length of first and second fingers: (0) first finger not reaching the tip of the second; (1) first finger equal in length or extending beyond the second.

Previously used by Wu (1994) 10*, Glaw, Vences & Böhme (1998) 18*, Vences (1999) 30*. This character is similar to Ford (1990) 114, which used the relative length of the metacarpals. The first finger equal in length or longer than the second (state 1) is synapomorphic for (*Colostethus* + *Mannophryne*), for (Brevicipitinae + *Hemisus*), for the Arthroleptidae, for the Tomopterninae and at node 55 for the Raninae. Within the Raninae, reversals to state 0 are synapomorphic for the Ptychadeninae and for (*Amolops* + *Nannophrys*).

162. Relative length of first and third fingers: (0) third finger longer than first; (1) third finger equal in length to first; (2) third finger substantially longer than first.

Previously used by Blommers-Schlösser (1993) 19*. Mentioned extensively in species diagnoses by Inger (1954). The third finger being equal in length to the first is synapomorphic for the (Pyxicephalinae + *Conraua*), and for (*Nanorana* (*Euphlyctis* + *Hoplobatrachus*)), and occurs in the ranines *Limnonectes* and *Platymantis*, as well as the astylosternids *Leptodactylon* and *Trichobatrachus*. The third finger being much longer than the first (state 2) is a unique synapomorphy for the Arthroleptinae.

163. Relative length of second and fourth fingers: (0) second finger shorter than or equal in length to the fourth; (1) second finger longer than fourth.

Previously used by Wu (1994) 13. The relative length of the metacarpals was used by Ford (1990) 114, which may surrogate for this. The second finger being longer than the fourth (state 1) is synapomorphic for (Brevicipitinae + *Hemisus*), and independently for the Arthroleptinae, node 18 in the astylosternids, for the Tomopterninae, and occurs independently in *Hildebrandtia*. This distribution of state 1 suggests that it may be correlated with a burrowing habit.

164. Feet, small conical spicules on ventrolateral surfaces of soles in breeding males: (0) absent; (1) present.

These small hardened conical spines appear to be better developed in males, although they are present in females. Presence of spines on the soles (state 1) is a unique synapomorphy for (*Phrynobatrachus krefftii* (*P. versicolor* + *P. dendrobates*)).

165. Colour pattern on the posteroventral surface of thighs: (0) solidly dark and extending onto soles of feet or uniform; (1) reticulate blotches or broken stripes not extending onto feet; (2) mottled.

The use of colour pattern as a phylogenetic character is usually avoided in systematics. However, the patterns described here appear to contain useful phylogenetic signal. The specifics of this colour pattern are diagnostic for various species of *Ptychadena* (Poynton 1964; Stewart 1967) in which they are highly consistent (see Stewart for illustrations). The uniform wide dark brown bands seen on the thighs of many African and Asian ranoids, which usually extend from around the cloaca down onto the soles of the feet, are here not considered as a separate state from absence. This pattern is assumed to be plesiomorphic based on its distribution. The presence of reticulating blotches or a broken striped colour pattern (state 1) is synapomorphic at node 55 for the Raninae, but also occurs in *Tomopterna tandyi*. Within the Raninae, reversals to the absence of the pattern (state 0) are synapomorphic for (Pyxicephalinae + *Conraua*), for (*Phrynoglossus* (*Discodeles* + *Platymantis*)) and from node 69, whereafter three taxa independently revert to state 1. Mottling only (state 2) is uniquely synapomorphic for the astylosternids, wherein a reversal to no pattern occurs in *Leptodactylon* and *Trichobatrachus*.

166. Tip of the terminal phalanx of the fourth toe: (0) does not terminate in a small, narrow, hard bead; (1) terminates in small, narrow, hard bead.

The presence of this hardened bead is best determined by feel, since its hard texture can be assessed by running the frog's toe tips over your fingertips. The tips of the digits also appear narrower than those of frogs with non-expanded digit tips and no beads. The beads usually

occur on both finger and toe tips, but are usually better developed on the toes. Beads (state 1) are uniquely synapomorphic at node 55 for the Raninae, and reverse synapomorphically therein to absent in (*Discodeles* + *Platymantis*) and at node 73.

167. Shape of the terminal phalanx of the fourth toe: (0) deltoid or triangular disc; (1) slightly to notably enlarged semicircular disc; (2) tapering or pointed, not notably enlarged.

Previously used by Heyer (1975) 5*, Wu (1994) 15*. Digital discs are thought to be correlated to an arboreal habit (Laurent 1964, Lynch 1971), whilst deltoid discs appear to be an adaptation to fast-flowing riparian habitats, where grip on slippery rocks is essential. Discs on the fingers are usually as for the toes, with a few notable exceptions, such as *Natalobatrachus*. Slightly to notably enlarged semicircular discs (state 1) are postulated to have evolved at the basal node (reversing to state 0 at node 25), and are synapomorphic for the phrynobatrachids excluding *Natalobatrachus*, for (*Phrynoglossus* (*Discodeles* + *Platymantis*)) and for (*Amnirana* + *Hydrophylax*). Tapering toes (state 2) unite (Brevicipitinae + *Hemisus*), the Tomopterninae, the cacosternids, and the Raninae at node 55.

168. Tip of the terminal phalanx of the fourth toe: (0) with a ventral circum-marginal groove; (1) without a ventral circum-marginal groove.

Previously used by Liem (1970) 33, Heyer (1975) 5*, Heyer & Liem (1976), Blommers-Schlösser (1993) 27*, Glaw, Vences & Böhme (1998) 19. This character was used by Inger (1954) in his species diagnoses. Circum-marginal grooves are common in many families of frogs with expanded toe tips. This character would probably be more informative if two states were made of the presence of grooves, i.e. completely round or semi-circular (horse-shoe shaped), but assessment of this was not always unambiguous in some of the material examined here. Absence of circum-marginal grooves (state 1) is synapomorphic for (Brevicipitinae + *Hemisus*), for the astylosternids, the Tomopterninae, the cacosternids, and for the Raninae. In the latter clade, a reversal to state 0 is synapomorphic for (*Phrynoglossus* (*Discodeles* + *Platymantis*)).

169. Outer two metatarsals: (0) deeply incised and separated by web almost to base; (1) forming part of a fleshy sole, separated only distally.

Previously used by Vences (1999) 32*. Inger (1954) mentions whether this characteristic is present in his species diagnoses, referring to it as the outer metatarsal region being united for at least 2/3 of length or separated for at least 2/3 of length, and illustrates the distinction in his Figs 34 and 35. Poynton (1963, 1964) and Poynton & Broadley (1985) often refer to 'outer metatarsals bound into a fleshy sole' to describe state 1 of this character, which is illustrated in Lynch (1971) Fig. 45B, whilst state 0 is illustrated in Perret (1994) Fig. 3. Deeply incised and

separated metatarsals (state 0) occur in heavily webbed aquatic forms, and are probably an adaptation to increase the surface area of the webbing. Similarly, metatarsals bound into a fleshy sole appear to be an adaptation to a terrestrial habit. Under Acctran optimization, metatarsals bound into fleshy soles (state 1) originate at the basal node and is present in most basal ranoids. A reversal to deeply incised metatarsals (state 0) is synapomorphic at node 20 for the Ranidae, whereafter transitions to state 1 unite taxa from node 26 onwards, and independently the petropedetids.

170. Inner metatarsal tubercle, length compared to that of the fifth toe (measured from the base of the subarticular tubercle to tip): (0) short, up to the same length as the fifth toe; (1) longer than fifth toe but flattened and indistinct; (2) longer than fifth toe, but expanded into a protruding digging flange.

Previously used by Heyer (1975) 8*, Heyer & Liem (1976) 38*, Wu (1994) 16*. The inner metatarsal tubercle is always present, but its size varies. Heyer (1975) considered a short inner metatarsal tubercle to be plesiomorphic, and an enlarged one to be derived. Long but flattened and indistinct tubercles (state 1) are synapomorphic for the petropedetids, node 63 in the Raninae and for (*Amolops* + *Nannophrys*). A long protruding digging flange (state 2) is synapomorphic for the microhylids including *Hemisus*, for the arthroleptids (wherein it reverses in the astylosternids), the Tomopterninae, and (*Cacosternum capense* + *C. namaquense*). State 2 also occurs sporadically in the burrowing forms *Hildebrandtia*, *Pyxicephalus* and in *Poyntonia*, suggesting that the latter genus is at least partly fossorial.

171. Outer metatarsal tubercle: (0) absent; (1) present.

Previously used by Lynch (1973) 29, Heyer & Liem (1976) 39*, Lynch (1978) 18, Wu (1994) 17, Vences (1999) 35. Lynch (1973) states that the Archeobatrachian families uniformly lack an outer metatarsal tubercle, and suggests that its absence is thus plesiomorphic, as polarized here. He notes that this character is prone to secondary loss. Heyer (1975) accepts this polarization. Presence of the tubercle (state 1) is synapomorphic for (dendrobatids + sooglossids), and under Acctran optimization for node 26 in the Ranidae, reversing to state 0 in most cacosternids. State 1 is also synapomorphic for (*Discodeles* + *Platymantis*) and at node 73 in the Raninae. Other single-taxon transformations frequently occur.

172. Tarsal fold: (0) absent; (1) present; (2) present to mid-tarsal tubercle only.

Previously used by Heyer (1975) 6* state B. Tarsal folds are common in some taxa, such as the bufonids, but within the ranids, they are mostly confined to the Raninae. Inger (1954) mentions tarsal folds in his descriptions of Philippine ranids. Presence of a tarsal fold (state 1) is synapomorphic at node 55 for the Raninae, whereafter its loss is synapomorphic for node 73 and

for (*Discodeles* + *Platymantis*). The presence of a tarsal fold to the mid-tarsal tubercle only (state 2) is synapomorphic for the dendrobatids, and independently for the phrynobatrachids excluding *Natalobatrachus*.

173. Lateral margin of fifth toe and metatarsal, loose flap of skin: (0) absent; (1) present; (2) absent, but strongly or weakly developed dermal seam separating dorsal and ventral surfaces of the foot.

Previously used by Heyer (1975) 6 state F, but no description presented. Mentioned by Inger (1954) in his diagnoses of the large ranids of the Philippines. A loose flap of skin on the outside of the fifth toe and metatarsal (state 1) is found in many aquatic forms, probably assisting in swimming, and is well developed in the large aquatic Raninae. The flap is illustrated in Perret (1994) Fig. 3 for *Aubria occidentalis*, and in various figures throughout Inger (1954). The skin flap (state 1) is synapomorphic for (*Nyctibates* + *Trichobatrachus*), for the two species of *Conraua* and for (*Euphlyctis* + *Hoplobatrachus*). The presence of a seam (state 2) is synapomorphic for the dendrobatids, the rhacophorids, at node 34 in the phrynobatrachids, and for (petropedetids + Raninae). Within the Raninae, reversals to state 0 unite node 69 and (*Discodeles* + *Platymantis*).

174. Mid-tarsal tubercle: (0) absent; (1) present.

Previously used by Heyer (1975) 6 state C. In combination with the presence of a medial lingual process, this character was previously thought to be diagnostic for the genus *Phrynobatrachus* (Poynton 1964), but this combination also occurs in some *Colostethus* of the dendrobatids, e.g. *C. atopoglossus* Grant, Humphrey & Myers, 1997 (Grant *et al.* 1997). The structure is morphologically identical in both groups. The mid-tarsal tubercle is synapomorphic for the phrynobatrachids excluding *Natalobatrachus*, and independently for the dendrobatids.

175. Heel tubercle: (0) absent; (1) small and round to spike-like; (2) not single, present in a row of three.

The presence of small rounded to spike-like heel tubercles (state 1) is synapomorphic for the phrynobatrachids (reversing to state 0 in *Phrynobatrachus plicatus*), but also occurs independently in *Mantidactylus* and *Tomopterna marmorata*. The sooglossids appears to have some form of tubercle on the heel, but this is here considered to differ from the state evident in *Phrynobatrachus*. A row of three tubercles (state 2) is autapomorphic in *Platymantis*.

176. Basal (proximal) row of subarticular tubercles of feet: (0) abnormally large, tending to square; (1) large, round to oval; (2) very small and sharply defined, round to conical; (3) tubercles under the first to third digits large, those under the fourth and fifth small.

This character is inapplicable in the sooglossids and *Ericabatrachus*, which both lack subarticular tubercles. Large round to oval tubercles (state 1) arise at the basal node, and is exhibited by most taxa. A reversal to extra large square tubercles (state 0) is synapomorphic for the astylosternids. Small well-defined tubercles (state 2) are synapomorphic for the Tomopterninae, the species of *Cacosternum*, for (Pyxicephalinae + *Conraua*) and for (*Nanorana* (*Euphlyctis* + *Hoplobatrachus*)). Differentially-sized tubercles (state 3) are a unique synapomorphy for (*Hyperolius* + *Kassina*).

177. Subarticular tubercles of feet: (0) spherical or conical; (1) oval, long, flattened; (2) raised perpendicularly and half disc-shaped, each joined by a ridge to that of next phalanx.

Most taxa display spherical or conical subarticular tubercles (state 0). Oval tubercles (state 1) are synapomorphic for node 73 in the Raninae, although raised disc-shaped joined tubercles (state 2) are autapomorphic for *Nannophrys*.

178. Outer metacarpal tubercle: (0) divided, mid section smaller than outer section; (1) divided, sections equal in size; (2) divided, mid section larger than outer; (3) entire on smooth palm; (4) entire, palm of hand granular.

The surface of the manus usually bears an outer metacarpal (sometimes called the palmar) tubercle and an inner metacarpal (sometimes called thenar) tubercle proximally. In many Neobatrachia, the outer metacarpal tubercle is divided, and may even be separated into two sections (resulting in what Lambiris (1989) refers to as the middle metacarpal tubercle). Divided outer metacarpal tubercles with the mid section smaller than outer section (state 0) occurs in the outgroup, and a reversal to this is synapomorphic in the cacosternids for (*Anhydrophryne* + *Arthroleptella hewitti*) and (*Cacosternum capense* + *C. namaquense*). Under Acctran optimization, outer metacarpal tubercles divided with sections equal in size (state 1) arise at node 9 for the Ranoidea and persist for most taxa. Entire outer metacarpal tubercles on a smooth palm (state 3) arises at the basal node and occurs in the sooglossids, the dendrobatids, *Leptodactylus*, microhylids including *Hemisus* and *Kassina*, but within the Ranidae this state unites only the cacosternid genera *Ericabatrachus* and *Poyntonia*. Entire outer metacarpal tubercles on a granular palm (state 4) is a synapomorphy for the rhacophorids, but also occurs in *Hyperolius*. Divided outer metacarpal tubercles with the mid section larger than outer section (state 2) is synapomorphic at node 26 in the Ranidae, and synapomorphically for the two species of *Ptychadena* and (*Euphlyctis* + *Hoplobatrachus*).

179. Outer metacarpal tubercle, if divided: (0) parts touching or fused; (1) parts distinctly separate.

This character is an extension of c178, applicable only to taxa with divided outer metacarpal tubercles. Distinctly separated outer metacarpal tubercles (state 1) are synapomorphic at node 20 for the Ranidae, wherein a reversal to fused or touching parts (state 0) is synapomorphic for the (cacosternids + phrynobatrachids), for (*Discodeles* + *Platymantis*) and for (*Euphlyctis* + *Hoplobatrachus*).

180. Number of subarticular tubercles present on the third finger (including the basal or proximal tubercle): (0) two; (1) one.

Some frogs, notably some cacosternids, lack subarticular tubercles on the third finger. This is also a useful characteristic to separate *Afrana fuscigula* from *Afrana angolensis*, which is difficult on the basis of external morphology alone. No tubercles on the third finger (state 1) is synapomorphic for the cacosternids, but reverses synapomorphically in that clade for the species of *Cacosternum*. State 1 arises independently in the sooglossids and in *Afrana angolensis*.

181. Palmar supernumerary tubercles: (0) indistinct or absent; (1) distinct in one or two rows; (2) indistinguishable from granular palms.

The palmar tubercles (*sensu* Lambiris 1989), also referred to as supernumerary tubercles, can be faint or distinct within a species, but are always present or always absent in any given species. Distinct palmar tubercles (state 1) occur in many ranids, with many sporadic reversals between state 0 and 1 occurring throughout the tree. Palmar tubercles indistinguishable from granular palms (state 2) are synapomorphic for the two species of rhacophorids included. These also occur independently in *Leptopelis* and *Hyperolius*, and reflect an adaptation to arboreality.

182. Tubercle on ventrolateral surface of wrist: (0) absent; (1) present.

This weak tubercle is laterally displaced off the palm. Its presence (state 1) is synapomorphic for node 35 in the phrynobatrachids, but is also present independently in *Platymantis*, *Batrachylodes* and *Philautus*.

183. Dorsal raphe (narrow inverted skin fold) running along spine: (0) absent; (1) present.

The raphe is a very narrow indented fold of the dorsal skin. Laurent (1957) mentioned this feature in his work on the Arthroleptidae. Presence of the raphe (state 1) is synapomorphic for the two species of *Arthroleptis*, and also occurs in *Leptopelis*, the Brevicipitinae, *Batrachylodes*, *Petropedetes cameroniensis* and *Nannophrys*. This character appears to be polymorphic in *Hemisus*. This state is also present in many species of microhylids, as seen in figures from Zweifel (1985) and Dunn (1949), and *Mantella*, as seen in figures from Glaw & Vences (1994).

A slight indent that is much wider and more distinct posteriorly is evident in *Petropedetes parkeri*, *P. palmipes* and *Hoplobatrachus*, but is not here classified as a raphe.

184. Transverse fold across head behind eyes: (0) absent; (1) present.

A transverse fold across the back of the head is illustrated in Dunn (1949) Figs. 5 and 7, and appears to be common in the microhylids, although not used as a character by Wu (1994). The presence of the transverse fold (state 1) occurs only *Hemisus* of this lineage examined here. This state is synapomorphic for the two species of *Conraua*, but occurs also in many of the large fanged Asian ranids, e.g. *Limnonectes*, *Hoplobatrachus* and *Phrynoglossus*.

185. Abdominal colouration: (0) uniform or slightly mottled to plain; (1) small, regular round spots; (2) irregular spots to plain; (3) small reticulations; (4) large reticulations, semi-circular, may fade to uniform in adult. (5) bull's-eye pattern.

This character was included as it may provide insight regarding terminal sister species relationships, especially in the Petropedetinae. Small, regular round spots (state 1) are synapomorphic for (*Poyntonia* + *Ericabatrachus*), but also occur in *Leptodactylon*. Irregular spots to plain (state 2) are synapomorphic for (*Cacosternum* + *Nothophryne*). Small reticulations (state 3) are synapomorphic at node 41 in the cacosternids but occur independently in *Nanorana*. Large reticulations (state 4) are synapomorphic for the two species of *Afrana*, for the Pyxicephalinae and for (*Euphlyctis* + *Hoplobatrachus*). A bull's-eye pattern is autapomorphic for *Phrynobatrachus cricogaster*.

186. Abdominal skin: (0) coarsely granular; (1) smooth; (2) showing some granulation on the posterior half of abdomen, chest region smooth.

Previously used by Heyer & Liem (1976) 35*. Care was taken to code this character from photographs of live animals, or very well-preserved specimens, since granulations can be distorted in preservation, and may disappear (C. W. Myers, personal communication). Granular abdomens were considered plesiomorphic according to Heyer & Liem (1976), using the common equals primitive criterion. Outgroup comparison here indicates the same polarity. Smooth abdomens (state 1) are synapomorphic for (dendrobatids + sooglossids), for the astylosternids, and under Acctran optimization at node 25 in the Ranidae. Some granulation on the posterior half of the abdomen (state 2) appears to be intermediate between state 0 and state 1. Under Acctran optimization, state 2 is synapomorphic for the petropedetids excluding *Petropedetes natator*, and for node 66 in the Raninae. Within the Raninae, reversals to granular abdomens (state 0) are synapomorphic for (*Phrynoglossus* (*Discodeles* + *Platymantis*)) and for (*Amolops* + *Nannophrys*).

187. Gular skin of females, texture: (0) granular or rippled; (1) smooth.

The extent of granulation of the gular skin of females does not appear to be correlated with the granulation of the abdomen skin. Smooth gular regions (state 1) arise at the basal node. Under Acctran optimization, a reversal to granular gular regions (state 0) is synapomorphic for the arthroleptids, for (*Staurois* + rhacophorids), for (*Phrynobatrachus dendrobates* + *P. versicolor*), for (*Phrynoglossus* (*Discodeles* + *Platymantis*)) and for (*Amolops* + *Nannophrys*).

188. Additional dorsal glands: (0) none; (1) sacral gland; (2) two dorso-lateral strips of glands, continuous and complete, or incomplete and broken into paired oval glands in the lumbar and sacral regions; (3) glandular region above eyelids; (4) poorly-defined glandular patch in the inguinal region.

Body glands were used in inferring leptodactylid relationships by Heyer (1975) 4*, and described in detail by Lynch (1971), whose terminology is adopted here. A sacral gland (state 1) occurs independently in *Phrynomantis* and *Astylosternus*, but is synapomorphic for (*Cacosternum boettgeri* + *C. nanum parvum*). Two dorso-lateral strips of glands (state 2) is a unique synapomorphy for (*Cacosternum capense* + *C. namaquense*). Glandular regions above the eyelids (state 3) are autapomorphic for *Nanorana*, whilst inguinal glands (state 4) are autapomorphic for *Poyntonia*.

189. Chevron-shaped glands in scapular region, or running down length of body: (0) absent; (1) present.

Chevrons are ridges of skin starting in the scapular region, which can be short or run the entire body length to the level of the groin (see Stewart, 1967 Fig. 37 for illustration). They are usually rounded in profile and contain a distinct point of inflection. The presence of chevron-shaped glands (state 1) is synapomorphic for the phrynobatrachids (but appear to have reversed in *Phrynodon* and *Phrynobatrachus natalensis*). In its original description, the figures of *Ericabatrachus* show chevrons (Largen 1991), but these were not present on the specimens examined for this study, and accordingly were coded as absent for that taxon.

190. Skin ridges on dorsum: (0) none; (1) only a few, broken or discontinuous; (2) more than six; (3) two continuous, glandular dorsolateral ridges.

The number and form of the dorsal skin ridges has been used in keys for African ranids (e.g., Poynton 1964; Poynton & Broadley 1985). Inger (1954) mentions the form of this character in his diagnoses of the Philippine ranids. The plastic nature of this character between species requires that it be coded very conservatively for this higher-level analysis. A few broken ridges (state 1) are synapomorphic for the two included species of *Afrana* and occur independently in *Pyxicephalus*. More than six ridges (state 2) occur in *Leptodactylus*, but is synapomorphic for

species of *Ptychadena*. Under Acctran optimization, two continuous, glandular dorso-lateral ridges (state 3) is an unambiguous synapomorphy at node 72 in the Raninae, but apparently occurs in many other ranids (Inger, 1954).

191. Amplexus position: (0) inguinal; (1) male's forearms placed along female's flanks, male vent placed half a body length back from female vent; (2) cephalic; (3) weak contact or straddling; (4) gluing of male to female; (5) axillary.

Previously used by Lynch (1973) 23, Duellman & Trueb (1986) P, Blommers-Schlösser (1993) 15* and 29*, Glaw, Vences & Böhme (1998) 15a*. Lynch (1973) argued that inguinal amplexus (state 0) is plesiomorphic, and this state occurs here in the outgroup *Heleophryne*. Duellman & Trueb (1986) propose a transformation series from inguinal to axillary to cephalic. Glaw *et al.* (1998) suggest that weak or straddling amplexus may occur in some of the petropedetids that display femoral glands, but due to lack of information, these were coded here as having axillary amplexus. Amplexus characterised by the males' forearms along the females' flanks (state 1) is synapomorphic for the hyperoliids, with the amplexus position for *Leptopelis* coded as unknown. Cephalic amplexus (state 2) is a unique synapomorphy for the dendrobatids. Although a poorly defined state, weak or straddling amplexus (state 3) is synapomorphic for the mantellids. Gluing of male to female (state 4) is autapomorphic for the Brevicipitinae. The vast majority of the Ranidae and Neobatrachia exhibit axillary amplexus (state 5).

Appendix 3. Multiple sequence alignment of the partial 12S rDNA sequences.

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                                0    5    10   15   20   25   30   35   40   45   50   55   60   65
                                |    |    |    |    |    |    |    |    |    |    |    |    |    |
Heleophryne natalensis          CGCCAGGGTA-TTACGAG-CCCAAGCTTAAAACCCAAAGGACTTGACGGTGCCCC-AAT-CCCCCTA-G
Probreviceps species            CGCCAGG-TA-TTACGAG-CAAAAGCTTAAAACCCAAAGGACTTGACGGnnTCCC--AC-CCACCTA-G
Hemisus marmoratus              CGCCAAAGGn-TTACAAG-TGCAAGCCTAAAA-CTTAAGGACTTGACGGTGTCTC--AT-CCTCCTA-G
Nesomantis thomasseti           CACCTGGGAA-CTACAAG-CAAAAGCTTGAAACCTAAAGGACTTGACGGTGCCCCAAAC-CCACCTA-G
Leptodactylus pentadactylus     CGCCAGGGAG-CTACGAG-CC-AAGCTTAAAACCCAAAGGACTTGACGGCACCCCAATT-CCCTCTA-G
Dendrobates speciosus           CGCCCGGGTAATTACGA--CT-ATGTCC---GTCCATAGGA--T-AC-GTGCCCCATAT-CCCCCTAAG
Dendrobates pumilio             CGCCTGGGGA-CTACAAG-CT-AAGCTTAAAACCCAAAGGACTTGACGGTACCCCATAT-CCCCCTA-G
Leptopelis vermiculatus         CGCCCGAGAA-CTACGAG-CACACGCTTAAAACTCAAAGGACTTGACGGTGTCCC--AC-CCAACTA-G
Hyperolius viridiflavus         CGCCAAAGAA-CTACAAG-CGCAAGCTTAAAACTTAAAGGACTTGACGGTGCCCC--AT-CTACCTA-G
Kassina maculata                CGCCAGAGAA-TTACGAG-CACAAGCTTAAAACTCAAAGGACTTGACGGTGTCCC--AT-CTGCCTA-G
Mantella aurantiaca             ?????GGGAA-TTACGAG-CGTAnnnTTAAAATCCAAAGGATTTGACGGTGTCCC--AC-CCACCTA-G
Mantidactylus femoralis         AGCCAGGGAA-TTACGAG-CGCAAGCTTAAAACCCAAAGGATTTGACGGTGTCCC--AC-CCACCTA-G
Chiromantis xerampelina         CGCCAGGGTAACTACGAG-CCTTAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCAACTA-G
Philautus petersi               CGCCAGGGTA-TTACGAG-CCT-AGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCCACTA-G
Arthroleptis variablis          CGCCAGAGCA-CTACGAGTAACTAACTTAAAACTCAAAGGACTTGACGGCGTCTC--AC-CTACCTA-G
Arthroleptis species            CGCCAGAGTA-CTACGAGTAACCAACTTAAAACTCAAAGGACTTGACGGCGTCTC--AC-CTACCTA-G
Cardioglossa gracilis           ???????TA--CTACAAG-CCCAAGCTTAAAACTCAAAGGACTTGACGGCGTCCC--AC-CCACCTA-G
Astylosternus diadematus        ???????TA--TTACGAG-CACAAGCTTAAAACTCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Scotobleps gabonicus            ????????TA-CTACGAG-CCCAGGCTTGAAACTCAAAGGACTTGACGGTGTCCC--AC-CCCCTA-G
Trichobatrachus robustus        ????????????????????????AACTTAAAACTCAAAGGACTTGACGGTGTCCC--AC-CCACCTAnG
Leptodactylon mertensi          CGCCAGAGTA-TTACGAG-CCCAAGCTTAAAACTCAAAAGACTTGACGGTGTCCC--AC-CCACCTA-G
Tomopterna marmorata            CGCCCGGGTA-TTACGAG-CTCAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Tomopterna tandyi               CGCCCGGGTA-TTACGAG-CGGAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Anhydrophryne rattrayi          ????????TA-TAACGAG-CATAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AT-CCATCTA-G
Arthroleptella landdrosia       ????????TA-TTACGAG-CTTAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Arthroleptella lightfooti       ????????TA-TAACGAG-CTTAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Poyntonia paludicola            CGCCCGGGTA-TTACGAG-CTTAAGCTTAAAACCCAAGGGACTTGACGGTGCCCC--AT-CCATCTA-G
Cacosternum capense             CGCCCGGGTA-TTACGAG-CTGAAGCTTAAAACCCAAGGGACTTGACGGTGTCCC--AC-CCATCTA-G
Cacosternum namaquense          CGCCAGGGTA-TTACGAG-CTGAAGCTTAAAACCCAAGGGACTTGACGGTGTCCC--AC-CCACCTA-G
Cacosternum nanum parvum        CGCCCGGGTA-TTACGAG-CTTAAGCTTAAAACCCAAGGGACTTGACGGTGTCCC--AC-CCACCTA-G
Cacosternum boettgeri           CGCCAGGGTA-TTACGAG-CTGAAGCTTAAAACCCAAGGGACTTGACGGTGTCCC--AC-CCACCTA-G
Microbatrachella capensis       CGCCCGGGTA-TTACGAG-CTGAAGCTTAAAACCCAAGGGACTTGACGGTGTCCC--AC-CCACCTA-G
Phrynobatrachus natalensis      ????????????????????????????CTTAAAACCCAAAGGAATTGACGGTGTCCC--AC-CCACCTA-G
Phrynobatrachus acridoides      ???????????TT---AG-CCT-AGCTTAAAACCCAAAGGAATTGACGGTGTCCC--AC-CCACCTA-G
Phrynobatrachus cricogaster     CGCCAGGGAA-TTACGAG-TTT-AACTTAAAACCCAAAGGATTTGACGGTGTCCC--AC-CCACCTA-G
Dimorphognathus africanus       ????????GA-CTACGAG-CCTT-GCTTAAAACCTAAAGGATTTGACGGTGTCCC--AC-CCACCTA-G
Phrynodon sandersoni            CGCCCGGGAA-TTACGAG-CTTAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCGCCTA-G
Phrynobatrachus auritus         CGCCCGGGGA-CTACGAG-TCT-AACTTAAAACCCAAAGGATTTGACGGTGTCCT--AC-CCACCTA-G
Arthroleptides martiensseni     CGCCAGGGTA-TTACGAG-CTGAAGCTTAAAACCCAAGGGACTTGACGGTGTCCC--AC-CCACCTA-G
Petropedetes parkeri            CGCCAGGGTA-TTACGAG-CCTCAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCATCTA-G
Petropedetes cf. parkeri        CGCCAGGGGA-CTACGAG-CAA-TGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Petropedetes cameroniensis      ????????CA-TTACGAG-TCTTAGCTCAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Ptychadena chrysogaster         ???????TA--TTACAAG-CTC-AGCTTAAAATCCAAAGGACTTGACGGTGTCCCACAT-CCTTCTA-G
Ptychadena anchiete             CGCCAGGATA-TTACGAG-CAATAGCTTAAAATCCAAAGGACTTGACGGTGTCCCTTAC-CCATCTA-G
Hildebrandtia ornata            CGCCTGGATA-TTACGAG-CTTTAGCTTGAAATCCAAGGGACTTGACGGTGTTCT--AC-CCTCCTA-G
Amnirana albolabris             CGCCAGGGAA-TTACGAG-CAA-TGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Hydrophylax galamensis          ????????AA-TTACGAG-CTA-TGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AT-CCCCCTA-G
Afrana fuscigula                ???????TA--TTACGAG-CTTAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCCCCTA-G
Afrana angolensis               CGCCCGGGTA-TTACGAG-CTTTAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCCCCTA-G
Strongylopus grayii             ???????TA--TTACGAG-CTTAAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCCCCTA-G
Pantherana pipiens              CGCCAGGGAA-CTACGAG-CAA-TGCTTAAAACCCAAAGGATTTGACGGTGTCCC--AC-CCAGCTA-G
Pyxicephalus adspersus          CGCCAGGGAA-TTACGAG-CCA-AGCTTAAAACCCAAAGGACTTGACGGTGTCCT--AT-CCACCTA-G
Conraua crassipes               CGCCAGGGAA-TTACGAG-CCC-AGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AT-CCACCTA-G
Conraua goliath                 ????????AA-TTACGAG-CCC-AGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AT-CCACCTA-G
Hoplobatrachus occipitalis      CGCCAGGGAA-TTACGAG-CTTTAGCTTAAAACCCAAAGGACTTGACGGTGCCCC--AC-CCAGCTA-G
Euphlyctis cyanophlyctis        CGCCAGGGAA-CTACGAG-CTTTAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCAACTA-G
Limnonectes blythii             CGCCAGGGAA-CTACGAG-C-CTAGCTTAAAACCCAAACCACTTGACGGTGTCCT--AT-CCAACTA-G
Nannorana pleskei               CGCCC-GGTA-CTACGAG-CCCCAGCTTAAAACCCAAAGGACTTGACGGTGTCCC--AC-CCACCTA-G
Phrynoglossus laevis            CGCCAGGGAA-TTACGAG-CTT-AGCTTAAAACCCAAAG-ACTTGACGGTGTCCC--ATCCCA-CTA-G
Nannophrys ceylonensis          CGCCAGGGGA-CTACGAG-CCTCAGCTTAAAACCCAAAGGACTTGACGGTGACCC--AC-CCGACTA-G
Amolops ricketti                CGCCAGGGAA-CTACGAG-CC-ATGCTTAAAACCCAAAGGACTTGACGGTGTCC---ATACCAACTA-G
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Appendix 3. Continued

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                                69   74   79   84   89   94   99   104  109  114  119  124  129  134
                                |    |    |    |    |    |    |    |    |    |    |    |    |    |
Heleophryne natalensis          AGGAGCCTGTTCTATAATCGATGATCCCC------------GTTAAACCTCACCACTTCT-CGCC--
Probreviceps species            AGGAGCCTGTTCTATAATCGACACCACCC------------GCTATACCCCACTGCTTTT-TGCA--
Hemisus marmoratus              AGGAGCCTGTCCTATAATCGATAACCCCC------------GATATACCCGACTGCTTTT-TGCC--
Nesomantis thomasseti           AGGAGCCTGTTCTATAACCGACACTACCC------------GATAAACCTCACCACCACT-AGCCAT
Leptodactylus pentadactylus     AGGAGCCTGTCCTGTAATCGATAACCCCC------------GCTTAACCTCACCACTTCT-AGCA--
Dendrobates speciosus           AGGAGCCTGTCCTATAATCGATAC-CCCCC-----------GTTCAACTTCACCATTTCT-AGTAA-
Dendrobates pumilio             AGGAGCCTGTCCTATAACCGATAATCCCCC-----------GTTTAACCTCACCATTTCT-AGCTA-
Leptopelis vermiculatus         AGGAGCCTGTTCTATAATCGATAATCCCC------------GATAAACCTCACCACTTCT-AGCC--
Hyperolius viridiflavus         AGGAGCCTGTTCTATAATCGATAATCCTC------------GCTATACCTCACCTTTTTT-AGCT--
Kassina maculata                AGGAGCCTGTTCTATAATCGATACTCCCC------------GATTTACCTCACCACTTTT-AGCC--
Mantella aurantiaca             AGGAGCCTGTTCTATAATCGATAATCCTC------------GATATACCCAACCATTTCT-TGCT--
Mantidactylus femoralis         AGGAGCCTGTTCTATAATCGATGATCCTC------------GATATACCTCACCATTTTT-TGCTT-
Chiromantis xerampelina         AGGAGCCTGTCCTATAATCGATACTCCACATCGATACTCCACGTTATACCTAGCCACTTTT-TGCT--
Philautus petersi               AGGAGCCTGTTCTATAATCGATAATCCAC------------GTTATACCTAACCATTTTT-TGCT--
Arthroleptis variablis          AGGAGCCTGTTCTATAATCGATACCCCCC------------GATACACCTAACCACTTTT-TGCT--
Arthroleptis species            AGGAGCCTGTTCTATAATCGACATCCCCC------------GATACACCTAACCACTCTTTTGCT--
Cardioglossa gracilis           AGGAGCCTGTTCTATAATCGATAATCCCC------------GATAAACCCAACCACTTCT-TGCT--
Astylosternus diadematus        AGGAGCCTGTTCTATAATCGATACTCCCC------------GCTAAACCTAACCACTTCT-CGCC--
Scotobleps gabonicus            AGGAGCCTGTTCTATAATCGACAATCCCC------------GCTTAACCTCACCACTTTT-TGTC--
Trichobatrachus robustus        AGGAGCCTGTTCTATAATCnATATTCCCC------------GCTAAACCTACCCATTTCT-TGCT--
Leptodactylon mertensi          AGGAGCCTGTTCTATAATCGATTTTCCCC------------GCTACACCCAACCACTTTT-TGC---
Tomopterna marmorata            AGGAGCCTGTTCTATAATCGATACTCCCC------------GCTTCACCTCACCATTTTT-AGCC--
Tomopterna tandyi               AGGAGCCTGTTCTATAATCGATACCCCCC------------GCTTCACCTCACCATTTTT-AGCC--
Anhydrophryne rattrayi          AGGAGCCTGTTCTATAATCGATATTCCCC------------GCTATACCTCACCATTTCT-AGCC--
Arthroleptella landdrosia       AGGAGCCTGTTCTATAATCGACACTCCCC------------GCTTCACCTCACCATTTTT-AGCC--
Arthroleptella lightfooti       AGGAGCCTGTTCTATAATCGACACTCCCC------------GCTTCACCTCACCATTTTT-AGCC--
Poyntonia paludicola            AGGAGCCTGTTCTATAATCGACACCCCCC------------GCTACACCTCACCATTTTT-AGCC--
Cacosternum capense             AGGAGCCTGTTCTATAATCGACACCCCCC------------GCTTTACCTTACCATTTTT-AGCC--
Cacosternum namaquense          AGGAGCCTGTTCTATAATCGACACCCCCC------------GCTTCACCTCACCATTTTT-AGCC--
Cacosternum nanum parvum        AGGAGCCTGTTCTATAATCGACACCCCCC------------GCTTAACCTCACCATTTTT-AGCC--
Cacosternum boettgeri           AGGAGCCTGTTCTATAATCGACACCCCCC------------GCTTTACCTCACCATTTTT-TGCC--
Microbatrachella capensis       AGGAGCCTGTTCTATAATCGACACCCCAC------------GCTTTACCTCACCCTCTTT-AGCC--
Phrynobatrachus natalensis      AGGAGCCTGTCCCATAATCGATTATACCC------------GCTTTACCCTACCGCTTCT-ATCC--
Phrynobatrachus acridoides      AGGAGCCTGTCCCATAATCGATTATACCC------------GCTTTACCCTACCGCTTCT-ATCC--
Phrynobatrachus cricogaster     AGGAGCCTGTCCCATAATCGATAACCCCC------------GCTCTACCTTACCGCTTCT-TACC--
Dimorphognathus africanus       AGGAGCCTGTCCCATAATCGATAATCCCC------------GCTCCACCCTACCACTTCT-TACC--
Phrynodon sandersoni            AGGAGCCTGTCCTATAATCGATACCCCCC------------GCTATACCTCACCACTCCT-TGC---
Phrynobatrachus auritus         AGGAGCCTGTCCCATAAACGATAATCCCC------------GATTCACCCGACCCCTTCT-TACT--
Arthroleptides martiensseni     AGGAGCCTGTTCTATAATCGACACCCCCC------------GCTTTACCTCACCATTTTT-AGCC--
Petropedetes parkeri            AGGAGCCTGTTCTATAATCGATACCCCCC------------GCTATACCCTACCACTTTT-AGCC--
Petropedetes cf. parkeri        AGGAGCCTGTCCTGTAATCGATGACCCCC------------GTTATACCCAACCATTCCT-AGCT--
Petropedetes cameroniensis      AGGAGCCTGTTCTATAATCGATACCCCCC------------GCTATACCTCACCACTTTT-AGCC--
Ptychadena chrysogaster         AGGAGCCTGCCCTACAATCGATTATTCCC------------GCTAGACCCTACCATCTCT-TGCAA-
Ptychadena anchiete             AGGAGCCTGCCCTATAATCGATTATCCCC------------GCTAGACCCTACCATCTCT-TGCC--
Hildebrandtia ornata            AGGAGCCTGTCCTACAATCGATGATCCCC------------GCTACACCCAACCATTTCT-TGCCT-
Amnirana albolabris             AGGAGCCTGTCCTGTAATCGATGATCCCC------------GCTATACCCAACCATTCCT-AGCC--
Hydrophylax galamensis          AGGAGCCTGTTCTATAATCGATGATCCCC------------GATATACCCGACCACCCTT-AGCT--
Afrana fuscigula                AGGAGCCTGTTCTATAATCGATACTCCCC------------GCTAAACCTCACCATTTTT-TGCC--
Afrana angolensis               AGGAGCCTGTTCTATAATCGATACCCCCC------------GCTACACCTCTCCATTTTT-AGCC--
Strongylopus grayii             AGGAGCCTGTTCTATAATCGATACTCCCC------------GCTAAACCTCACCATTTTT-TGCC--
Pantherana pipiens              AGGAGCCTGTTCTTTAATCGATGATCCCC------------GCTACACCTGACCATTTCT-TGCT--
Pyxicephalus adspersus          AGGAGCCTGTTCTATAATCGATACTCCAC------------GCTACACCCCACCATTTCT-TGTT--
Conraua crassipes               AGGAGCCTGTTCTATAATCGATACCCCCC------------GCTATACCTAACCATTTCT-AGCC--
Conraua goliath                 AGGAGCCTGTTCTATAATCGATACCCCCC------------GCTATACCTAACCATTTCT-AGCC--
Hoplobatrachus occipitalis      AGGAGCCTGTTCTATAATCGATGATCCCC------------GCTTAACCTAACCCTTTCT-TGCTT-
Euphlyctis cyanophlyctis        AGGAGCCTGTTCTATAACCGATAATCCCC------------GTTCTACCTAACCCCCCTT-TGCCT-
Limnonectes blythii             AGGAGCCTGTTCTATAATCGATAACCCCC------------GATTCACCTAACCCTATTT-TGCC--
Nannorana pleskei               AGGAGCCTGTTCTATAATCGATGATCCCC------------GCTAAACCCAACCTCCCCT-TGC---
Phrynoglossus laevis            AGGAGCCTGTTCTAGAATCGATACTCCCC------------GCTTAACCTCACCACTTCT-TGCTT-
Nannophrys ceylonensis          AGGAGCCTGTTCTACAACCGATGATCCCC------------GTTACACCCAACCCCCCCT-TGCTT-
Amolops ricketti                AGGAGCCTGTTCTATAATCGATGATCCCC------------GCTATACCTAACCATCCCT-TGCTT-
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Appendix 3. Continued

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                                138  143  148  153  158  163  168  173  178  183  188  193  198  203
                                 |    |    |    |    |    |    |    |    |    |    |    |    |    |
Heleophryne natalensis          CAT-CCGCCTGTATACCTCCGTCGCCAGCCCACCGCATGAGCGTGAG-AAAGTGGGCCTAA--AGAA-
Probreviceps species            TAT-CAGCCTGTATACCTCCGTCGCAAGCCTGCCATATGAAkGTCTT-AAAGCAAGCCCAA--TGAT-
Hemisus marmoratus              TCT-CAGCCTGTATACCTCCGTCGAAAGCTTACCTTGTGAAAGCCAC-TTAGTGAGCCAAT--AGGC-
Nesomantis thomasseti           ACC-CAGCCCGTATACCTCCGTCGTCAGCTTATCACTCAAGTGAATT-TTAATAAGCCAAA--TGGC-
Leptodactylus pentadactylus     AAT-CAGCCTGTATACCTCCGTCGTCAGnTTACCTCGTGAGCGCCTT-TAAGTGAGCCCAA--TGCC-
Dendrobates speciosus           AAT-CAGCCTGTATACCTCCGTCGTCAGCTTACCACGTGAGCGT-----TAGTGAGCTAAA--TGTT-
Dendrobates pumilio             AAA-CAGCCTGTATACCTCCGTCGTCAGCTCACCGCGTGAGCGT-----CAGTGAGCCTAA--TGTT-
Leptopelis vermiculatus         CAT-CAGTCTGTATACCTCCGTCGAAAGCTTACCCTGTGAACGATCA-TTAGTAAGCAGTA--AGGTC
Hyperolius viridiflavus         AAC-CAGTCTGTATACTTCCGTCGTAAGCTTACCATATGAATGCA---TCAGTAAGTTAAA--TAGTA
Kassina maculata                AAT-CAGCCTGTATACTTCCGTCGTAAGCTTACCATATGAATGC-----TAGTGAGCAAAA--TGATT
Mantella aurantiaca             TTT-CAGCCTGTATACCTCCGTCGCAAGCTTACCATTTGAATGTAAA-AGAGTAGGTTTAA---GGAT
Mantidactylus femoralis         TTT-CAGCCTGTATACCTCCGTCGCAAATCTACCACCTGAGTGTCCC-AAAGTAAATTCAA-CTGGGC
Chiromantis xerampelina         TAT-CAGCCTGTACACCTCCGTCGTAAGCTTACCATATGAACGCACA-ACAGTAGGCATAA---GGA-
Philautus petersi               TTT-CAGCCTGTATACCTCCGTCGCAAGCCTACCATATAAATGAACA-ATAGTAGGCCTAA--CAGC-
Arthroleptis variablis          AAT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATATGAATGTTAA-TTAGTAAGCAAAA--AGGTC
Arthroleptis species            AAT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATATGAGTGTCAA-TTAGTGAGCATAA--TGATC
Cardioglossa gracilis           AAT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATATGAATGACAA-TTAGTGAGCAAAA--TGATT
Astylosternus diadematus        TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCTTATGAACGATCA-TTAGTGAGCAACA--AGGCT
Scotobleps gabonicus            TAT-CAGTCTGTATACCTCCGTCGCAAGCTCACCACATGAGTGTAAA-TCAGTGGGCAACA--GGGTC
Trichobatrachus robustus        TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCCTATGAATGAC---TTAGTGAGCAAAA--AGGCT
Leptodactylon mertensi          CCC-CAGTCTGTATACCTCCGTCGCAAGCTTACCATATGAACGCCCA-TTAGTGAGCAGTA--AGGC-
Tomopterna marmorata            TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGC----TTAGTAAGCCCAA--AGGTC
Tomopterna tandyi               TCT-CAGCCTGTATACCTCCGTCGCAAGCTCACCATGTGAACGCTC--TCAGTAAGCTTAA--AGGTC
Anhydrophryne rattrayi          TTC-CAGCCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGTTA--CTAGTAAGCTCAA--TGAT-
Arthroleptella landdrosia       TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCTTATGAACGT-A--TTAGTAAGCCTAA--AGGTT
Arthroleptella lightfooti       TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCCTATGAACGT-A--TTAGTAAGCCCAA--AGGTT
Poyntonia paludicola            TCT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGTAT--TTAGTAAGCCTAA--TGGTT
Cacosternum capense             TAT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGTAT--ATAGTAAGCCTAA--TGGCC
Cacosternum namaquense          GCT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGAAT--ATAGTAAGCCTAA--TGGCC
Cacosternum nanum parvum        TAT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGAAT--ATAGTAAGCCTAA--TGGCC
Cacosternum boettgeri           TCT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGCAT--ATAGTAAGCCTAA--TGGCC
Microbatrachella capensis       TAT-CAGTCTGTATACCTCCGTCGCAAGCTTACCCTATGAACGTGG--ATAGTAAGCTTAA--TGGCC
Phrynobatrachus natalensis      ----GAGTCAGTATACCGCCGTCGTAAGTCTACCATGTGAGTGA-----AAGTGGGCTAAA--TAGCC
Phrynobatrachus acridoides      ----GAGTTAGTATACCGCCGTCGTAAGTCTACCATGTGAATGA-----AAGTGGGCTAAA--TAGCC
Phrynobatrachus cricogaster     ----TAGTCTGTATACCTCCGTCGCAAGCCCACCATGTGAATGC-----AAGTGGGCCAAA--TGGGG
Dimorphognathus africanus       ----TAGTCTGTATACCTCCGTCGCAAGCTCACCATGTGAATGT-----TAGTGGGCCAAC--TAGTA
Phrynodon sandersoni            TCT-CAGCCTGTATACCTCCGTCGTAAGCCTACCATGTGAACGC----TTAGTAGGCCCAA--CGGT-
Phrynobatrachus auritus         ----CAGCCTATATACCTCCGTCGTAAGCCCACCATGTAAATGA-----GAGTAGGCCAAA--CGGGT
Arthroleptides martiensseni     TTT-CAGTCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGCAC--ACAGTAAGCCTAA--TGGCC
Petropedetes parkeri            TAT-CAGCCTGTATACCTCCGTCGTAAGTTTACCGTGTGAACGTCT--ATAGTGAGCTAAA--TGAC-
Petropedetes cf. parkeri        TCT-CAGTCTGTATACCTCCGTCGAAAGCCTACCATGTAAACGTTC--TCAGTAGGCCCAA--TG---
Petropedetes cameroniensis      TAT-CAGCCTGTATACCTCCGTCGTAAGTTTACCGTGTGAACGCTT--GTAGTAAGCTAAA--TGAC-
Ptychadena chrysogaster         CCC-CAGCTTGTATACTTCCGACGCAAGTTTACCATTTGAACGA----TCAGTGGACCTAA--TGTTC
Ptychadena anchiete             AAT-CAGCTTGTATACTTCCGTCGTAAGCTTACCATGTGAAAGACCA-ATAGTGGGCCTAA--TGTTC
Hildebrandtia ornata            TATTCAGCCTGTATACCTCCGTCGCCAGCCCGCCATGTGAATGTAG--TGTTTTGGCCCAA--TGATC
Amnirana albolabris             ATT-CAGTCTGTATACCTCCGTCGAAAGCCTACCATGTAAACGTCC--CCAGTAGGCTCAA--TGACA
Hydrophylax galamensis          CTT-CAGTCTGTATACCTCCGTCGAAAGCTTACCATGTAAACGTTAA-AAAGTAGGCTCAA--TGATG
Afrana fuscigula                TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCCTGTGAACGCCA--TCAGTAAGCCTAA--TGGCC
Afrana angolensis               TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCATGTGAACGCTA--CTAGTAAGCCCAA--TGGCC
Strongylopus grayii             TCT-CAGCCTGTATACCTCCGTCGCAAGCTTACCCTGTGAACGCCA--TCAGTAAGCCTAA--TGGCC
Pantherana pipiens              CAT-CAGTCTGTATACCTCCGTCGAAAGCTTACCATGTGAACGTCT--TCAGTAGGCTCAA--TGATC
Pyxicephalus adspersus          GAT-CAGCCTGTATACCTCCGTCGTAAGCTTACCATATGAATGACCT-GCAGTAAGCTCAACTAGGTC
Conraua crassipes               -CT-CAGCCTGTATACCTCCGTCGCAAGCCTACCCTATGAATGAACT-ACAGTAAGCCCAA--AGGCC
Conraua goliath                 -CT-CAGCCTGTATACCTCCGTCGCAAGCCTACCCTATGAATGAACT-ACAGTAAGCCCAA--AGGCC
Hoplobatrachus occipitalis      TAT-CAGCCTGTATACCTCCGTCGTAAACCCGCCATATGAGTGTTT--TTAGCGGATTCAA--TGGCC
Euphlyctis cyanophlyctis        TTT-CAGCCTGTATACCTCCGTCGCAAGTCCGCCATATGAATGCCCT-TCAGCGGATTAAA---GGAT
Limnonectes blythii             CCC-CAGTCTGTATACCTCCGTCGCAAACTTACCATATGAATGCTT--ACAGTAAGTACAA--AGGCC
Nannorana pleskei               AAT-CAGCCTGTATACCTCCGTCGTAAGCTTACCATATGAATGTTT--TCAGTAAGTTTAA--TGGCT
Phrynoglossus laevis            TAT-CAGCTAGTATACTTCCGTCGCAAGCTTACCACATGAGTGTAC--GTAGTAGGCCCAA--TGATT
Nannophrys ceylonensis          TAT-CAGCCTGTATACCTCCGTCGTAAACTCACCATATGAATGCCTTCCAAGTGGGTTCAA--TGTTT
Amolops ricketti                TAT-CAGCCTGTATACCTCCGTCATAAGCCTACCATGTGAACGTCA--ACAGTGGGCCCAA--TGGTT
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Appendix 3. Continued

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                                207  212  217  222  227  232  237  242  247  252  257  262  267  272
                                 |    |    |    |    |    |    |    |    |    |    |    |    |    |
Heleophryne natalensis          ----CCTTTTCCAATACGTCAGGTCAAGGTGCAGCACATG-AAGTGGAAAGAAATGGGCTACACTCTCT
Probreviceps species            ---TCAyTCACCCCAACGTCAGGTCAAGGTGCAGCCCACA-AAGCAGTTCGAAATGGGCTACAATTTCT
Hemisus marmoratus              ---TATTACGCCATTATGTCAGGTCAAGGTGCAGCCAATA-TAGCAGCA-GAGATGGGCTACAGTTTCT
Nesomantis thomasseti           -----CCCCACCAATACGTCAGGTCAAGGTGCAGCATATG-TCGTGGGCAGAAATGGGCTACACTCCCT
Leptodactylus pentadactylus     ----AATACGCCAATACGTCAGGTCAAGGTGCAGCTAATG-AAATGGGAAGAGATCGGCTACACTCTCT
Dendrobates speciosus           ----TATTCAACCACACGTCAGGTCAAGGTGCGACACATG-AGATGGAAAGAGATGGGCTACACTCT-T
Dendrobates pumilio             ----AATTCAACTACACGTCAGGTCAAGGTGCAACATATG-TAATGGGAAGAGATGGGCTACACTCTCT
Leptopelis vermiculatus         ----TATCCACCAAAACGTCAGGTCAAGGTGCAGCTTACG-AAGTGGGAAGAAATGGGCTACAATTTCT
Hyperolius viridiflavus         AATAC-ATTACCAAAACGTCAGGTCAAAGTGCAGCCTACA-AAAAGGGAAGAAATGGGCTACAATTTCT
Kassina maculata                AATA----TACCCACACGTCAGGTCAAAGTGCAGCCGACA-AAGTGGCAAGAAATGGGCTACAATTTCT
Mantella aurantiaca             ----CCCCCATCAATACGTCAGGTCAAGGTGCAGCCAATG-TAATGGAAAGTAATGGGCTACAATTTCT
Mantidactylus femoralis         CC-CAATACGCCAATACGTCAGGTCAAGGTGCAGCCCATA-AAATGGGAAGCAATGGGCTACAATTTCT
Chiromantis xerampelina         ---CCACACGCCACAATGGCAGGTCAAGGTGCAGCTCACA-AAGTGGAAGA-GATGAGCTACAATTTCT
Philautus petersi               ---CCAAACACTATAACGTCAGGTCAAGGTGCAGCTTATA-AAATGGAAAGTAATGGGCTACAATTTCT
Arthroleptis variablis          ----ACCACACCAATACGTCAGGTCAAGGTGCAACCCACA-AAGTGGTAAGAAATGGGCTACACTTTCT
Arthroleptis species            ----CCTACATCAACACGTCAGGTCAAGGTGCAGCCTACA-AAGTGGAAAGAAATGGGCTACAATTTCT
Cardioglossa gracilis           ----ACTACACCAACACGTCAGGTCAAGGTGCAACCTATG-AACTGGAAAGAAATGGGCTACAATTTCT
Astylosternus diadematus        ----ATTACACCTACACGTCAGGTCAAGGTGCAGCTCACG-AAGTGGTGTGAAATGGGCTACAATTTCT
Scotobleps gabonicus            ----TCTTCACCAATACGTCAGGTCAAGGTGCAACTTATA-GAGTGGCAAGTAATGGGCTACAATTTCT
Trichobatrachus robustus        ----ATTACnCCCACnCTTCGGGTCAAGGTGCAnCCTACA-AAATGGTnAGAAATGGGCTACAATTTCT
Leptodactylon mertensi          ----CCCACGCCAACACGTCAGGTCAAGGTGCAGCCAACA-AAGTGGAGAGAAATGGGCTACAATTTCT
Tomopterna marmorata            ----CTCTCACCAACACGTCAGGTCAAGGTGCAGCTCATG-AAATGGGAAGCAATGGGCTACAATTTCT
Tomopterna tandyi               ----CTCTCACCAATACGTCAGGTCAAGGTGCAGCTCATG-AAATGGGAAGCAATGGGCTACAATTTCT
Anhydrophryne rattrayi          -----CCACATCAATACGTCAGGTCAAGGTGCAGCTCACG-CAATGGAAAGCAATGGGCTACAATTTCT
Arthroleptella landdrosia       ----CACCCACCAACACGTCAGGTCAAGGTGCAGCTTATA-AAATGGAAAGCAATGGGCTACAATTTCT
Arthroleptella lightfooti       ----CACCCACCAGCACGTCAGGTCAAGGTGCAGCTCATA-AAATGGAAAGCAATGGGCTACAATTTCT
Poyntonia paludicola            ----ACTTCACCAACACGTCAGGTCAAGGTGCAACCTATA-AAATGGGAAGTAATGGGCTACAATTTCT
Cacosternum capense             ----CATTCACCCGCACGTCAGGTCAAGGTGCAACTTATA-AAATGGAAAGCAATGGGCTACAATTTCT
Cacosternum namaquense          ----TATTCACCAACACGTCAGGTCAAGGTGCAACTCATA-AAATGGAAAGCAATGGGCTACAATTTCT
Cacosternum nanum parvum        ----TATTCACCAACACGTCAGGTCAAGGTGCAACTTATA-AAATGGGAAGTAATGGGCTACAATTTCT
Cacosternum boettgeri           ----CGTACACCAACACGTCAGGTCAAGGTGCAACTTATA-AAATGGGAAGTAATGGGCTACAATTTCT
Microbatrachella capensis       ----TTTTCACCAATACGTCAGGTCAAGGTGCAACTAATA-AAAGGGGAAGCAATGGGCTACAATTTCT
Phrynobatrachus natalensis      T----CCCCGCACATACGTCAGGTCAGGGTGCAGCTTATG-GAGCGGAAGGCGATGGGCTACAATTTCT
Phrynobatrachus acridoides      T----CCCCGCACATACGTCAGGTCAGGGTGCAGCTTATG-GAGCGGGAAGCGATGGGCTACAATTTCT
Phrynobatrachus cricogaster     T-----TTTCCCAACACGTCAGGTCAAGGTGCAGCTTATG-AAACGGAGTGAGATGGGCTACAATTTCT
Dimorphognathus africanus       ----GCTACCCTCATACGTCAGGTCAAGGTGCAGCTTATG-AAGTGGCGTGAGATGGGCTACAGTTTCT
Phrynodon sandersoni            ----CACTCACCAATACGTCAGGTCAAGGTGCAGCCTATG-AAGTGGTA-GTGATGGGCTACAATTCCT
Phrynobatrachus auritus         T--CACTTCCCCCCCACGTCAGGTCAAGGTGTAGCCTATG-AAGAGGTGTTAGATGGGCTACAATCTCT
Arthroleptides martiensseni     ----TATACACCAGCACGTCAGGTCAAGGTGCAACTTATA-AAATGGGAAGTAATGGGCTACAATTTCT
Petropedetes parkeri            ----TTTTCGCCAATACGTCAGGTCAAGGTGCAGCCCATG-AAGTGGCAAGCAATGGGCTACAATTTCT
Petropedetes cf. parkeri        ----ATTCCGTCAACACGTCAGGTCAAGGTGCAGCTTACG-GAATGGGA-GAGATGGGCTACAATTTCT
Petropedetes cameroniensis      ----TTTCCGTCAGTACGTCAGGTCAAGGTGCAGCCCATA-AAGTGGCAAGCAATGGGCTACAATTTCT
Ptychadena chrysogaster         C--AGTTTAACCAGTACGTCAGGTCAAGGTGCAGCCTATG-AGATGGGA-GAGGTGGGCTACAATTTCT
Ptychadena anchiete             C---GTTTCACCAGTACGTCAGGTCAAGGTGCAGCCTATG-AGATGGGAAAGGGTGGGCTACAATTTCT
Hildebrandtia ornata            A---GCCTAATAAATACGTCAGGTCAAGGTGCAGCCTATG-AGATGGAATGAGATGGGCTACAATTTCT
Amnirana albolabris             -------CCATCAACACGTCAGGTCAAGGTGCAGCTTACG-GAATGG-AAGAGATGGGCTACAATTTCT
Hydrophylax galamensis          -------TCATCAATACGTCAGGTCAAGGTGCAACTCACG-GAGTGGTAAGTAATGGGCTACAGTTTCT
Afrana fuscigula                ----CTTTCGCCAATACGTCAGGTCAAGGTGCAGCTCATA-AAATGGGAAGCGATGGGCTACAATTTCT
Afrana angolensis               ----CTTCCACCAACACGTCAGGTCAAGGTGCAGCTCATG-AAATGGAAAGCAATGGGCTACAATTTCT
Strongylopus grayii             ----CTTTCGCCAATACGTCAGGTCAAGGTGCAGCTCATA-AAATGGGAAGCGATGGGCTACAATTTCT
Pantherana pipiens              AT-AATTACATCAATACGTCAGGTCAAGGTGCAGCTTAAG-AAATGGGAAGCAATTGGCTACAATTTCT
Pyxicephalus adspersus          ----CCTCCACCAATACGTCAGGTCAAGGTGCAGCTTATG-AAATGGAAAGCAATGGGCTACAATTTCT
Conraua crassipes               -----CCCCGCCAACACGTCAGGTCAAGGTGCAGCTTATG-AAATGGCAAGCAATGGGCTACAATTTCT
Conraua goliath                 -----CCCCGCCAACACGTCAGGTCAAGGTGCAGCTTATG-AAATGGCAAGCAATGGGCTACAATTTCT
Hoplobatrachus occipitalis      T---TAGCCACCAGCACGTCAGGTCAAGGTGCAGCCAATGAAAGAGGTAAGCAATGGGCTACAATTTCT
Euphlyctis cyanophlyctis        ----TTTTTATCAATACGTCAGGTCAAGGTGCAGCCTATA-GGGTGGCAAGCAATGGGCTACAATTTCT
Limnonectes blythii             -----CTTCGCCAATACGTCAGGTCAAGGTGCAACTTATA-ATAGGGGAAGTAATGGGCTACAATTTCT
Nannorana pleskei               A--TAAAACACCAATACGTCAGGTCAAGGTGCAGCTCATG-GGGTGGTAAGCAATGGGCTACAATTTCT
Phrynoglossus laevis            -----ATACATAAACACGTCAGGTCAAGGTGCAGCATAAG-AAGTGGC-TGAGATGGGCTACAATTTCT
Nannophrys ceylonensis          T---ATTACACCAGTACGTCAGGTCAAGGTGCAGCCCATG-GTGAGGTAAGCAATGGGCTACAATTTCT
Amolops ricketti                ---TGTATAACCAAAATGCCAGGTCAAGGTGCAGCTCACG-GAATGGTAAGTAATGGGCTACAATTTCT
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Appendix 3. Continued

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                                276  281  286  291  296  301  306  311  316  321  326  331  336  341
                                 |    |    |    |    |    |    |    |    |    |    |    |    |    |
Heleophryne natalensis          AACCT--AGAAAACA-CGAAAGA----CTGCC--TGAAACACCAGTCT--GAAGGCGGATTTAGTAGT
Probreviceps species            ATATT--AGAACAAA-CGAAAGG----CCAC--ATGAAA-TCTAGCCA-TGAAGGCGGATTTAGTAGT
Hemisus marmoratus              ATAAT--AGAACATA-CAGATGGATTTCCA---ATGAAA---CAGACC-AGAAGGCGGATTTAGAAnT
Nesomantis thomasseti           CACAACCAGGAAAAA-CAAAAGA---CCTAG---AGAAA-CAAAGTCA--AAAGGCGGATTTAGTAGT
Leptodactylus pentadactylus     ATTTA-TAGAAAAAA-CGAAAGA----CCACTTATGAAA-CCTGGTCA--GAAGGAGGATTTAGCAGT
Dendrobates speciosus           ATCTT--AGAGAATA-CGAAAGA----CTAATTATGAAA-TCTAGTCA--GCAGGCGGATTTAGAAGT
Dendrobates pumilio             AACTT--AGAATATA-CGAAAGA----CTACTTATGAAA-TCTAGTCA-TAAAGGTGGATTTAGAAGT
Leptopelis vermiculatus         AAACT--AGAACAAA-CGAAAAG--ATCTGC--ATGAAA-CACAGTCA-TGAAGGCGGATTTAGTAGT
Hyperolius viridiflavus         AATAA--AGAACACA-CGAATTT----AAGTAATTGAAA-ACTACT-A-TGAAGGCGGATTTAGAAGT
Kassina maculata                AACTT-TAGAACATA-CGAAAAA----CCAC--ATGAAA-ACTGGTCA-CGAAGGCGGATTTAGCAGT
Mantella aurantiaca             ATAAT--AGAACAAA-CGAAACA----CTGC--ATGAAA-AACAGTCA-TGAAGGCGGATTTAGTAGT
Mantidactylus femoralis         AAAAT--AGAACAAA-CATAAAA----CTAC--ATGAAA-CATAGTCA-TAAAGGCGGATTTAGCAGT
Chiromantis xerampelina         AAATT--AGAACATA-CGAAACA----TTAT--ATGAAA-CATAATCA-TGAGGGTGGATTTAGTAGT
Philautus petersi               AGTCT--AGAACAAA-CGAATTA----CTAC--ATGAAA-CACAGTCA-TGAAGGCGGATTTAGCAGT
Arthroleptis variablis          AATTT--AGAAAATA-CGAATAG----TCAT--ATGAAA-AATGACAA-TGAAGGCGGATTTAGTAGT
Arthroleptis species            AATCT--AGAACACA-CGGATAG----TCAT--ATGAAA-AATGACAA-TGAAGGAGGATTTAGAAGT
Cardioglossa gracilis           AATTA-TAGAACAAA-CGAAAAA---ATTAT--ATGAAA-AATAATTA-TGAAGGCGGATTTAGTAGT
Astylosternus diadematus        ATAATTTAGAACACA-CGAAA-G----ACCCC-ATGAAA-TTAAGTCA-TGAAGGCGGATTTAGTAGT
Scotobleps gabonicus            ATAGT--AGAACACA-CGAAAAG----ACAC--ATGAAA-ACATGTCT-TGAAGGCGGATTTAGTAGT
Trichobatrachus robustus        ACCAC--AAAACATA-CAAAAnA----CCCT--ATGAAA-CTAAATCA-TGAAGGAGGATTTAGTAnT
Leptodactylon mertensi          GCCAC--AGAACACA-CGAAAGA----CCCA--ATGAAA-ACCAGTCA-CGAAGGCGGATTTAGCAGT
Tomopterna marmorata            AATGC--AGAACAAA-CGAAGGA----CTAT--ATGAAA-CACAGTCA-CGAAGGCGGATTTAGTAGT
Tomopterna tandyi               CATGC--AGAACAAA-CGAAAGA----CTAC--ATGAAA-CACAGTCA-TGAAGGCGGATTTAGCAGT
Anhydrophryne rattrayi          AACAT--AGAACCTA-CGAAAAA----CTGT--ATGAAA-TATAGTTA-TGAAGGCGGATTTAGTAGT
Arthroleptella landdrosia       AACAT--AGAATAAA-CGAAAAA----CTGT--ATGAAA-CACAGTAA-TGAAGGCGGATTTAGTAGT
Arthroleptella lightfooti       AGTAT--AGAATAAA-CGAAAAA----CTGT--ATGAAA-CACAGTAA-TGAAGGCGGATTTAGTAGT
Poyntonia paludicola            AACTT--AGAACAAA-CGAAAAA----CTGC--ATGAAA-AACAGTTA-TGAAGGCGGATTTAGTAGT
Cacosternum capense             AATGT--AGAACAAA-CGAAAAA----CTGC--ATGAAA-CACAGTTA-TGAAGGCGGATTTAGTAGT
Cacosternum namaquense          AATGT--AGAACAAA-CGAAAAA----CTGC--ATGAAA-CACAGTTA-TGAAGGCGGATTTAGTAGT
Cacosternum nanum parvum        AACGT--AGAACAAA-CGAAGAA----CTGT--ATGAAA-CACAGCTA-TGAAGGCGGATTTAGTAGT
Cacosternum boettgeri           AACCT--AGAACAAA-CGAAAAA----CTGC--ATGAAA-CACAGTT--TGAAGGCGGATTTAGTAGT
Microbatrachella capensis       AATTT--AGAACACA-CGAAAAA----CTGC--ATGAAA-CACAGTTA--GAAGGCGGATTTAGCAGT
Phrynobatrachus natalensis      AACAT--AGAACATAACGGAAAA----CCTA--ATGAAA-CCCAGATATTGAAGGTGGATTTAGCAGT
Phrynobatrachus acridoides      AACAT--AGAACATAACGGAAAA----CTAA--ATGAAA-CCCAGTTATTGAAGGTGGATTTAGCAGT
Phrynobatrachus cricogaster     ATCAT--AGAACATA-CGAAAAG----ATAA--ATGAAA-CTCATCTA-TGAAGGTGGATTTAGTAGT
Dimorphognathus africanus       --GTT-CAAAGCACA-CAGAAAA---ACGTA-AATGAAA-CTCAACTA-TGAAGGAGGATTTAGAAGT
Phrynodon sandersoni            AACCT--AGCACAAA-CGGAAAG----CTGC--ATGAAA-CACAG-CA-TAAAGGTGGATTTAGTAGT
Phrynobatrachus auritus         ACCAT--AGAACAAA-CGAAAAG----TCAA--ATGAAA-ATTAACTA-TGAAGGTGGATTTAGCAGT
Arthroleptides martiensseni     AATTT--AGAACAAA-CGAACAA----CTGC--ATGAAA-CACAGTT--TGAAGCCGCATTTAGTAGT
Petropedetes parkeri            AACCT--AGAACAAA-CGGATGA---ACTGT-AATGAAA---CAGTTT-AGAAGGAGGATTTAGTAGT
Petropedetes cf. parkeri        AATTT--AGAACAAA-CGAAATA----CTAT--GTGAAATCATAGTCACTGAAGGTGGATTTAGTAGT
Petropedetes cameroniensis      AATTT--AGAACAAA-CGGATAA---ACTGT--ATGAAA--CCAGTTT-AGAAGGCGGATTTAGTAGT
Ptychadena chrysogaster         AATCT--AGAACAAA-CGAACTA----CTGC--ATGAAAACACAGT-A-TGAAGGAGGATTTAGTAGT
Ptychadena anchiete             ATAAT--AGAACACA-CGAAACC----CTGC--ATGAAAACCCAGAAA-TGAAGGTGGATTTAGTAGT
Hildebrandtia ornata            AGATT--AGAACATA-CGGAAAC----CTAT--ATGAAG-TATAGTTA-TGAAGGTGGATTTAGTAGT
Amnirana albolabris             AAATT--AGAACAAA-CGAAATA----CTAT--GTGAAATCATAGTAACTGAAGGTGGATTTAGTAGT
Hydrophylax galamensis          AGACT--AGAACAAA-CGAAAGA----CATT--GTGAAA-CATAATCA-TGAAGGCGGATTTACTAGT
Afrana fuscigula                AAGTT--AGAACAAA-CGAAAGA----CTGC--ATGAAA-CACAGTCA-TGAAGGCGGATTTAGTAGT
Afrana angolensis               AACAT--AGAACAAA-CGAAAGA----CTGT--ATGAAA-CACAATCA-TGAAGGTGGATTTAGTAGT
Strongylopus grayii             AAGTT--AGAACAAA--GA--------CTGC--ATGAAA-CACAGTCA-TGAAGGCGGATTTAGTAGT
Pantherana pipiens              AATAT--AGAACAA--CGAAAGG----CTAT--GTGAAATCATAGCAG-CGAAGGTGGATTTAGTAGT
Pyxicephalus adspersus          AACTT--AGAACATA-CCAAACG----CTGC--ATGAAA-CACAGCTA-CAAAGGCGGATTTAGTAGT
Conraua crassipes               AACTT--AGAACAAA-CGGAAGA----CTAC--ATGAAA-CACAGTCG-TGAAGGCGGATTTAGTAGT
Conraua goliath                 AACTT--AGAACAAA-CGGAAGA----CTAC--ATGAAA-CACAGTCG-TGAAGGCGGATTTAGTAGT
Hoplobatrachus occipitalis      AATCT--AGAACATA-CGAACTA----CTGC--ATGAAAACACAGTCA-TGAAGGAGGATTTAGTAGT
Euphlyctis cyanophlyctis        AACCT--AGAACATA-CGAAGTA----CTGC--ATGAAA-CACAGTCA-TGAAGGAGGATTTAGTAGT
Limnonectes blythii             AACAT--AGAACACA-CGAAACA----CTGC--ATGAAA-TACAGTTA-TGAAGGCGGATTTAGTAGT
Nannorana pleskei               AATCT--AGAACAAA-CGAAACA----CTGT--ATGAGA-CTCAGTTA-T-AAGGCGGATTTAGTAGT
Phrynoglossus laevis            AGCTT--AGAACACA-CGAAATG----CTGA--ATGAAA-CACGGGCA-TGAAGGAGGATCTAGTAGT
Nannophrys ceylonensis          ATATT--AGAACAAA-CGAAATA----CTGC--ATGAAA-TACAGTCA-TGAAGGAGGATCTAGTAGT
Amolops ricketti                AATCT--AGAACAAA-CGGAAAG----CTAT--GTGAAATCACAGCC--TAAAGGTGGATTTAGTAGT
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Appendix 3. Continued

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                                345  350  355  360  365  370  375  380  385
                                 |    |    |    |    |    |    |    |    |
Heleophryne natalensis          AAAAAGAAACAATGAGAGTTCTTTTTAACTC-GGCCCTGGGGTGTGT
Probreviceps species            AAAnAGAAAA-TAGAGAGTTCTTTTTAATAA-GGCACTGGGACATGT
Hemisus marmoratus              AAAAAGAAAA-TAAAnATTCCTTTTTAATTA-GGTCCGTTTAGCCGT
Nesomantis thomasseti           AAAAAGAAAA-CAGAGTGTTCTTTTTAACTC-GGCCCTGGGACACGT
Leptodactylus pentadactylus     AAAAAGAGAC-AT-AGTGCTCTTTTTAACCCGGGAACTGGGGTGTG?
Dendrobates speciosus           AAAATGGAAC-CAGAGAGTCCCTTTGAACAC-CCCAC??????????
Dendrobates pumilio             AAAACGGAAC-AAGAGAGTCCTTTTTAACAT-GGC???????????
Leptopelis vermiculatus         AAAAAGAAAA-TAGAGTGTTCTTTTTAACCG-AGCACTGGnTACCG?
Hyperolius viridiflavus         AAAACGAAAA-CAAAGTGTTCGTTTTAACAA-TGCTCTGGGACGCGT
Kassina maculata                AAGGGGAAAA-TAGAGTGTnCCCCTTAAATA-TGCCCTGGGACGTGT
Mantella aurantiaca             AAAAGGGGAA-TAGAGAGCCCCTTTTAACA--GGCCCTGGGACGTGT
Mantidactylus femoralis         AAAAGAAGAA-TAGCAAGCTTCTTTTAACAG-GGCCCTGGGACGTGT
Chiromantis xerampelina         AAGTGGGGAA-TAGAGAGCCCCACTTAACTC-GGCCCTGGGACGTGT
Philautus petersi               AAACGGGAAA-TAAAGAGCCCCGTTTAATCT-GGCCCTGGGACGTGT
Arthroleptis variablis          AAGGGGCAAA-TAGAGCGTCCCCCTTAACCC-AGCAATGAGACGTGT
Arthroleptis species            AAGGGGCAAA-TAGAGTGTCCCCnnnTnC---AGCAAT--CAC-TAT
Cardioglossa gracilis           AAGGGGCAAA-TAAAGTGTTCCCCTTAATTC-GGCACTGGGAC-TGT
Astylosternus diadematus        AAAAAGGAAA-TAGAGTGT-CTTTTTAATCC-GGCACTGGGACGCGT
Scotobleps gabonicus            AAAGGGGAAA-TAGAGTGTCCCCTTTAACCC-GGCACTGGGACGTGT
Trichobatrachus robustus        AAAAAGGAAA-TAnATTnTCCTTTTTAACCC-GGCACTGGGACnCnT
Leptodactylon mertensi          AAGAAGAAAA-CAAAGTGT-CTCTnT?????-GGC??TG??????GT
Tomopterna marmorata            AAAAAGAAAA-TAGTGTGTTCTTTTTAATTA-GGCACTGGGACGCGT
Tomopterna tandyi               AAAAAGAAAA-TAGTGTGTTCTTTTTAACTA-GGCACTGGGACGCGT
Anhydrophryne rattrayi          AAAAAGAAAA-CAGTATGTTCTTTTTAACCC-GGCACTGGGACGCGT
Arthroleptella landdrosia       AAAAAGAAAA-TAGTGTGTTCTTTTTAATCA-GGCTCTGGGACGCGT
Arthroleptella lightfooti       AAAAAGAAAA-TAGTGTGTTCTTTTTAATCA-GGCTCTGGGACGCGT
Poyntonia paludicola            AAAAGGAGAA-CAGCGTGCTCTTTTTAACCC-GGCACTGGGACGTGT
Cacosternum capense             AAAAAGAAAT-CAGCGTGTTCTTTTTAACTA-GGCACTGGGACGTGT
Cacosternum namaquense          AAAAAGAAAT-CAGCGTGTTCTTTTTAACTA-GACAC??????????
Cacosternum nanum parvum        AAAAAGAAAA-CAGAGTGTTCTTTTTAACCT-GGCACTGGGACGnGT
Cacosternum boettgeri           AAAAAGAAAA-CAGCGTGTTCTTTTTAACTA-GGCACTGGGACGTG?
Microbatrachella capensis       AAAAAGAAAA-CAGCATGTTCTTTTTAACTA-GGCACTGGGACGTGT
Phrynobatrachus natalensis      AAAAAGACAA-TAGAGT---CTTTTTAACAA-GGCACTGGGACGTGT
Phrynobatrachus acridoides      AAAAAGACA--TAGAGTAGTCTTTTTAACAA-GGCACTGGGACGTGT
Phrynobatrachus cricogaster     AAAAAGAAAG-TAGAATATTCTTTTTAATTTAGGCCCTGGA-CGTGT
Dimorphognathus africanus       AAAAGGAAAA-TAGAGTGTTCTTTTTAATTA-GGCACTGGGACGTGT
Phrynodon sandersoni            AAAAAGAGAC-CAGTGTGTTTTTTTTAATAC-GGCCCTGGGACG-GT
Phrynobatrachus auritus         AAAAGGAGAA-TAAAACTCCCCTTTTAACTC-GGCACTAGGAC?TG?
Arthroleptides martiensseni     AAAAAGAACCC-??????????????????????????????????
Petropedetes parkeri            AAAAAGAAAACATAAGTGTTCTTTTTAATTT-GGCACTGGGACGTGT
Petropedetes cf. parkeri        AAAAAGAAAA-TAGAGAGTTCTTTTTAACCn-GGCTCTGG???????
Petropedetes cameroniensis      AAAAAGGAAG-TAGTG----CTTTTTAATTC-GGCACTGGGACGTGT
Ptychadena chrysogaster         AAAAAGAAAT-CAGCGAGTTCTTTTTAACAT-GGCCCTGGGGCGTGT
Ptychadena anchiete             AAAAAGAAAA-TAGAGTGTTCTTTTTAATGA-GCCGCTGGGGCGAGT
Hildebrandtia ornata            AAAAAGAACC-CCGCG??????-TnTA-CTG-GG????????????
Amnirana albolabris             AAAAAGAAAA-TAGAGAGTTCTTTTTAACCC-GGCTCTGGGACGTGT
Hydrophylax galamensis          AAAAAGAAAA-TAGAGAGTTCTTTTTAACTA-GGCACTGGGAC????
Afrana fuscigula                AAAAAGAAAA-TAGTGTGTTCTTTTTAACAC-GGCACTGGGACGTGT
Afrana angolensis               AAGAAGAAAT-CAGAGAGTAATG-nTAACAC-GGCACT-GCTAT???
Strongylopus grayii             ??????????????????????????????????????????????
Pantherana pipiens              AAAAAGAAAA-TAGAGTGTTCTTTTTAACCC-GGCTCTGGGATGCGT
Pyxicephalus adspersus          AAAAAGAAAA-TAGCATGTTC??????????????????????????
Conraua crassipes               AAAA-GGGAA-CAGAGTGT-C??????????????????????????
Conraua goliath                 AAAA-GGGAA-CAGAGTGTCC??????????????????????????
Hoplobatrachus occipitalis      AAAAAGAAAT-CAGCGAGTTCTTTTTAACAT-GGCCCTGGGGC????
Euphlyctis cyanophlyctis        AAAAAGAAAA-TAGCGTGTTCTTTTTAACGC-GGCCCTGGGACGTGT
Limnonectes blythii             AAAAAGA???????????????????????????????????????
Nannorana pleskei               AAAAAGAAAAGTAGCGTATTCTTTTTAACTA-GGCCCTGGGACGTGT
Phrynoglossus laevis            AAAAAGA???????????????????????????????????????
Nannophrys ceylonensis          AAAGAGAAAA-TAGCGAGTTCTTTTTAATGC-GGCCCTGGGACATGT
Amolops ricketti                AAAAAGAAAA-TAGAGTGTTCTTTTTAACCC-GGCTCTGGGACACGT
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Appendix 4. Multiple sequence alignment of the partial 16S rDNA sequences.

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                          0    5    10   15   20   25   30   35   40   45   50   55   60   65
                          |    |    |    |    |    |    |    |    |    |    |    |    |    |
Heleophryne purcelli      TGACC-A-CAAGTTTTTGGGTGGGGCGACCACGGAGAACAACTAAACCTGCGAGATGTATAGA-GTA-
Probreviceps species      TGTCT-C-TTGGTTTTAGGTTGGGGTGACCACGGAGCACAAAAACACCTCCGAGATGAATGGG-GCT-
Nesomantis thomasseti      TACAT-A-TTCATCTTCGGTTGGGGTGACCACGGAGAAAAACAAACCCTCCACGACAAACAAG-CCT-
Leptodactylus pentadactylus TGATT-T-CTAGTTTTAGGTTGGGGTGACCACGGAGkAAAAACCAnCCTCCGCAATGAACAGG-G-C-
Dendrobates speciosus     TAATT-T-CTAGTTTTAGGTTGGGGTGACCACGGAGTAAAAACTAACCTCCACGCTGAAAGAA-TCC-
Dendrobates pumilio       TAATT-T-CTAGTTTTAGGTTGGGGTGACCACGGAGTAAAAACTAACCTCCACGCTGAAAGAA-TCC-
Colostethus pratti        TTATT-T-CTAATTTTAGGTTGGGGCGACCACGGAGCAAAATTAAACCTCCACGACGAAGGAG-ACT-
Leptopelis vermiculatus   TGACG-G-GTAGTTTTCGGTTGGGGTGACCGCGGAGTAAAACAAAACCTCCACAATGAATGTA--AT-
Hyperolius viridiflavus   TGTTT-G-TTAGCTTTCGGTTGGGGTGACCGCGGAGTATAATATATCCTCCACGACGAATAGG-CCT-
Kassina senegalensis      TCTAT-G-ATGGTTTTTGGCTGGGGTGGCCCTGGAGTAAAATAAACCCTCCAGACTGAATGAT-TTA-
Mantella aurantiaca       TGCAT-TCTTGGTTTTAGGTTGGGGTGACCGCGGAGCACAATACAGCCTCCACGATGAACGGG-ATT-
Mantidactylus femoralis   TATAT-ACTTGGTTTTAGGTTGGGGCGACCACGGAGTAAAACCAAACCTCCATGATGTACGGA-ACA-
Chiromantis xerampelina   TGCAT-A-AAAGTTTTGGGTTGGGGTGACCGCGGAGCAAAAATTAACCTCCACAACGAAAAGA-ATT-
Philautus petersi         TGCTT-A-ACAGTCTTAGATTGGGGCGATCGCGGAGTAAAAATTAACCTCCATGACGAAAAGA-ACT-
Arthroleptis variablis    TAATT-A-TTAATTTTAGGTTGGGGTGACCACGGAGCACAACAAAACCTCCACAATGAAAAGG-CCT-
Arthroleptis adolfifriderici TAATT-A-TTAATTTTAGGTTGGGGCGACCACGGAGTAAAACAAAACCTCCACAATGAAAGGG-CCT-
Cardioglossa gracilis     TGACT-G-TTGACTTTCGGTTGGGGTGACCACGGAGTAAAATAAAACCTCCACAATGAATGGG--CT-
Nyctibates corrugatus     GTACT-A-TTAGTTTTCGGTTGGGGTGACCACGGAGCAAAGCACAACCTCCATGATGAACGGA-----
Astylosternus diadematus  TGACT-A-CTAGTTTTTGGTTGGGGTGACCGCGGAGTAAAACTTAACCTCCACAATGAACGGA-ATT-
Scotobleps gabonicus      TAATT-A-CTAGTTTTCGGTTGGGGCAACCACGGAGTAAAGTAAAACCTCCGCGATGTATAGA-CCT-
Trichobatrachus robustus  TGACT-A-CTAGTTTTCGGTTGGGGTGACCACGGAGTAAAACACAACCTCCATAATGAACGGA-ACT-
Leptodactylon mertensi    TGACT-A-CTTGTTTTTGGTTGGGGTGACCGCGGAGCAAAACACAACCTCCACAATGAACGGG-ACT-
Tomopterna marmorata      TGTCT-G-CTAGCTTTAGGTTGGGGTGACCGCGGAGTATAACACAACCTCCACGACGAACAGG-CCT-
Tomopterna tandyi         TGTTT-G-TTAGCTTTAGGTTGGGGTGACCGCGGGGTATAATATAACCCCCACGACGAATAGG-CCT-
Anhydrophryne rattrayi    TGTTC-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTATAATTAAACCTCCATAACGAACGGG-ATT-
Arthroleptella landdrosia TGTCT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTATAATATAACCTCCACGACTGACGGG-ACT-
Arthroleptella lightfooti  TGTCT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTACAATATAGCCTCCACGACTAACGGG-ACT-
Poyntonia paludicola      TGCTT-G-TTAGCTTTCGGTTGGGGTGACCGCGGAGCACAAACAAACCTCCACGACGAACGGG-TTA-
Cacosternum capense       TGATT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTACAATACAGCCTCCACGACGAACGGG-CTTC
Cacosternum namaquense    TGATT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTACAACACAACCTCCACGACGAACGGG-CTTC
Cacosternum nanum parvum  TGATT-A-TTAGCTTTAGGTTGGGGTGACCGCGGAGTAAAATGTAACCTCCACGACGAATGGG-CTTC
Cacosternum boettgeri     TGATT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTATAACATAACCTCCACGACGAATGGG-ATTC
Microbatrachella capensis TGATT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTACAACAAAGCCTCCACGCTGAACGGG-CCTT
Phrynobatrachus natalensis TGTTA-A-CTAGCTTTTGGATGGGGCATCCGAGGAGTACAATCTAACCTCCCTGACAA----------
Phrynobatrachus acridoides TGTTA-A-CTAGCTTTTGGATGGGGCATCCAAGGAGTATAATCTAACCTCCCTGACAA----------
Phrynobatrachus cricogaster TGTTA-G-CTAGTTTTTGGCTGGGGCATCCGAGGAGTATAACATAACCTCCCTGATAAAC--------
Dimorphognathus africanus TGTTA-C-CTA-CTTTTGGCTGGGGCATCCAGGGAGTATAACGCAACCTCCTTGACAAA---------
Natalobatrachus bonebergi TGTAA-G-TTAGTTTTAGGTTGGGGTGACCGCGGAGAATAATAAAACCTCCATAACGAACGGG----C
Phrynodon sandersoni      TGTAT-G-TTAGTTTTAGGTTGGGGCGACCACGGAGAACAATTAAACCTCCACAATGAACGG---TAA
Phrynobatrachus auritus   TGTTA-G-CTAGTTTTTGGCTGGGGCATCCAAGGAGTATAATAGATCCTCCCTGATAAAC--------
Phrynobatrachus krefftii  TGTTT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGAATAACATAACCTCCACGACAAACGGGACTAA
Arthroleptides martiensseni TGCCC-G-CTGGCTTTAGGTTGGGGCGACCACGAAGTACAATACAACCTTCATGACAAATGGA-ATT-
Petropedetes parkeri      TGTTT-A-C-CACTTTAGGTTGGGGCGACCACGAAGTATATTAAAACCTTCACGATAAAAGGA-GCC-
Petropedetes cameroniensis TGCTT-G-C-CACTTTAGGCTGGGGCGACCACGAAGTATACTAAAACCTTCATGATAGACGGA-ATT-
Ptychadena chrysogaster   TAACT-A-TTAATTTTAGGTTGGGGTGACCACGGAGAATAGCTTAACCTCCGCAATGAAAAGA--AA-
Ptychadena anchiete       TATCT-A-TTAGTTTTGGGTTGGGGTGACCGCGGAGAACAGCCTAACCTCCGCAATGAAAAGA--AT-
Hildebrandtia ornata      TATCT-A-TTAGTTTTGGGCTGGGGTGACCGCGGAGTAAAACCCAACCTCCGTAATGAATAGA--TT-
Amnirana albolabris       TGAGT-A-CAAGTTTTAGGTTGGGGAAACCGCGGAGAACAACTAAACCTCCACGACAAACGGC-CCT-
Hydrophylax galamensis    TGAAT-T-TTAGCTTTAGGTTGGGGGGACCGCGGAGTAAAAATTAACCTCCACGACAAACGGG--C--
Afrana fuscigula          TGTTT-G-TTAGCTTTAGGTTGGGGTGACCGCGGAGTATAATAAAACCTCCACGACAAACGGG-TTT-
Afrana angolensis         TGTTT-G-TCAGCTTTAGGTTGGGGTGACCGCGGAGTATAATTTAACCTCCACGACGAAACGG-CAT-
Pyxicephalus adspersus    TGCTT-A-TTGGCTTTGGGTTGGGGTGACCGCGGAGTACAATATAACCTCCACGATGTAAAGG-ATT-
Aubria subsigillata       TATAT-A-TTAG-TTTGGGTTGGGGA-ACCGnGGAA-AAAA-TTAACCTCCACGACAAATAGC-nAA-
Conraua crassipes         TGCCC-G-TTGGTTTTAGGTTGGGGTGACCGCGGAGAATAACTTAACCTCCACAATGAATGG--ACTA
Conraua robusta           TGTTT-G-TTGGTTTTAGGTTGGGGTGACCGCGGAGTATAATTTAACCTCCACGACGAACGGG-ACT-
Hoplobatrachus occipitalis TGTCC-A-TTGGTTTTAGGTTGGGGTGACCGCGGAGTATAATTGACCCTCCACGATGAATGGG-GCT-
Euphlyctis cyanophlyctis  TGTTA-G-TTGGTTTTAGGTTGGGGTGACCGCGGAGTACAAACCACCCTCCACGACGAATGGG-CCT-
Limnonectes blythii       TATCT-T-TTGGTTTTGGGTTGGGGTGACCACGGAGTAAAATAAAACCTCCCTGACGATAATCTACT-
Phrynoglossus laevis      TGTTCTG-TTAGTTTTGGGTTGGGGCGACCGCGGAGTAAAATAAAACCCCCACGACGAAAGGA-ACT-
Nannophrys ceylonensis    TGTCT-G-TTGGTTTTAGGTTGGGGTGACCGCGGAGTAAAACCTAACCTCCACGACGAATGGG-ACT-
Platymantis vitiensis     TGCCT-C-TTAGTCTTCGGTTGGGGCGACCACGGAGCAAAAATCAACCTCCATGATGAATGAA-CAT-
```

Appendix 4. Continued

```
                                69   74   79   84   89   94   99   104  109  114  119  124  129  134
                                |    |    |    |    |    |    |    |    |    |    |    |    |    |
Heleophryne purcelli            -TTACCCTAAGCCAAAAGCCACCGCTTTA-AGCATCAACACCTTGACATACATTGACCCATT-T----
Probreviceps species            AACC-CCTTATCTAAGAGCTACCTCTCTA-AGAATTAGTATTCTAACATAAAATGATCCGAT------
Nesomantis thomasseti           ------------AAACAC-ACAACTTAAAAGCA-CCAATAATTT--AACACTTGACCCAATTAC---
Leptodactylus pentadactylus     TCnTCCnTTACnCAAGGGCCTCAACCCTA-AGnATCCATAGnnTGTnATCAATTGATnCAAn-AA---
Dendrobates speciosus           TACGTTCTTAATTTAAAGTCACAACTTAA-AATATCAATACATTGACTTCCATTGACCCAAT------
Dendrobates pumilio             TACGTTCTTAATTTAAAGTCACAACTTAA-AACATCAACACATTGACTTCCATTGACCCAAT------
Colostethus pratti              CCTTCTCTTAGCTAAAAGCTACTCCTTTA-AGCATCAGCAAACTGACTTCTTTTGACCCAAT------
Leptopelis vermiculatus         AAAATACTAATAAAAGAACCACAATTCTA-ATAATCAAAAAATTGACATAT-TTGACCCAAACAC---
Hyperolius viridiflavus         AAAACCTTAATCCAAGAGCCACTGCTCTA-AGAATCATAAAATTGACGTAAAATGATCCGATT-----
Kassina senegalensis            AAA-CCCTAATCTAAGAATTACAATTCAA-AGAATCAATACTTTGACATAA-TTGACCCAATAAG---
Mantella aurantiaca             AC-CCCCTTATCTAAGAGCTACACCTCTA-AGAATTAGCATTCTAACATAAAATGATCCGA-------
Mantidactylus femoralis         AC-CTCCTCATCTAAGAGCTACAACTCTA-AGAATTAGCACACTATCATAAAACGACCCAT-------
Chiromantis xerampelina         AA-ATCTTTATCTAAGAACTACCATTCTA-AGAATCAACATATTGACGAACACTGATCCGA-------
Philautus petersi               AG-ATCTTTATCCAAGACCCACTACTCTA-AGAATTAGAACACTAACGTnnnnTGACCCGA-------
Arthroleptis variablis          AACCCCCTTATTCAAGAACAACAATTCTA-ACAATCAACATATTGACATACGTTGACCCAA------A
Arthroleptis adolfifriderici    ATT-CCCTAATCCAAGAACAACAACTCTA-ATAATCAACACATTGACATAACTTGACCCAA------A
Cardioglossa gracilis           AAACCCCTAATTTAAGAATTACACCTCTA-AAAATCAAGACATTGACATTTATTGACCCAA------A
Nyctibates corrugatus           TAACACCTTATTCAAGAGAGACATCTCGA-AACATCAAAACTTTGACATAACTTGACCCAAT-----T
Astylosternus diadematus        AAATTCCTAACTCTAGACCTACACCTCAA-AAAATTAAAACATTAACATAACTTGACCCAA------T
Scotobleps gabonicus            TATATCTTTATTTAAGAACTACACCTCTA-AAAATCAATATATTGACATAAATTGACCTAT-------
Trichobatrachus robustus        AAACTCCTAACTTAAGAGCTACAACTCAA-AAAATTAAAATACTAACACAC-TTGACCCAA------A
Leptodactylon mertensi          AACTCCCTAATTCAAGACCCACAACTCAA-TAAATCAGCATACTGACATAAATTGACCCAAG-----C
Tomopterna marmorata            AAAACCTTTATCCAAGAGCTACTGCTCTA-AGAATCATAAAATTGACGTAAAATGATCCGA-------
Tomopterna tandyi               AAAACCTTTATCCAAGAGCCACTGCTCTA-AGAATCATGAAATTGACGTAAAATGATCCGA-------
Anhydrophryne rattrayi          AAACCCTTTATCTAAGAGCCACCACTCTA-AGAATCATTAAATTGACGTAAAGTGATCCGA-------
Arthroleptella landdrosia       AA-CCCCTTATCCAAGAGCCACTGCTCTA-AGAATCATTAATTTGATGTAAAATGATCCGT-------
Arthroleptella lightfooti       AA-CCCCTTATCCAAGAGCCACTGCTCTA-AGAATCATTAATTTGATGTAAAATGATCCGA-------
Poyntonia paludicola            AA-CCCCTAATCCAAGAGCCACTGCTCTA-AGAATCATTAAACTGACGCAAAAAGATCCGA-------
Cacosternum capense             GA-CCCCTTATCTAAGAGCCACTGCTCTA-AGAATCATAAAATTGACG-AAAATGATCCGA-------
Cacosternum namaquense          AA-CCCCTTATCCAAGAGCCACTGCTCTA-AGAATCATAAAATTGACG-ACAATGATCCGA-------
Cacosternum nanum parvum        AACCCCCTTATCCAAGAGCCACTGCTCTA-AGAATCATTAAATTGACGAAAAATGATCCGA-------
Cacosternum boettgeri           AA-CCCCTTATCCAAGAGCCACTGCTCTA-AGAATCATTAAATTGACGAAAAATGATCCGA-------
Microbatrachella capensis       AA--CCCTTATCTAAGAGCTACTGCTCTA-AGAATCACTAAACTGACGCAAAATGATCCGA-------
Phrynobatrachus natalensis      ------CTTATCTCAGAGCTACTACTCTA-AGAAACAGTAAACTGATGTAATATGACCCGA-------
Phrynobatrachus acridoides      ------CTTATCTCAGAGCTACTACTCTA-AGAAACAGCAAACTGACGTAATATGACCCGA-------
Phrynobatrachus cricogaster     ---------ATCTTAGAACTACAATTCCA-AGAAACAGAAAACTGACGTAACGTGACCCGA-------
Dimorphognathus africanus       -------TCATCTTAGAACTACTATTCCA-AGAAACAGCAAACTGAAGTAATGTGACCCGA-------
Natalobatrachus bonebergi       ACAGTCCTAATCCAAGAGCAACTCCTCTA-AGAATCAACAAATTGACGCAATATGATCCGA-------
Phrynodon sandersoni            ACA-CCCTAATCCAAGAGCTACCGCTCTA-AGAATCAATAAGTTGACACTACATGACCCGAT-----A
Phrynobatrachus auritus         ---------ATCTAAGGGCGACAACCCTA-TGAGACAGCAAACTGACCTAAAATGATCCGA----CCC
Phrynobatrachus krefftii        A---CCCTTATCTATGAGCCACTGCTCTA-AGAATCATTAAATTGATGTAAAATGATCCGA-------
Arthroleptides martiensseni     TT-TTCCTTATCTTAGAGCTACCACTCCA-AGAATTAATAACTTAATGTAATATGATCCGAT-----T
Petropedetes parkeri            TG-CTCCTAATCTATGAACTACCCCTCTA-AGAATCAGAACCCCGATATAAAATGATCCGAT-----G
Petropedetes cameroniensis      TT-CTCCTTATCCATGAGCTACCCCTCTA-AGAATCAGCACACTGATATAAAATGACCCGAT-----T
Ptychadena chrysogaster         AATACCTTTATCTATGAGCAACACCTCTA-AGAATTAATAAATTAACATATAATGATCCGAT-CTCAC
Ptychadena anchiete             AATATCCTAATCTAAGAGGGACACCTCTA-AGAATTAATAAATTAACATATGATGATCCAAT-ACTTA
Hildebrandtia ornata            AACACCTTAATCTAAGAATTACACTTCTA-AGAATTAATAAATTAACATAAAATGATCCAAT-A--AA
Amnirana albolabris             AA-GTCCTTATCTACGAGCCACAGCTCTA-AGAATCAGCATACTGATGTTT-ATGACCCGAT-ACT--
Hydrophylax galamensis          AACGCCCTTATCCACGAATTACAACTCCA-AGAATCAGAATACTGATGTTAATTGACCCATT-T----
Afrana fuscigula                CTAACCCTAATCCAAGAGCCACAGCTCTA-AGAATCATTAATTTGATGTTTAATGATCCGAT------
Afrana angolensis               AAAACCCTTATCCAAGAGCCACTGCTCTA-AGAATCATTAAATTGACGTACAATGATCCAAT------
Pyxicephalus adspersus          TC-CCCCTTATCTAAGAACAACAGTTCGA-AGAACCTTAAAAATGTCATAAAATGATCCGA-------
Aubria subsigillata             A--GsCTTTATCTATGAACCACAATTCTA-AGAATCAATAAACTGATGTTTAATGATCCAAT------
Conraua crassipes               AC-ATCCTAATCCAAGAACAACACCTCCA-AGAATCAACAACTTGACATAAAATGATCCGA-------
Conraua robusta                 AT-GCCCTAATCCAAGAGCAACCACTCTA-AGAATCAAAAATTTGATGTAAAATGATCCGA-------
Hoplobatrachus occipitalis      ACCCCCCTAACCCAAGAGCCACTCCTCTA-AGAATCAATAAATTGACATAAAATGATCCAAT------
Euphlyctis cyanophlyctis        AC-CCCCTTACCCAAGAATTACACCTCTA-AGGATTAACACATTAACGTAAAATGATCCAAA------
Limnonectes blythii             AA--CTTAAATACAAGAGCCACTGCTCTA-AGAATCAAAAATTTGACGTAATATGATCCGG-------
Phrynoglossus laevis            AAA-CCCTTATC-AAGAACA-CATCTCTA-AGAATCAACAATATGACGC-CTATGACCCGA-------
Nannophrys ceylonensis          ACCCCTCTTATCCAAGAGCCACTTCTCTA-CGAATCAACAATTTGACGTTAAATGATCCAA------C
Platymantis vitiensis           TT----CTTATCCAAGAGATACATCTCAA-AGAAACAGAACACTGACAT--TCTGATCCGAA------
```

Appendix 4. Continued

	138 143 148 153 158 163
Heleophryne purcelli	--ATTGACCAACGAACCAAGTTACCCTGG
Probreviceps species	-TTTCGATCAACGAACCAAGTTACCCTGG
Nesomantis thomasseti	-AATTGATCAACGAACCAAGTTACCCTAG
Leptodactylus pentadactylus	-ATnTGCnCAATGAAnCAAGATACCCTAG
Dendrobates speciosus	TACTTGATCAACGAACCAAGTTACCCTAG
Dendrobates pumilio	TACTTGATCAACGAACCAAGTTACCCTAG
Colostethus pratti	AAATTGATCAACGAACCAAGTTACCCTAG
Leptopelis vermiculatus	---TTGATCAATGAACCAAGTTACCCTGG
Hyperolius viridiflavus	--TTCGATCAACGAACCAAGTTACCCTGG
Kassina senegalensis	---TTGATCAACGAACCAAGTTACCCTAG
Mantella aurantiaca	CAATCGATCAACGAACCAAGTTACCCTGG
Mantidactylus femoralis	TAnnnGATCAACGAACCAAGTTACCCTGG
Chiromantis xerampelina	TAATCGATCAATGGACCAAGTTACCCTGG
Philautus petersi	CAAACGATCAACGAACCAAGTTACCCTGG
Arthroleptis variablis	TTTTTGATCAATGAACCAAGTTACTCTGG
Arthroleptis adolfifriderici	TCTTTGATCAATGAACCAAGTTACTCTGG
Cardioglossa gracilis	CTTTTGATCAATGAACCAAGTTACCCTGG
Nyctibates corrugatus	TCATTGATCAACGAACCAAGTTACCCTGG
Astylosternus diadematus	TA-TTGATCAACGAACCAAGTTACCCTGG
Scotobleps gabonicus	TAA--GTTCAACGAACCAAGTTACCCTGG
Trichobatrachus robustus	TA-TTGATCAATGAACCGAGTTACCCTGG
Leptodactylon mertensi	CCATTGAACAATGAACCTAGTTACCCTGG
Tomopterna marmorata	CTTTCGATCAACGGACCAAGTTACCCTGG
Tomopterna tandyi	TTTTCGATCAACGAACCAAGTTACCCTGG
Anhydrophryne rattrayi	TTTTCGATCAACGGACCAAGTTACCCTGG
Arthroleptella landdrosia	TCTTCGATCAACGAACCAAGTTACCCTGG
Arthroleptella lightfooti	TTATCGATCAACGAACCAAGTTACCCTGG
Poyntonia paludicola	TTTTTGATCAACGGACCAAGTTACCCTGG
Cacosternum capense	TCTTCGATCAACGAACCAAGTTACCCTGG
Cacosternum namaquense	TCTTCGATCAACGAACCAAGTTACCCTGG
Cacosternum nanum parvum	TCTTCGATCAACGGACCAAGTTACCCTGG
Cacosternum boettgeri	TCTTCGATCAACGAACCAAGTTACCCTGG
Microbatrachella capensis	TCTTCGATCAACGGACCAAGTTACCCTGG
Phrynobatrachus natalensis	TTATCGATCAACGAACCAAGTTACCCTGG
Phrynobatrachus acridoides	TTATCGATCAACGAACCAAGTTACCCTGG
Phrynobatrachus cricogaster	CAATCGATCAACGAACCAAGTTACCCTGG
Dimorphognathus africanus	TAATCGATCAACGAACCAAGTTACCCTGG
Natalobatrachus bonebergi	TAATCGATCAACGAACCAAGTTACCCTGG
Phrynodon sandersoni	CAATCGATCAATGAACCAAGTTACCCTGG
Phrynobatrachus auritus	AACTCGATCAACGAACCAAGTTACCCTGG
Phrynobatrachus krefftii	TTTTTGATCAACGAACCAAGTTACCCTGG
Arthroleptides martiensseni	TATTCGATCAACGGACCAAGTTACCCTGG
Petropedetes parkeri	TAATCGATCAACGAACCAAGTTACCCTGG
Petropedetes cameroniensis	TAATCGATCAACGAACTAAGTTACCCTGG
Ptychadena chrysogaster	-GCTCGATCAATGAACCAAGTTACCCTGG
Ptychadena anchiete	TATTTGATCAATGAACCAAGTTACCCTGG
Hildebrandtia ornata	TATTTGATCAACGAACCAAGTTACCCTGG
Amnirana albolabris	-ATTCGACTAACGAACCAAGTTACCCTGG
Hydrophylax galamensis	TAT--GATCAACGAACCAAGTTACCCTGG
Afrana fuscigula	C-TTCGATCAACGGACCAAGTTACCCTGG
Afrana angolensis	-TTTTGATCAACGAACCAAGTTACCCTGG
Pyxicephalus adspersus	ACTTCGATCAACGGACCAAGTTACCCTGG
Aubria subsigillata	TTTTTGATCAACGAACCAAGTTACCCTGG
Conraua crassipes	CCCTCGATCAACGAACCAAGTTACCCTAG
Conraua robusta	TTTTCGATCAACGAACCAAGTTACCCTGG
Hoplobatrachus occipitalis	CATTTGATCAACGAACCAAGTTACCCTGG
Euphlyctis cyanophlyctis	TATTTGATCAACGAACCAAGTTACCCTGG
Limnonectes blythii	CAACCGATCAACGAACCAAGTTACCCTGG
Phrynoglossus laevis	CTATCGATCAACGAACCAAGTTACCCTGG
Nannophrys ceylonensis	TTCTTGATCAACGAACCAAGTTACCCTGG
Platymantis vitiensis	CTTTCGATCAACGAAACAAGCTACCCTGG

Appendix 5. Sankoff-style stepmatrices used in analyses employing direct optimization. Names of matrices refer to the costs of gaps: transversions: transitions.

111

0	1	1	1	1
1	0	1	1	1
1	1	0	1	1
1	1	1	0	1
1	1	1	1	0

411

0	1	1	1	4
1	0	1	1	4
1	1	0	1	4
1	1	1	0	4
4	4	4	4	0

121

0	2	1	2	2
2	0	2	1	2
1	2	0	2	2
2	1	2	0	2
2	2	2	2	0

421

0	2	1	2	8
2	0	2	1	8
1	2	0	2	8
2	1	2	0	8
8	8	8	8	0

141

0	4	1	4	4
4	0	4	1	4
1	4	0	4	4
4	1	4	0	4
4	4	4	4	0

441

0	4	1	4	16
4	0	4	1	16
1	4	0	4	16
4	1	4	0	16
16	16	16	16	0

211

0	1	1	1	2
1	0	1	1	2
1	1	0	1	2
1	1	1	0	2
2	2	2	2	0

110

0	1	0	1	1
1	0	1	0	1
0	1	0	1	1
1	0	1	0	1
1	1	1	1	0

221

0	2	1	2	4
2	0	2	1	4
1	2	0	2	4
2	1	2	0	4
4	4	4	4	0

210

0	1	0	1	2
1	0	1	0	2
0	1	0	1	2
1	0	1	0	2
2	2	2	2	0

241

0	4	1	4	8
4	0	4	1	8
1	4	0	4	8
4	1	4	0	8
8	8	8	8	0

410

0	1	0	1	4
1	0	1	0	4
0	1	0	1	4
1	0	1	0	4
4	4	4	4	0

Appendix 6. Complete command lines to implement direct optimization in POY, and the ratchet in NONA for the separate morphological data analysis. Detailed explanations can be found in the documentation for POY, obtainable at ftp.amnh.org/pub/molecular/poy. Words representing commands written in batch files are in boldface.

---

1) Example from the equally weighted analysis of molecular data only, invoking the text files 111 (step matrix), 12S.mol and 16S.mol, which included only taxa represented by molecular data, not those represented by morphology alone.

To generate the constrain file:

Poy -noleading -norandomizeoutgroup -molecularmatrix 111 -maxtrees 2 -jackboot -random 25 -seed -1 -nospr -notbr 12s.mol 16s.mol > m111.out

Outfile converted to a HENNIG86-style 50% majority-rule constrain file in the program JACK2HEN.exe using the commands:

Jack2hen 50 <m111.out> m111.con

Final analysis using the constrain file:

Poy -ratchettbr 20 -ratchetpercent 50 -ratchetseverity 3 -ratchettrees 2 -trailinggap 1 -noleading -molecularmatrix 111 -multibuild 20 -oneasis -maxtrees 20 -quick -fitchtrees -indices -seed -1 -slop 2 -checkslop 5 12s.mol 16s.mol -constrain m111.con > m111.tre

Treefile converted to a HENNIG86-style group inclusion matrix (GIM) of the strict consensus tree in JACK2HEN using the commands:

Jack2hen 100 <m111.tre> m111.ss

Standard HENNIG86 commands added to generate treefiles and calculate lengths.

2) Example from the equally-weighted analysis of molecular and morphological data simultaneously, invoking the files 111 (step matrix), 12S, 16S (including both taxa represented by molecular data and blank names for taxa present in the morphological matrix but lacking molecular data) and Mor (morphology in HENNIG86 format), weighing morphology equal to the change cost (mC).

To generate the constrain file:

Poy -noleading -norandomizeoutgroup -molecularmatrix 111 -maxtrees 2 -jackboot -random 25 -seed -1 -nospr -notbr 12s 16s -weight 1 mor > t111mC.out

Converted to a HENNIG86-style constrain file in the program JACK2HEN.exe with the commands:

Jack2hen 50 <t111mC.out> t111mC.con

Final analysis using the constrain file:

Poy -ratchettbr 20 -ratchetpercent 50 -ratchetseverity 3 -ratchettrees 2 -trailinggap 1 -noleading -molecularmatrix 111 -multibuild 20 -oneasis -maxtrees 20 -quick -fitchtrees -indices -seed -1 -slop 2 -checkslop 5 12s 16s -weight 1 mor -constrain t111mC.con > t111mC.tre

To calculate branch support values:

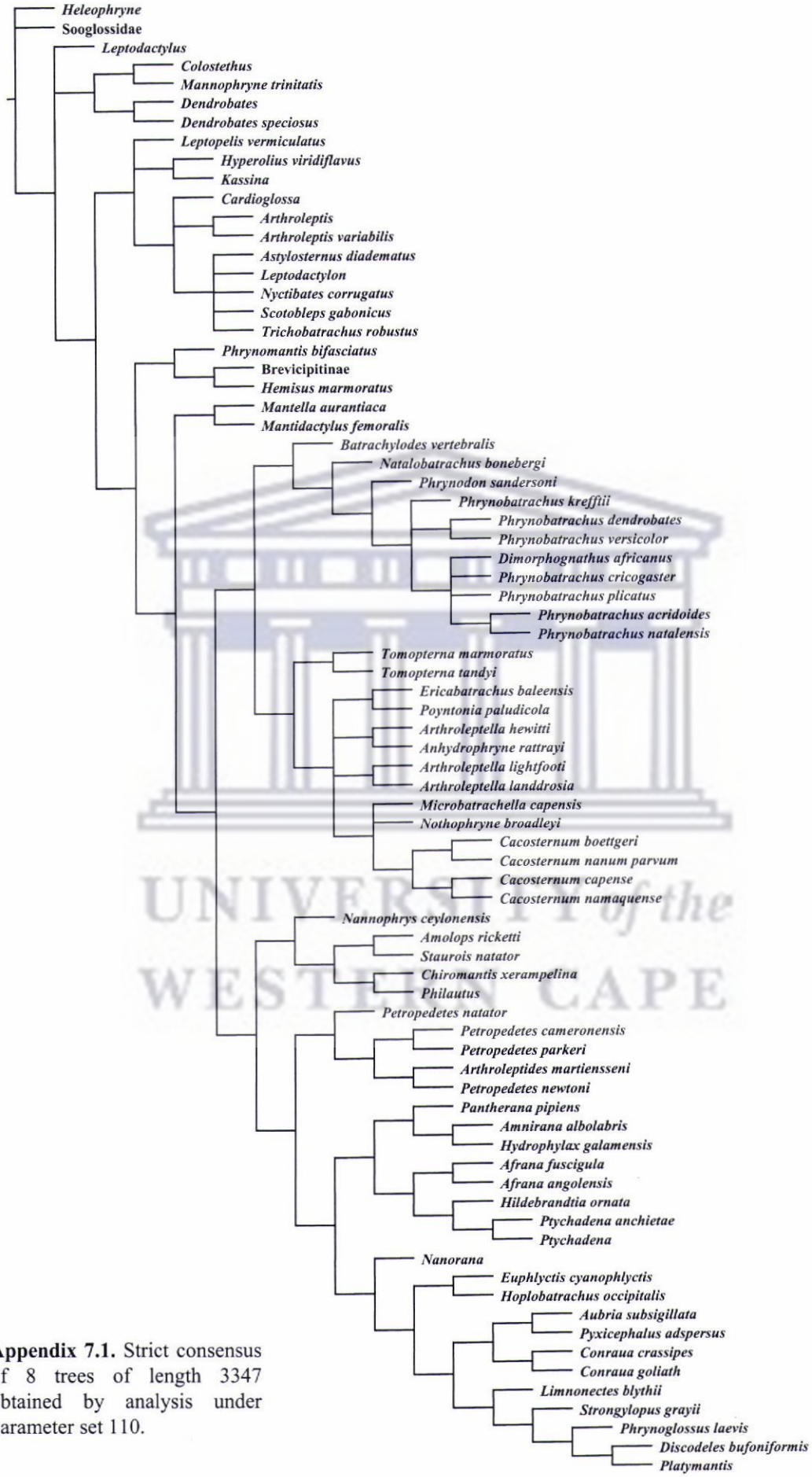
The command **-bremer** inserted into the original analysis commands, and re-running the original analysis using the consensus of the results as a constrain file.

3) NONA commands:

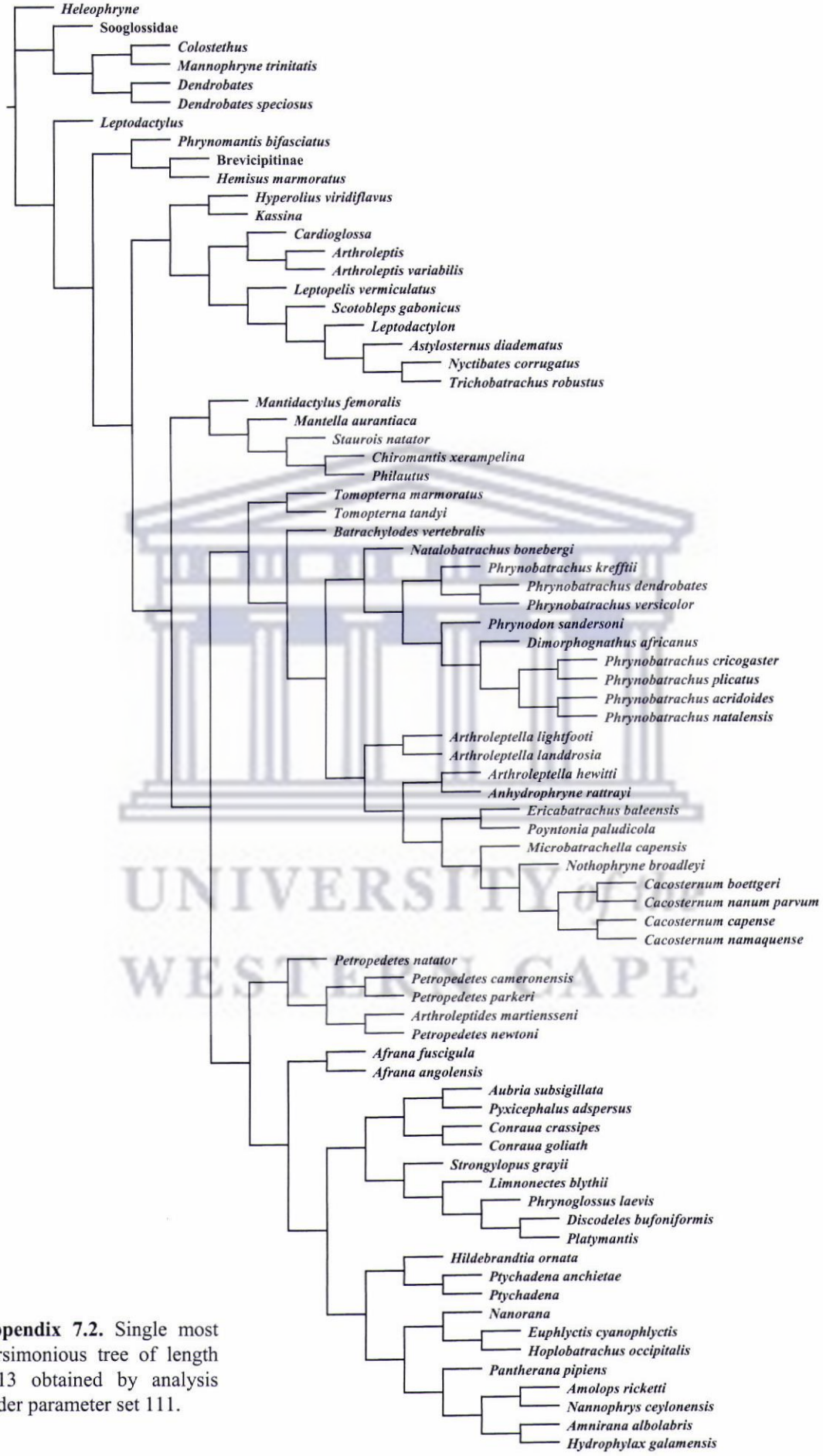
The ratchet was implemented in NONA v. 2.0 (Goloboff 1997), using the full command sequence **h10000; h/1000; mult*100; nix=50; h/3; nix[10; nix-10; 50 20; max*;.** The commands operate as follows: **h10000; h/1000; mult*100;** (holding 10000 trees in memory, hold 1000 starting trees in memory, perform tree bisection-reconnection branch swapping (Sofford 1993) implementing 100 random addition replicates); **nix=50; h/3; nix[10; nix-10; 50 20;** implement the ratchet, with the 'strength' or factor of the ratchet (i.e. proportion of the characters reweighed) set to 50% by the command **nix=50;**). Three starting trees were held in memory at each iteration (command **hold/3;**, or **h/3;**). Every 10 iterations, one of the best trees located at that stage in the search was randomly selected for continued swapping (command **nix[10;**). Subtree-pruning-regrafting (SPR) branch-swapping was applied in the first 10 iterations, followed by TBR branch swapping in the remaining 40 (command **nix - 10;**). Fifty initial iterations of the ratchet (command **nix 50;**) were conducted. When these initial iterations were completed, a further 20 iterations were conducted (command **nix 50 20;**). Finally, the command **max*** was used to initiate branch-swapping using tree bisection-reconnection.

4) Brief explanation of POY commands used in this analysis:

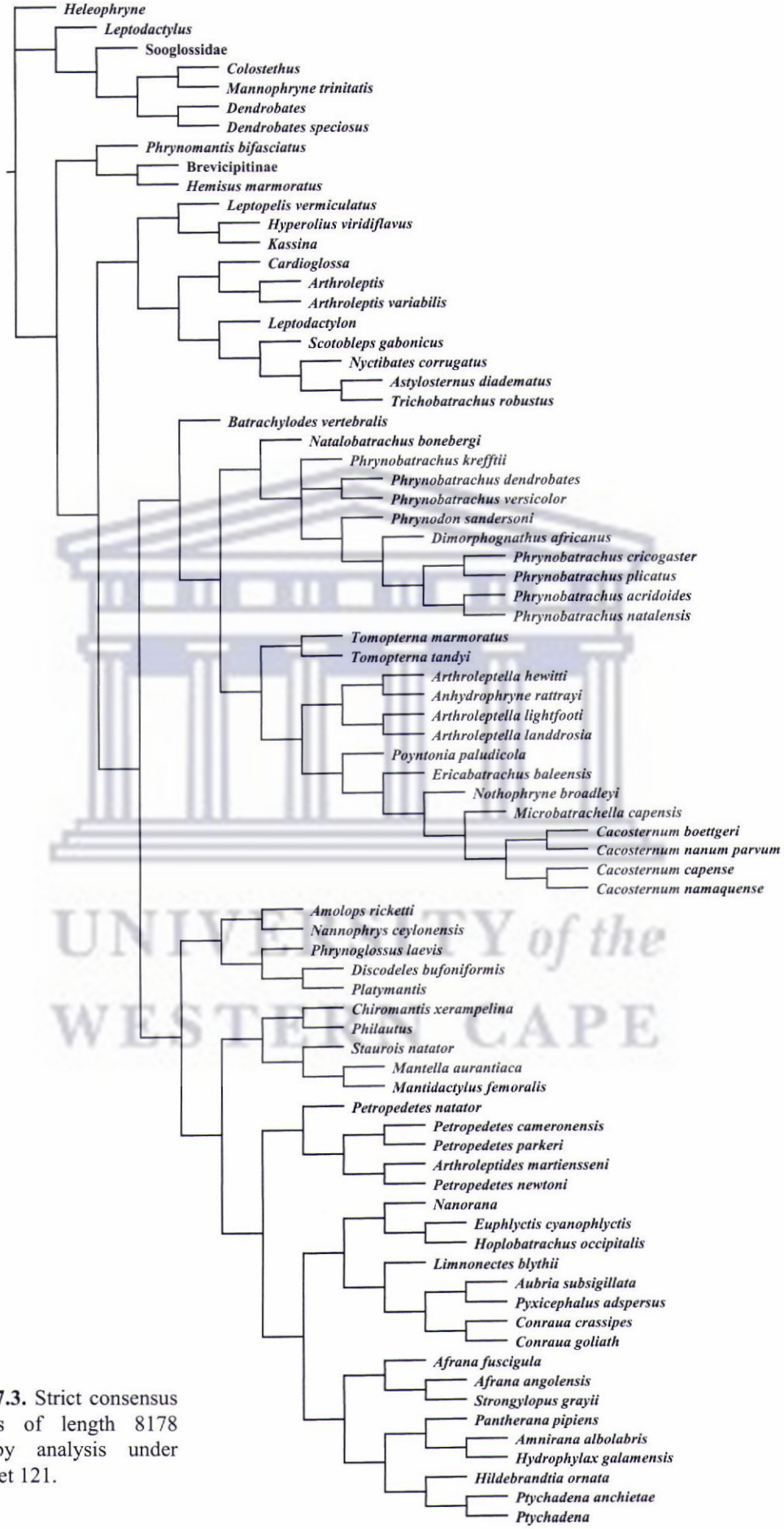
-checkslop ***n***: by adding an extra tbr branch swapping round, checks all cladograms that are within *n* tenths of a percent of the current minimum value.
-constrain ***x***: constrain the search to conform to the characters specified in the file *x* (HENNIG86 format).
-fitchtrees: ensures that the trees kept in buffer are a random subset of those that would have been kept if the tree buffer were larger.
-goloboff ck: sets implied weighting *sensu* Goloboff (1993), with mode of weight specified as ck, as in original paper.
-jackboot: performs Farris's parsimony jackknifing procedure with 'random *n*' replicates or 'multbuild *n*' replicates.
-kfactor ***n***: sets the *k* value of Goloboff (1993) to *n* for implied weighting.
-maxtrees ***n***: sets the number of trees held in the buffer to *n*.
-molecularmatrix ***n***: calls on the step matrix whose name is *n*.
-molecularmatrix ***x***: reads matrix *x* for molecular character transformation costs among molecular character states.
-multibuild ***n***: uses *n* random addition sequence builds (no swapping) to be performed
-multiplier ***n***: sets weights multiplier to *n* for implied weighting.
-noleading: does not count leading and trailing gaps.
-norandomizeoutgroup: does not allow the randomising of the outgroup in 'random' and 'multbuild'.
-nospr: 'spr' branch swapping suppressed.
-notbr: 'tbr' branch swapping suppressed.
-oneasis: when using **-multibuild** or **-random** the addition sequence will follow that of the first data file for the first replicate.
-quick: do not swap on minimal length trees during branch swapping.
-random ***n***: causes *n* random addition sequence searches (build through swapping) to be performed.
-ratchetpercent ***n***: sets the percentage of characters to be reweighed in each ratchet run to *n* %.
-ratchetseverity ***m***: weight multiplier for reweighed characters.
-ratchettbr ***n***: institutes *n* iterations of the parsimony ratchet.
-ratchettrees ***n***: number of trees saved during ratchet iterations.
-seed 1: sets seed for pseudorandom number generation using system clock time in seconds.
-slop ***n***: check all cladogram lengths which are within *n* tenths of a percent of the current minimum value.
-trailinggap ***n***: sets both leading and trailing gap weight to *n*.
-weight ***n x***: succeeding input files (named *x*) receive a weight of *n*.



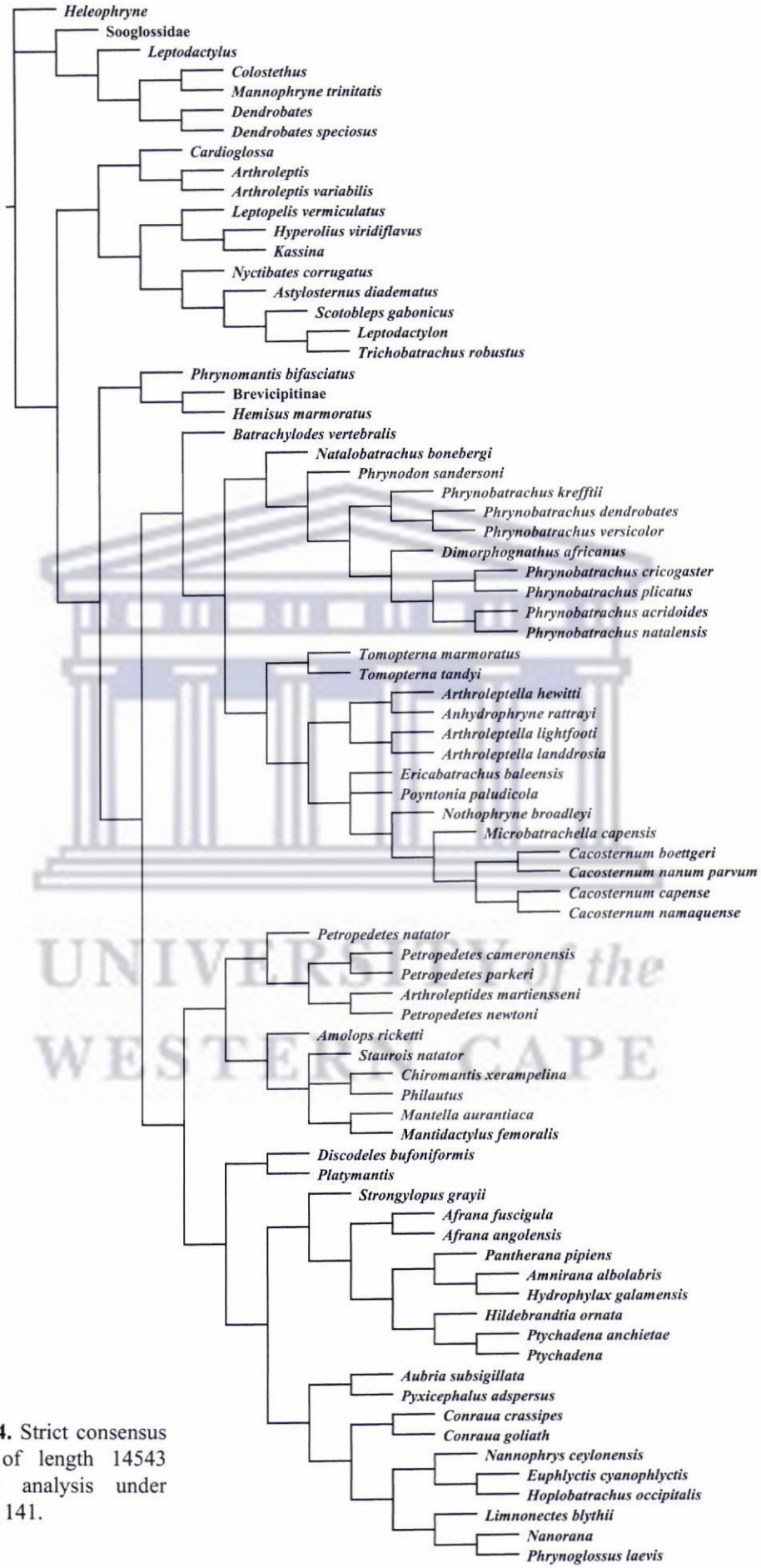
Appendix 7.1. Strict consensus of 8 trees of length 3347 obtained by analysis under parameter set 110.



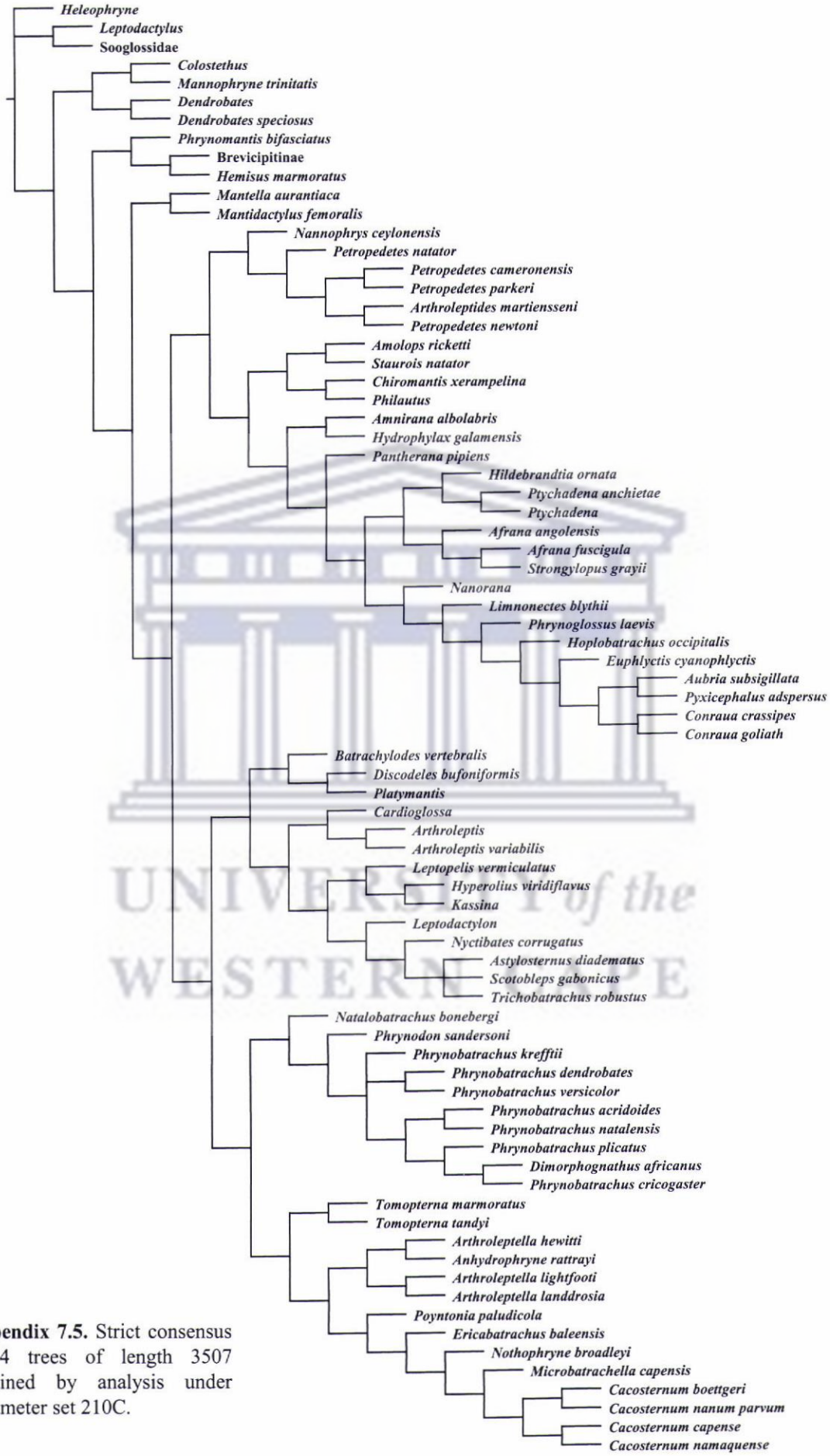
Appendix 7.2. Single most parsimonious tree of length 5113 obtained by analysis under parameter set 111.



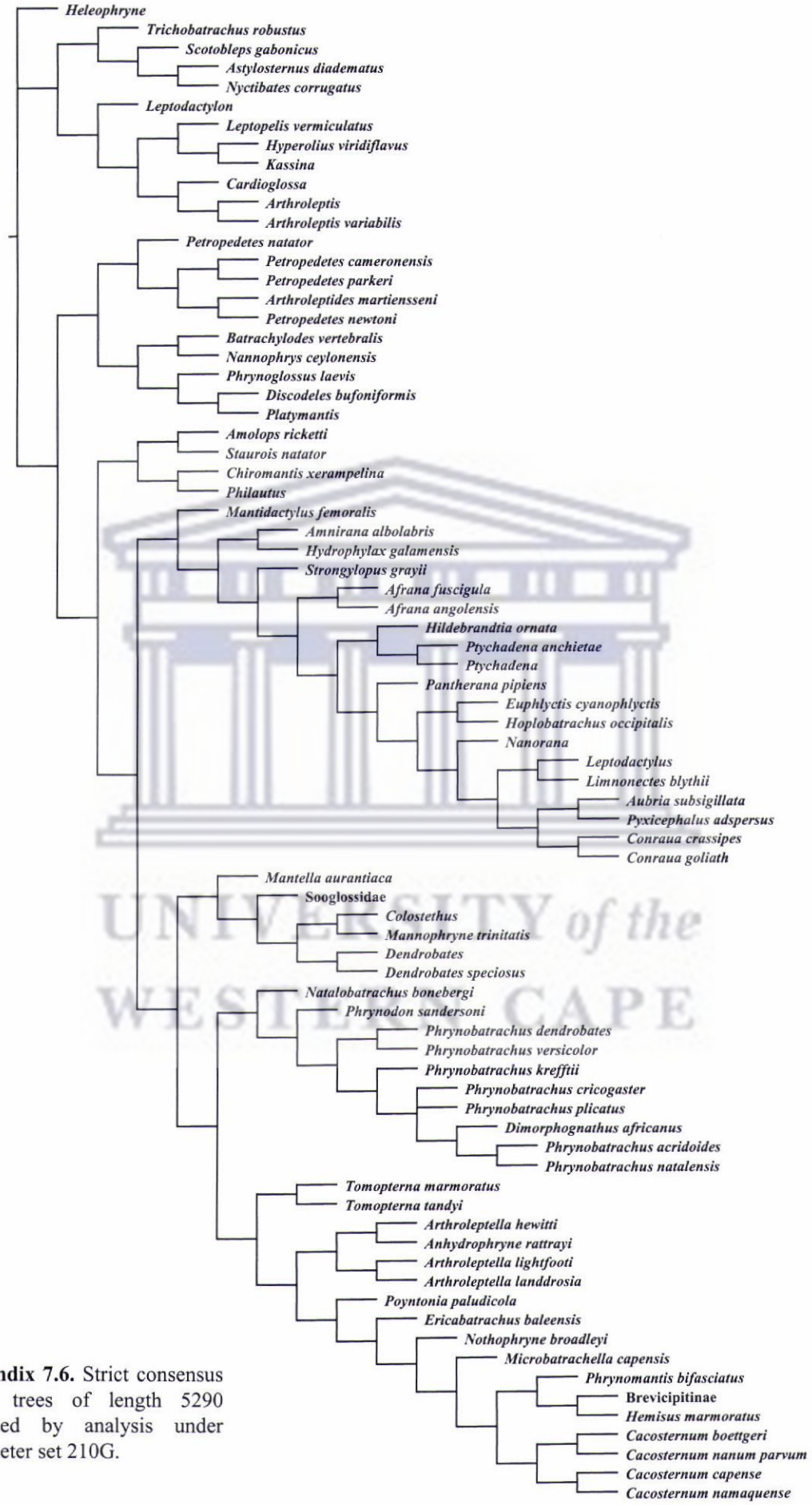
Appendix 7.3. Strict consensus of 2 trees of length 8178 obtained by analysis under parameter set 121.



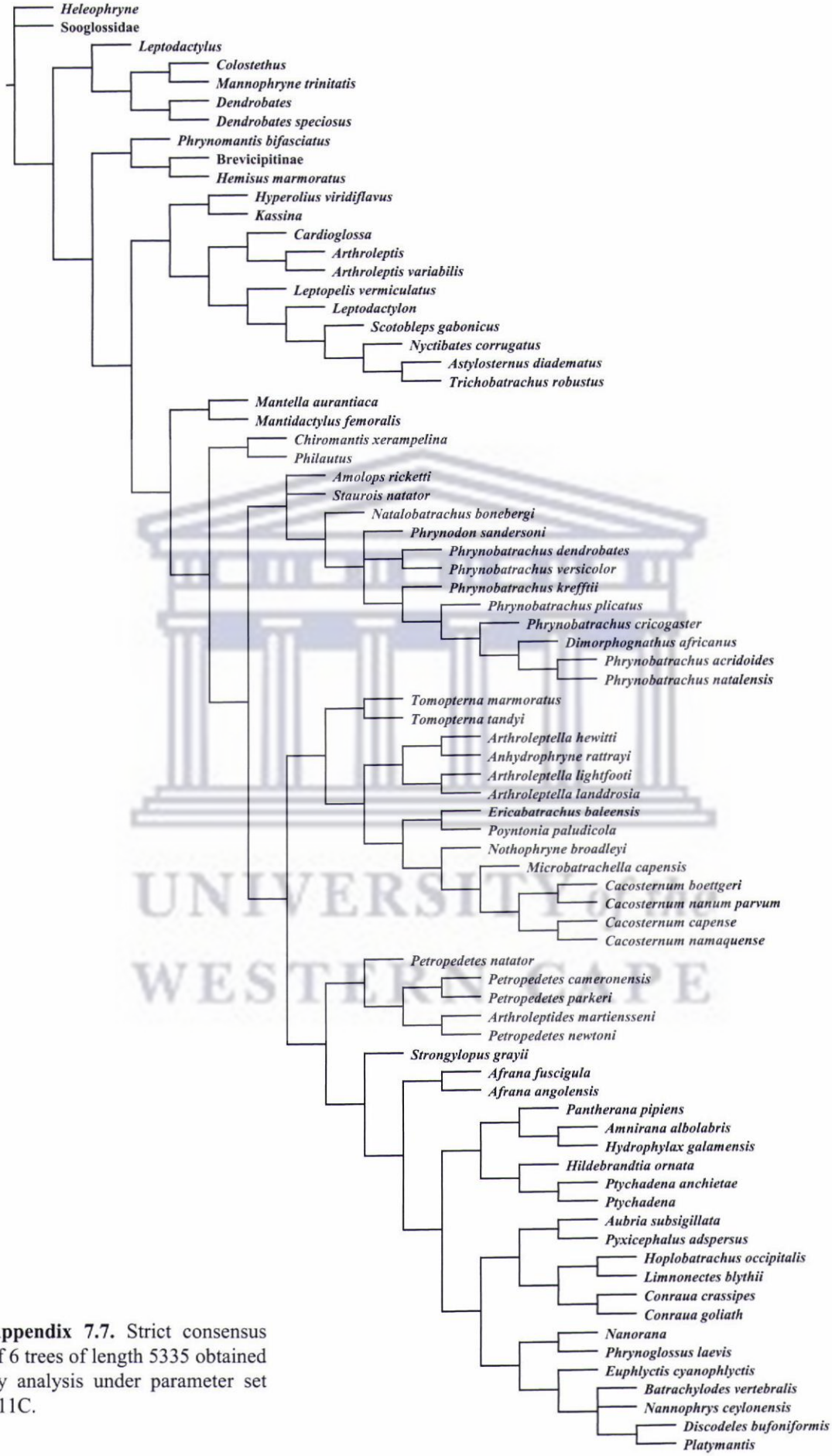
Appendix 7.4. Strict consensus of 4 trees of length 14543 obtained by analysis under parameter set 141.



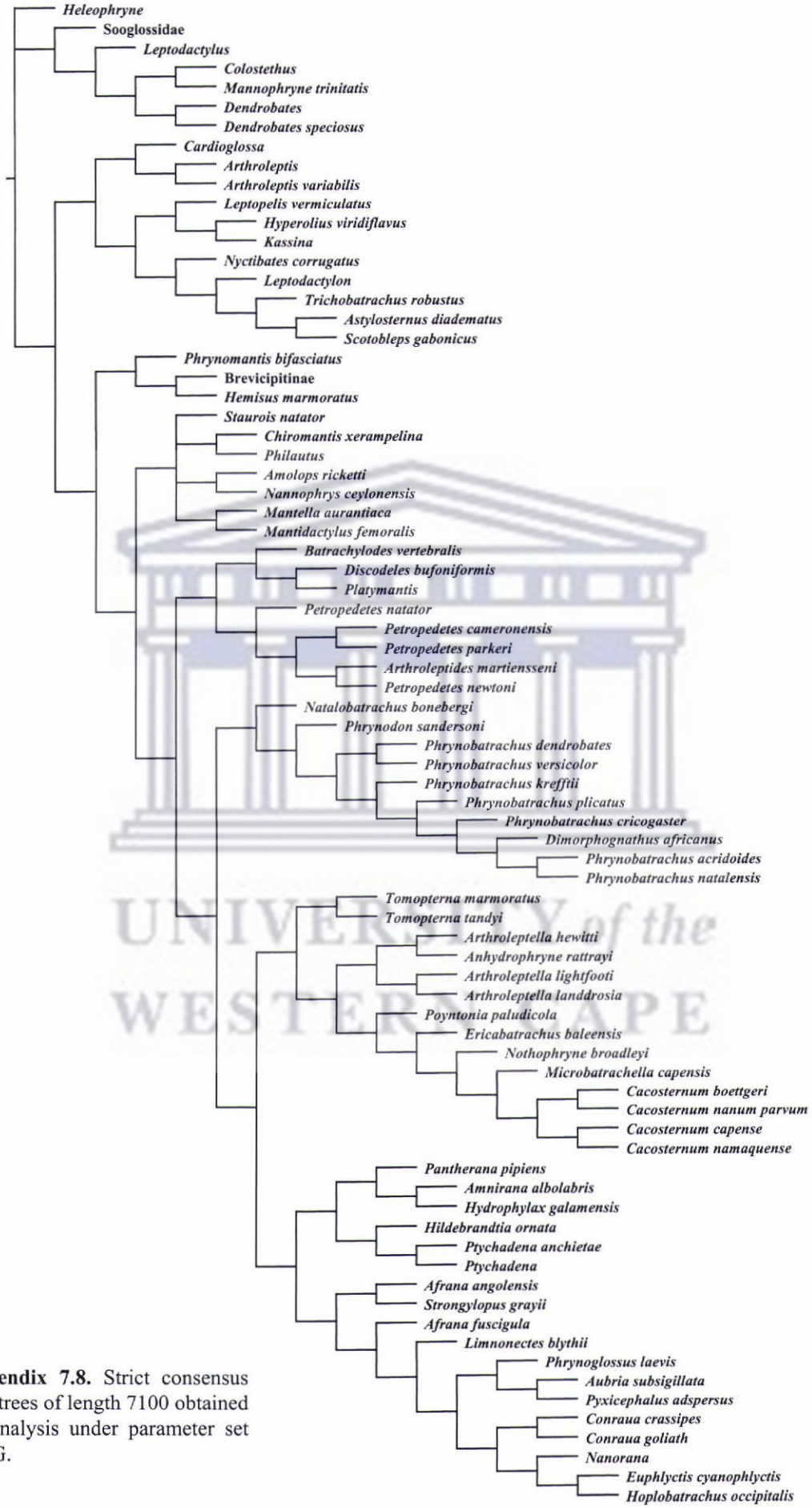
Appendix 7.5. Strict consensus of 4 trees of length 3507 obtained by analysis under parameter set 210C.



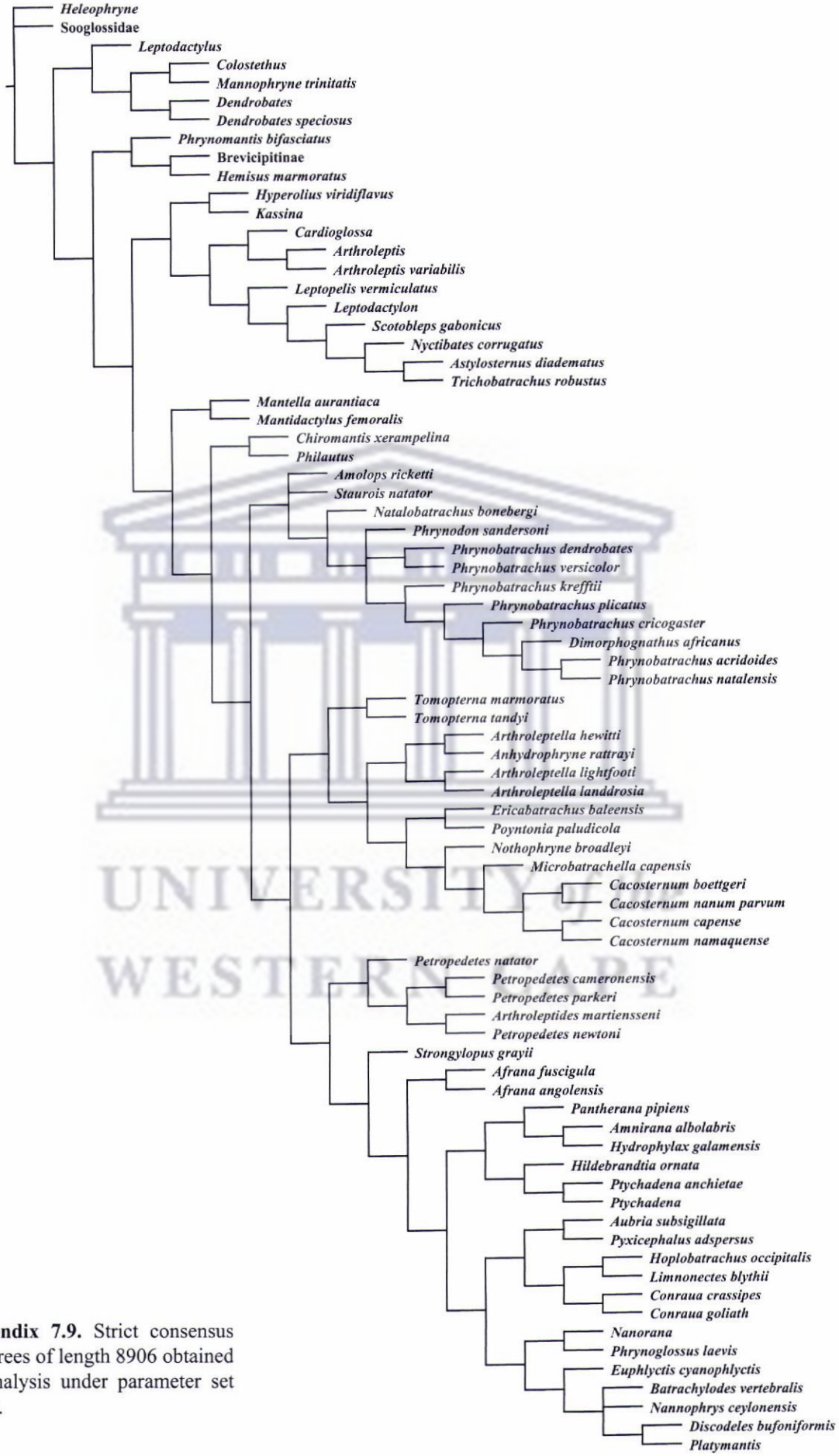
Appendix 7.6. Strict consensus of 2 trees of length 5290 obtained by analysis under parameter set 210G.



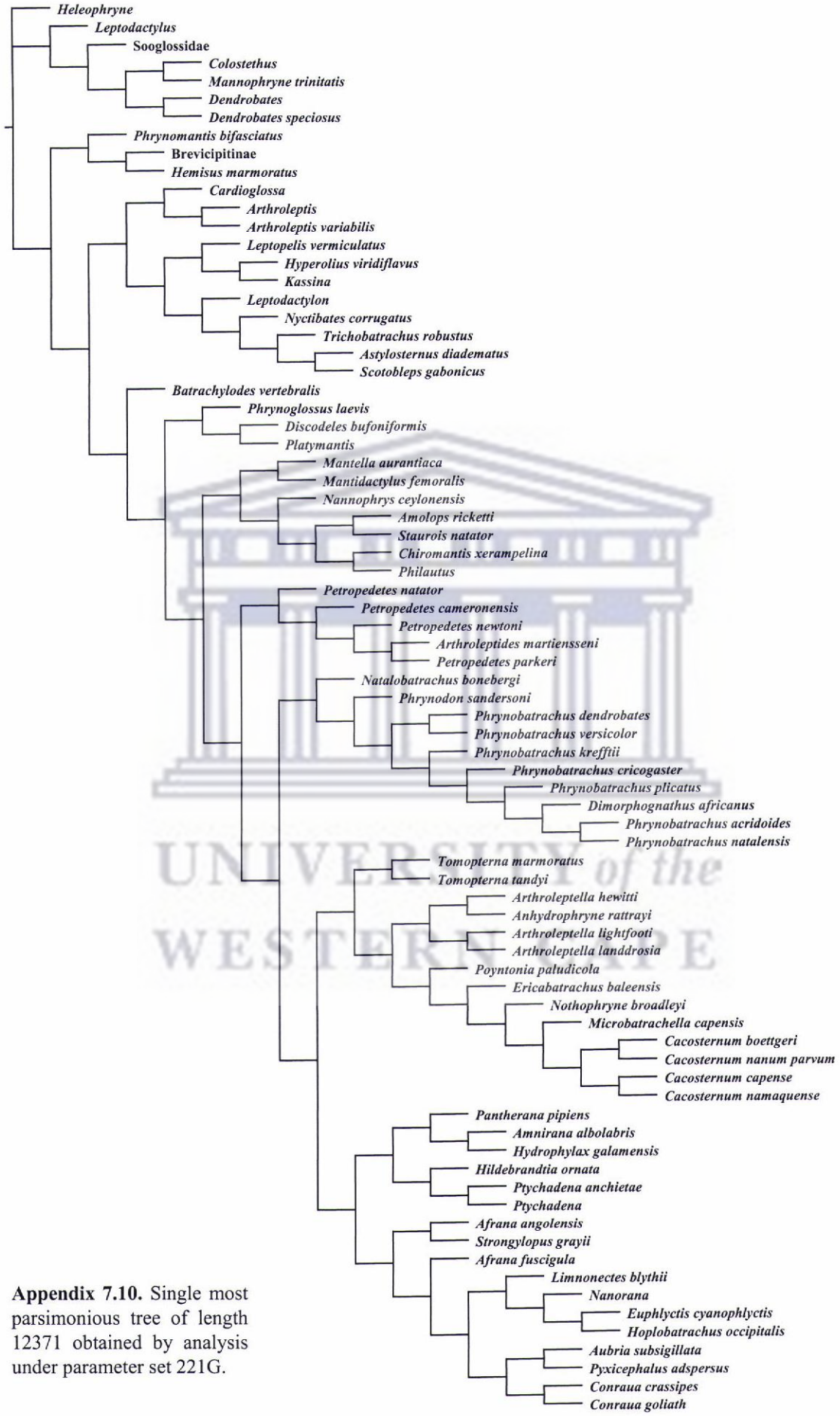
Appendix 7.7. Strict consensus of 6 trees of length 5335 obtained by analysis under parameter set 211C.



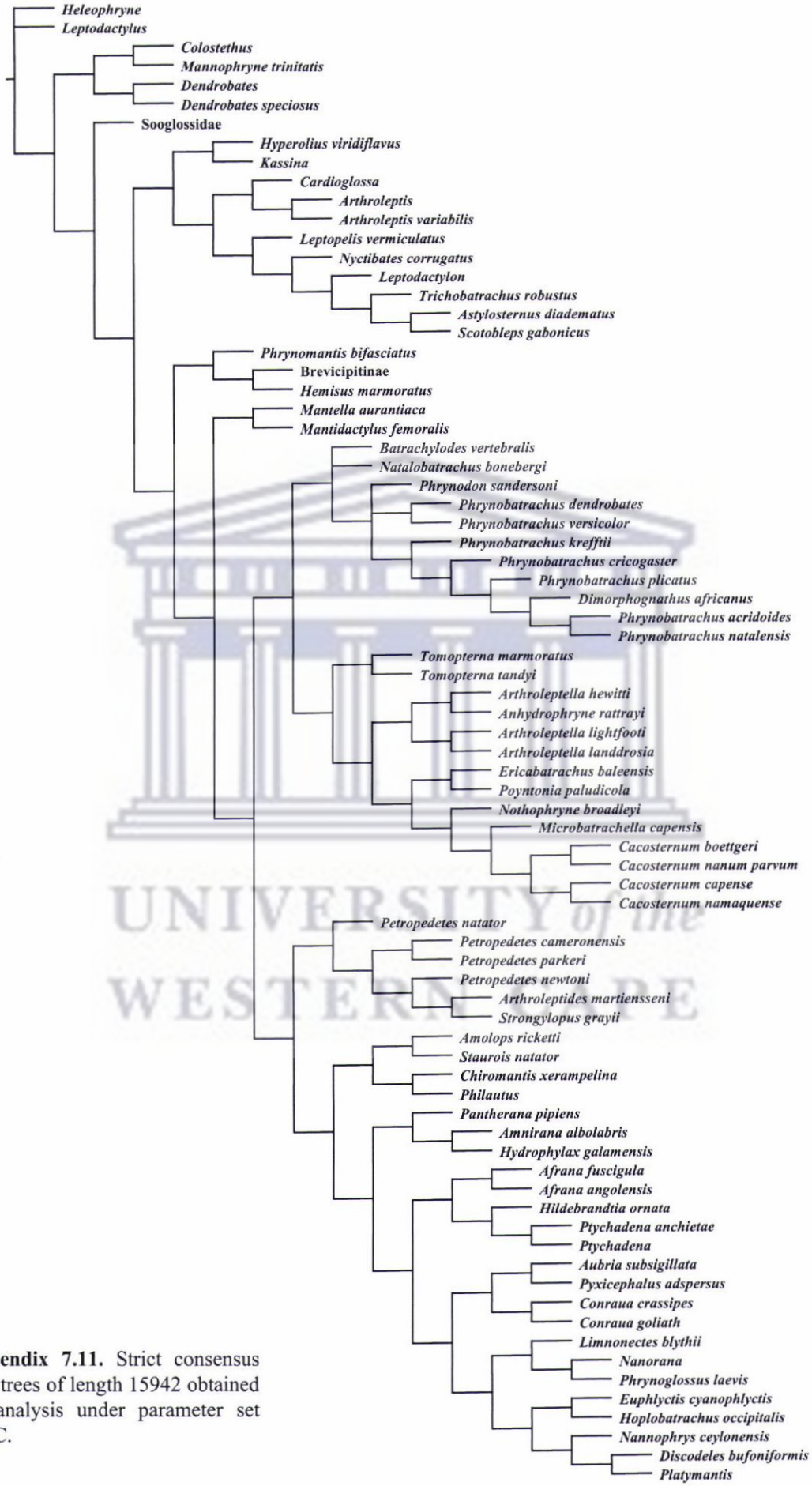
Appendix 7.8. Strict consensus of 2 trees of length 7100 obtained by analysis under parameter set 211G.



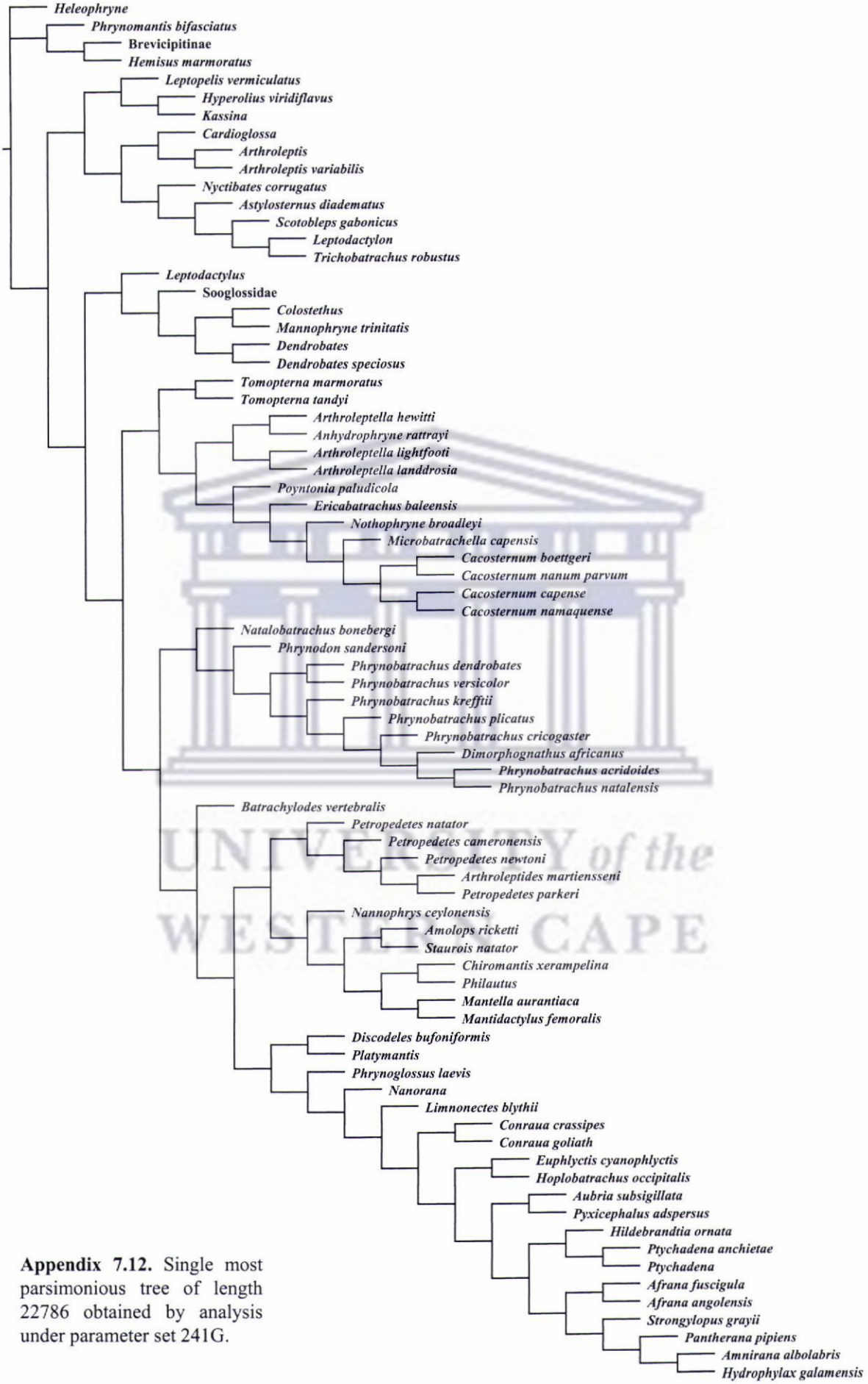
Appendix 7.9. Strict consensus of 2 trees of length 8906 obtained by analysis under parameter set 221C.



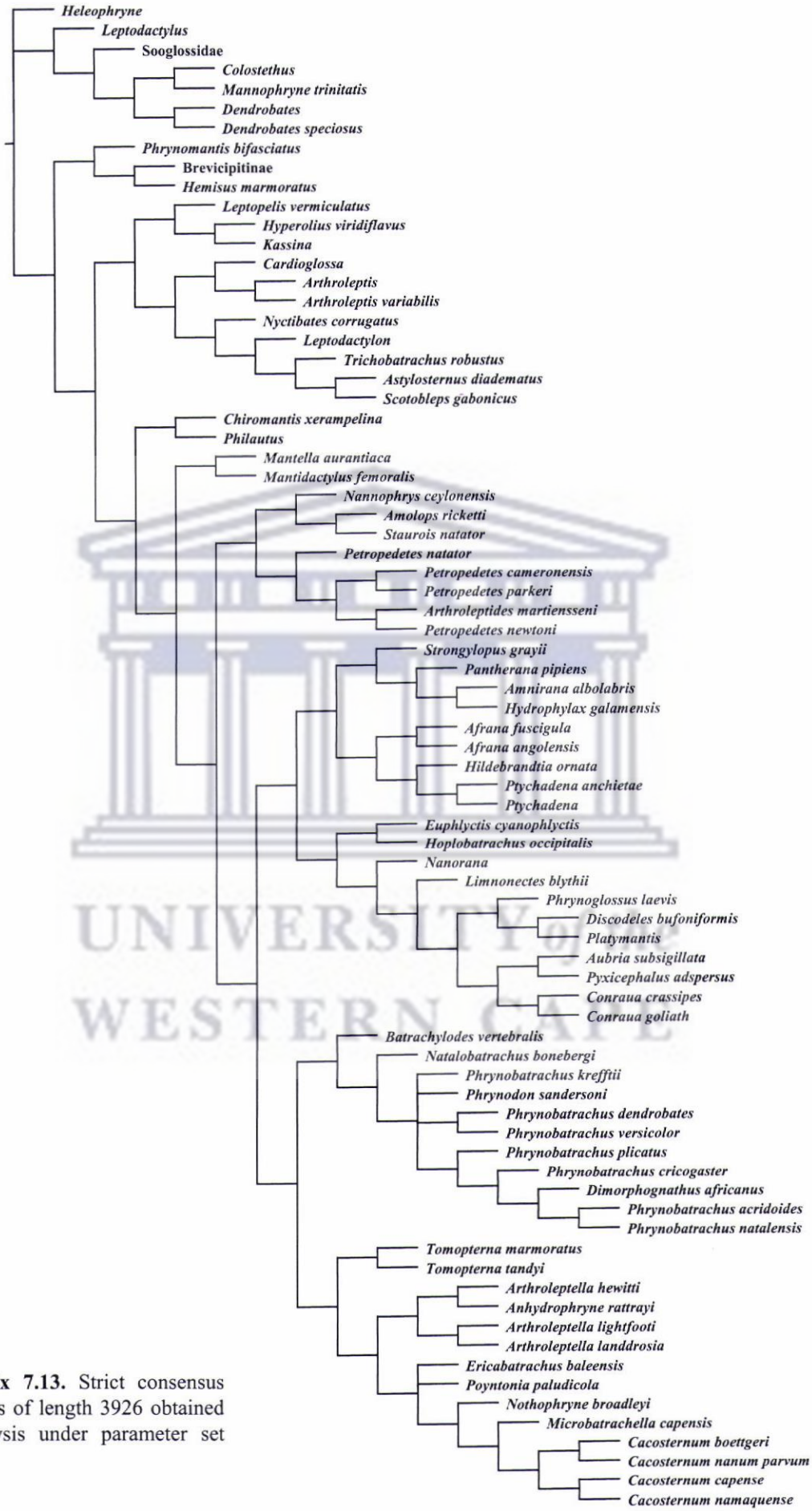
Appendix 7.10. Single most parsimonious tree of length 12371 obtained by analysis under parameter set 221G.



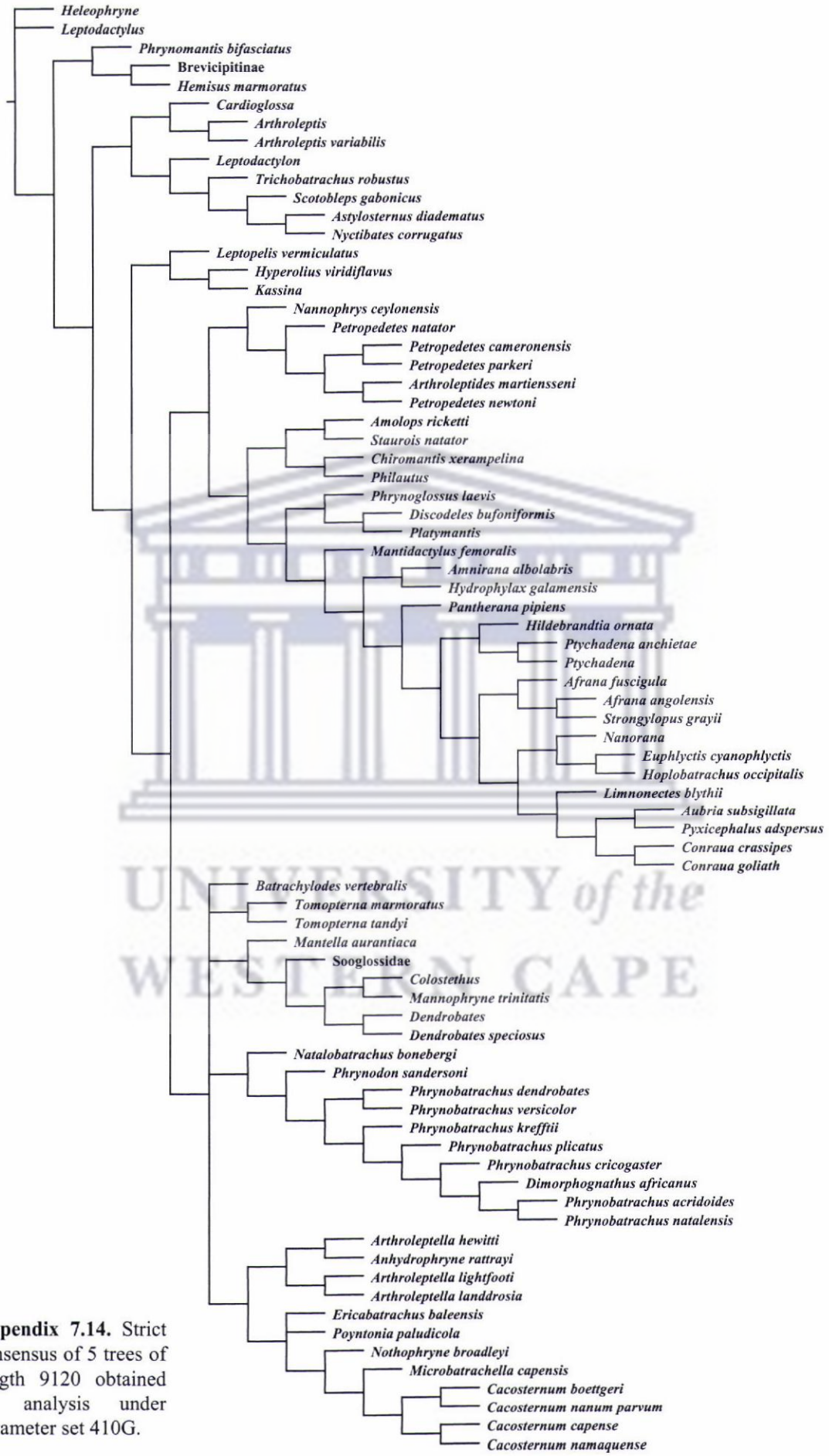
Appendix 7.11. Strict consensus of 2 trees of length 15942 obtained by analysis under parameter set 241C.



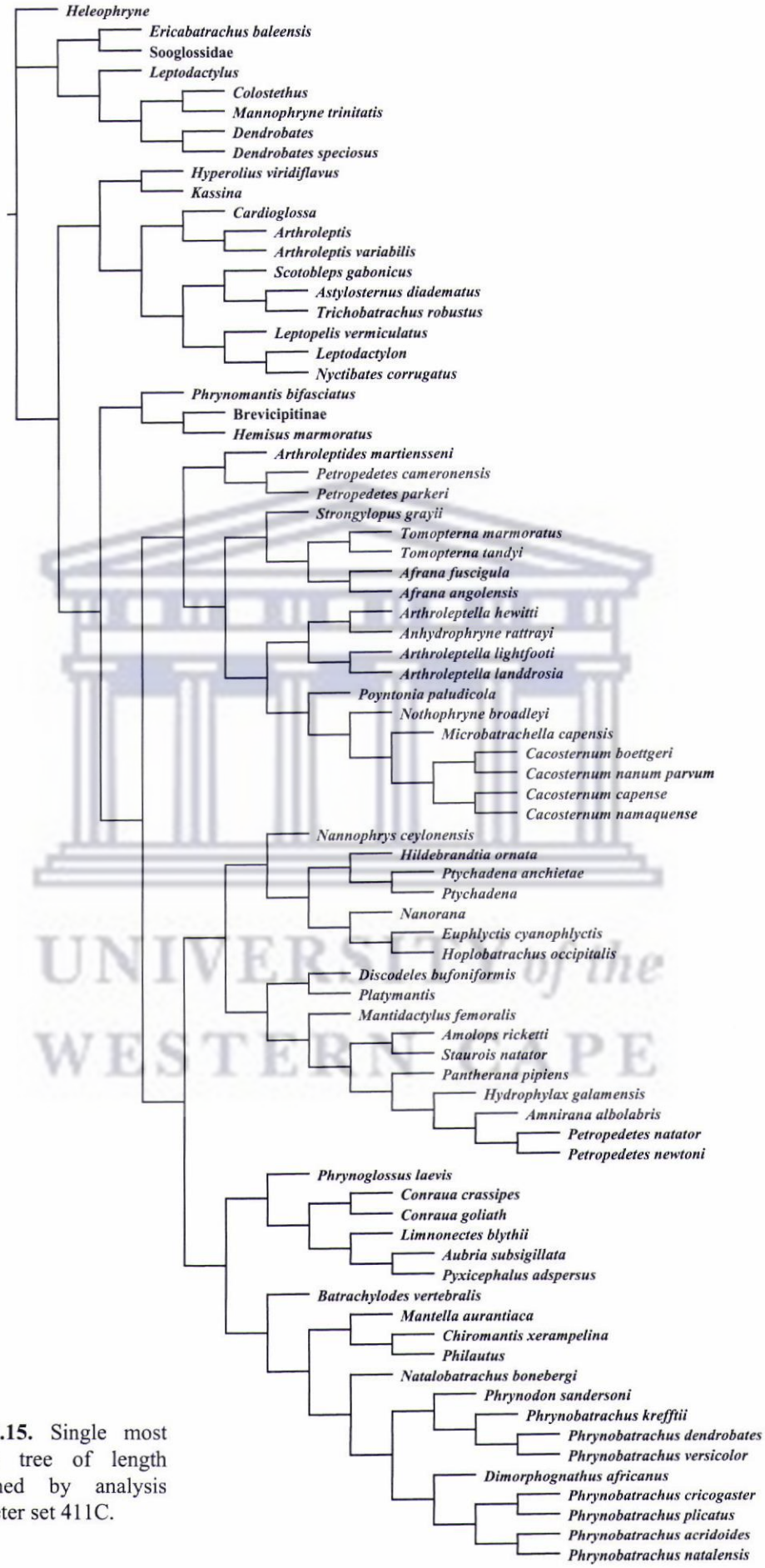
Appendix 7.12. Single most parsimonious tree of length 22786 obtained by analysis under parameter set 241G.



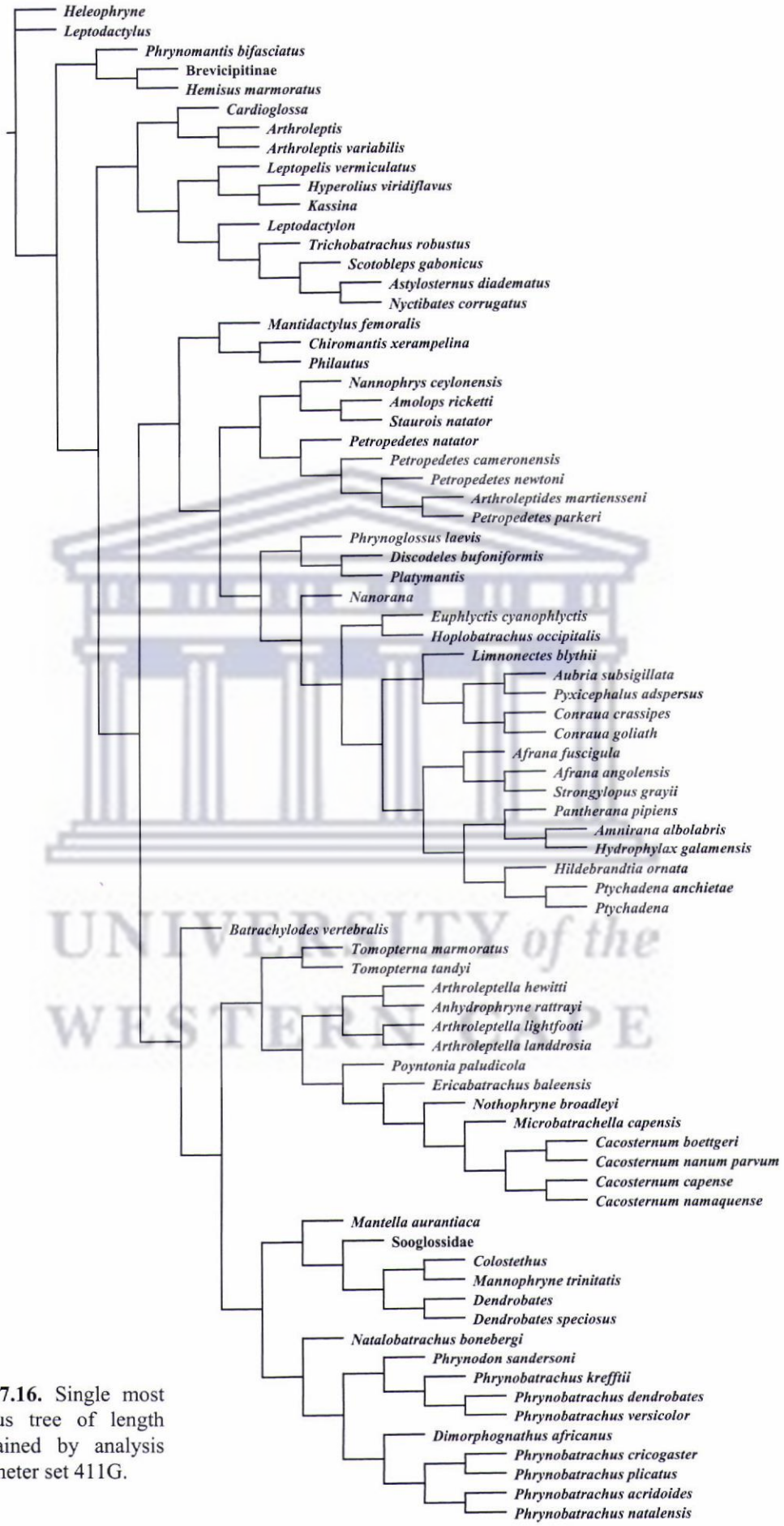
Appendix 7.13. Strict consensus of 4 trees of length 3926 obtained by analysis under parameter set 410C.



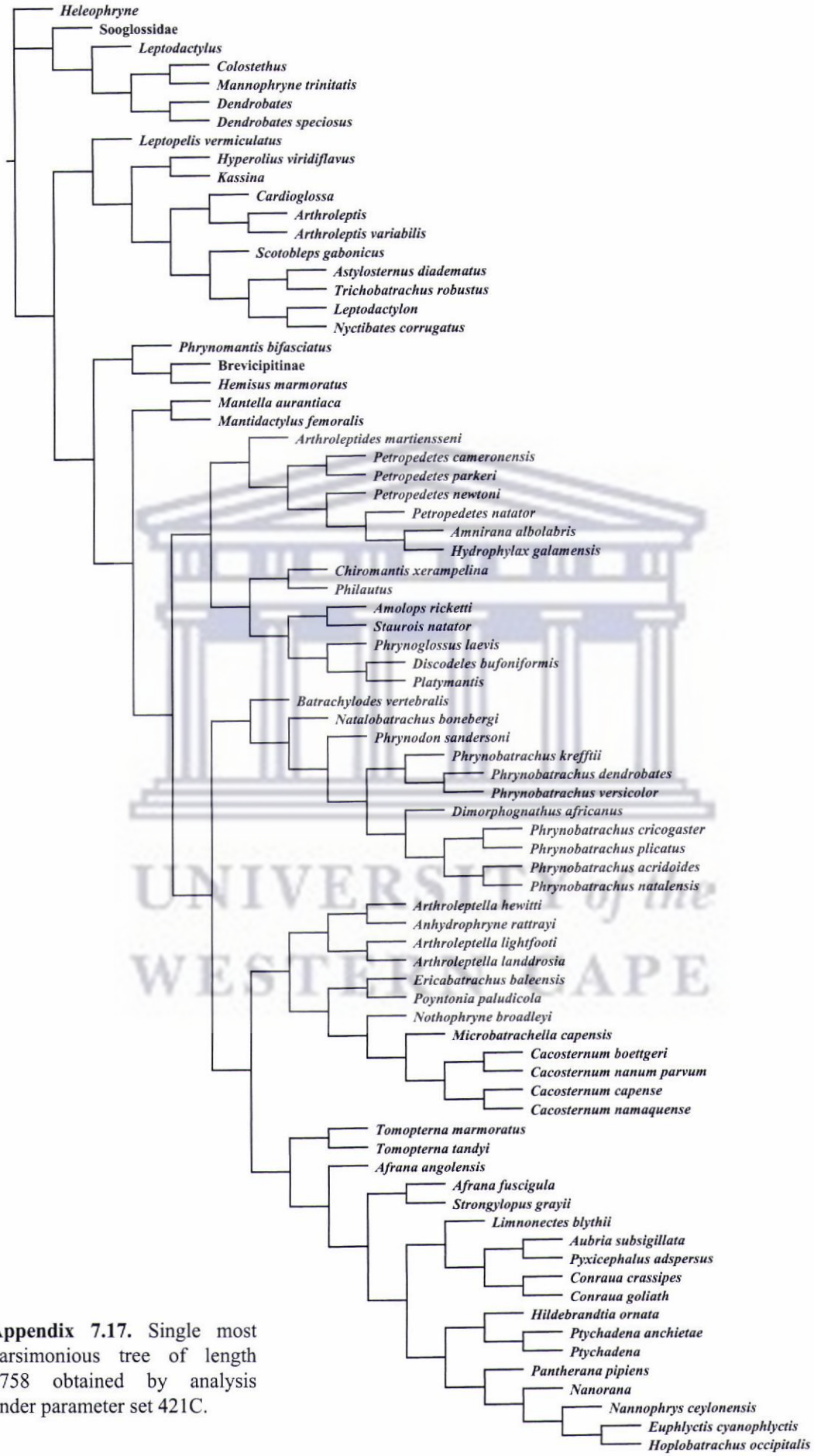
Appendix 7.14. Strict consensus of 5 trees of length 9120 obtained by analysis under parameter set 410G.



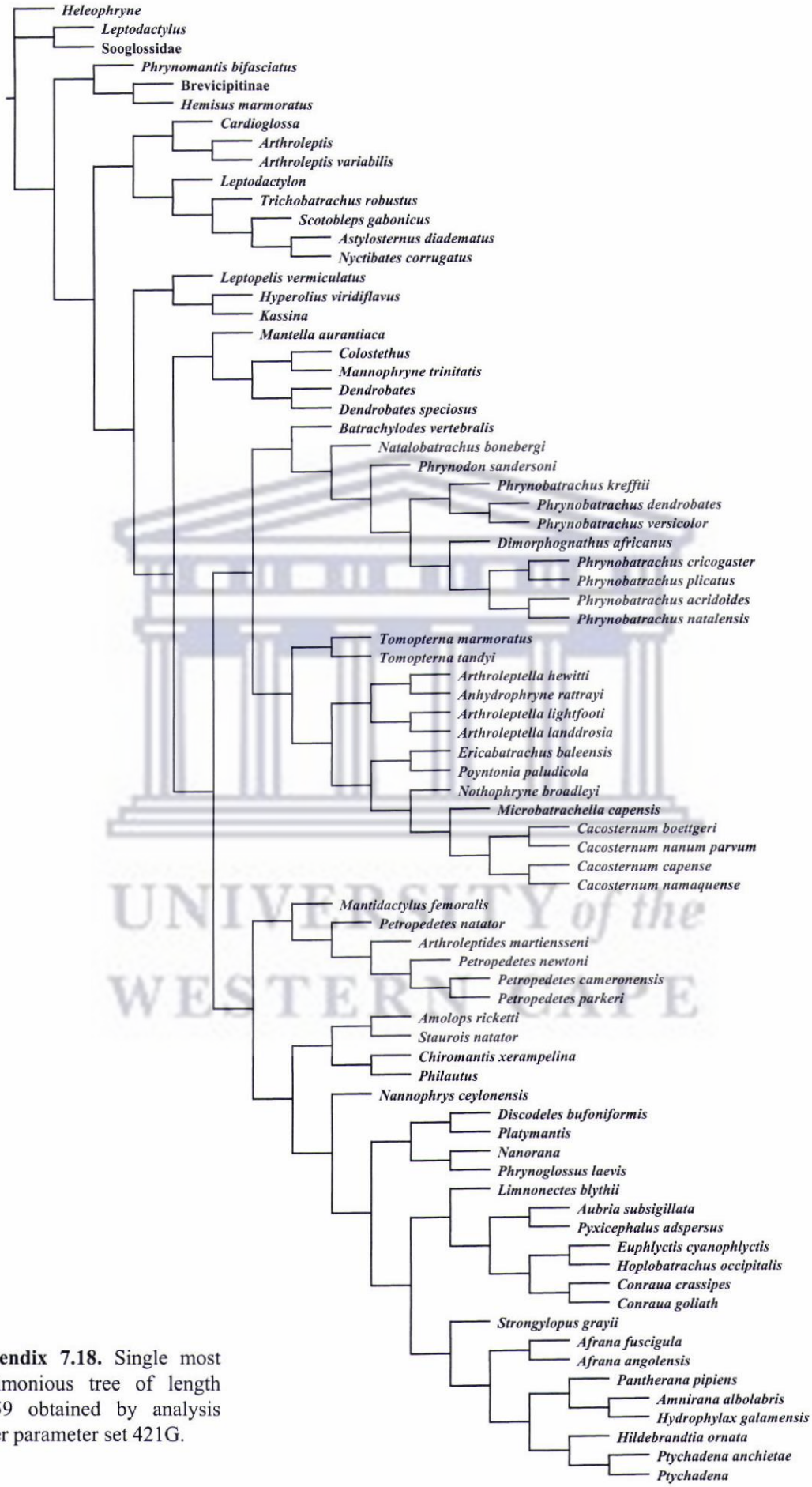
Appendix 7.15. Single most parsimonious tree of length 5827 obtained by analysis under parameter set 411C.



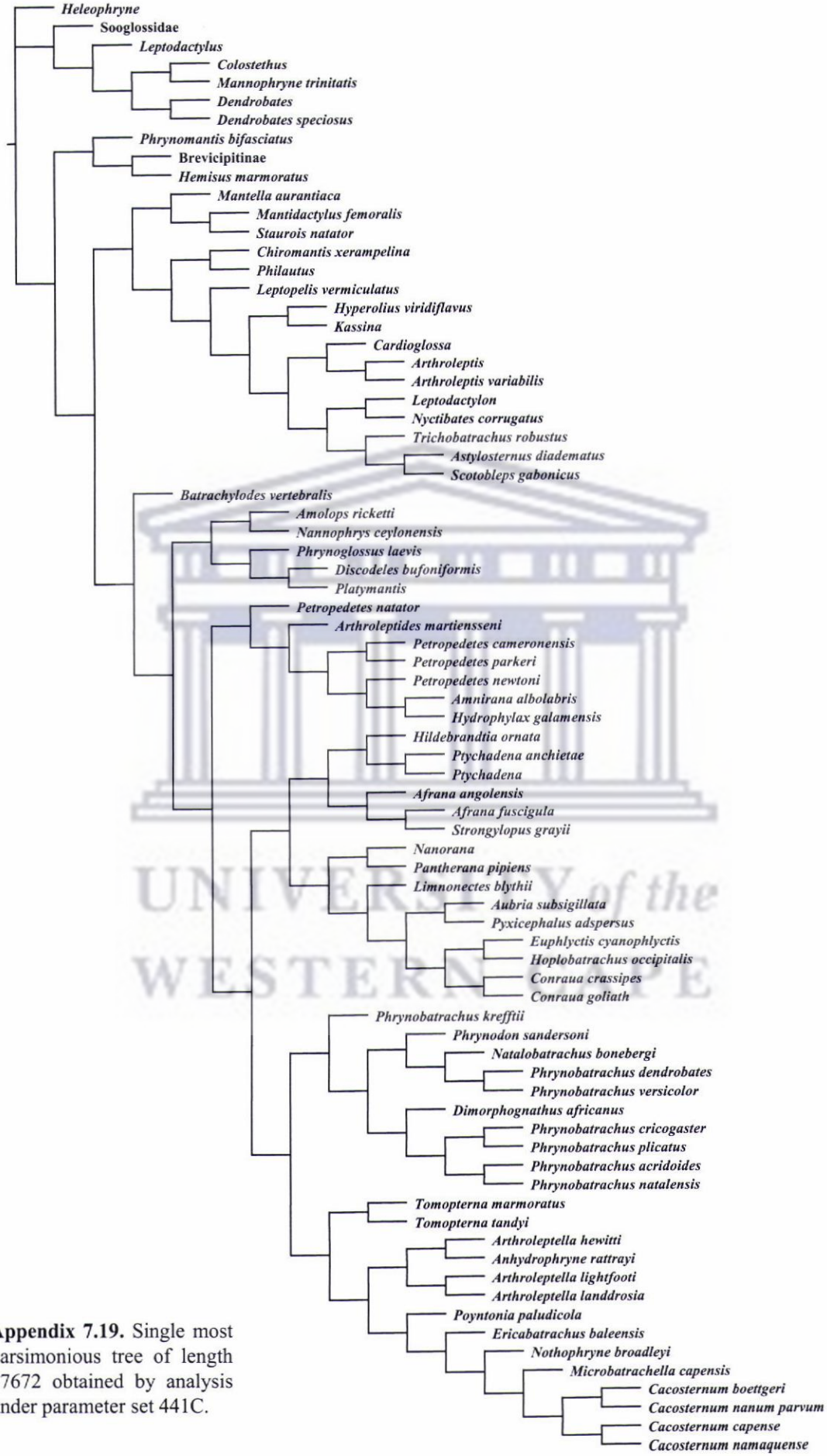
Appendix 7.16. Single most parsimonious tree of length 11051 obtained by analysis under parameter set 411G.



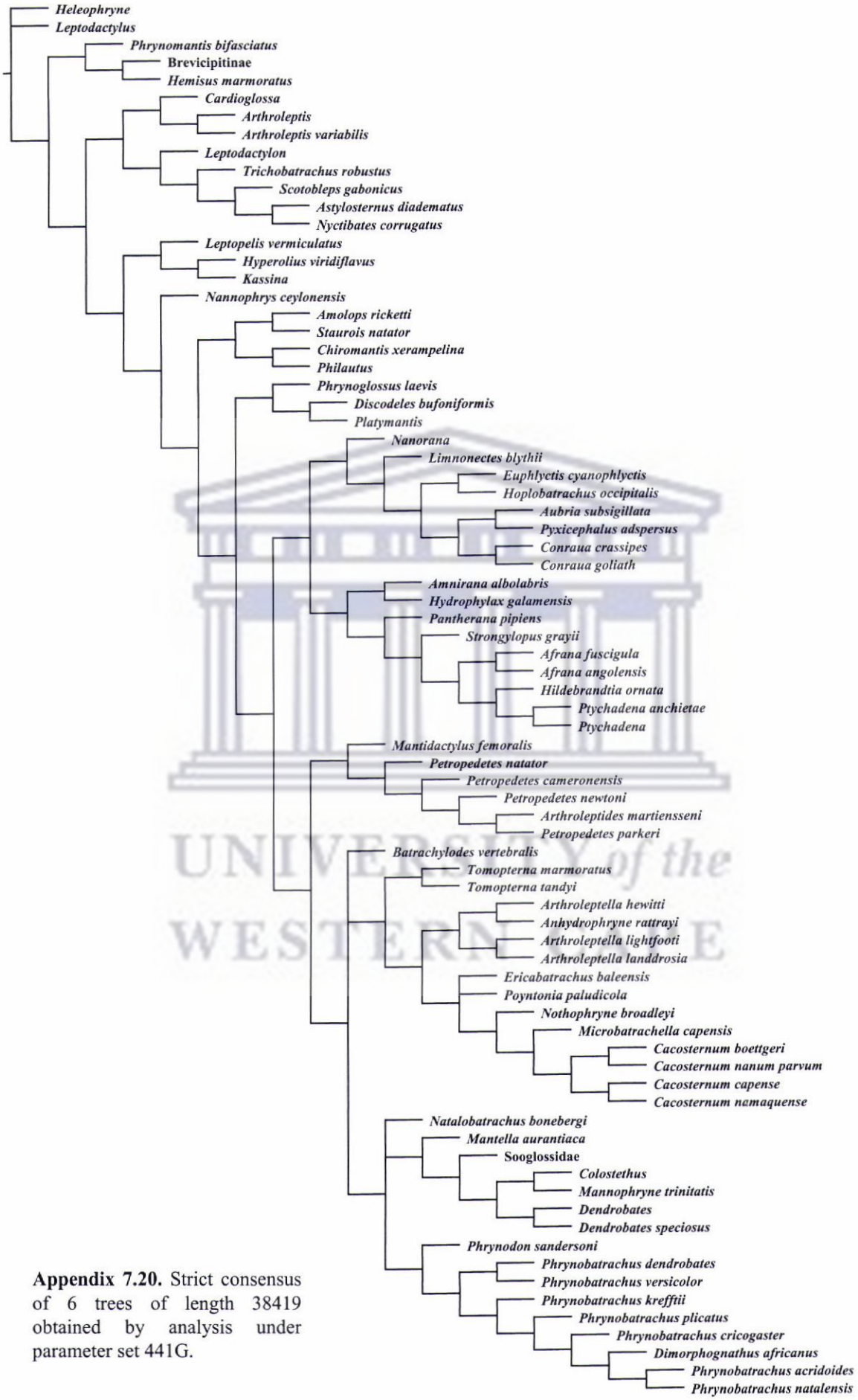
Appendix 7.17. Single most parsimonious tree of length 9758 obtained by analysis under parameter set 421C.



Appendix 7.18. Single most parsimonious tree of length 20259 obtained by analysis under parameter set 421G.



Appendix 7.19. Single most parsimonious tree of length 17672 obtained by analysis under parameter set 441C.



Appendix 7.20. Strict consensus of 6 trees of length 38419 obtained by analysis under parameter set 441G.

Appendix 8. Distribution of unambiguous synapomorphies on the tree obtained from the analyses under equal weights. Terminal taxa are listed alphabetically, and clades are referred to under the node number on the equally-weighted topology (Fig. 22). Character numbers are indicated first and refer to Table 3 and Appendix 2. Character transformations are denoted thereafter by listing the ancestral and derived states separated by a '>'.

Afrana angolensis 5:0>1, 70:0>2, 122:0>1, 180:0>1.
Afrana fuscigula 69:0>1, 107:1>0.
Amnirana albolabris 101:0>1, 168:1>0.
Amolops ricketti 1:1>0, 38:0>2, 39:0>1, 50:1>0, 58:0>1, 97:1>0, 107:1>0, 124:1>2, 126:0>1, 127:3>0, 138:0>1, 144:0>2, 150:1>0, 155:1>0, 167:2>0, 168:1>0.
Anhydrophryne rattrayi 24:1>2, 32:2>1, 40:0>1, 60:0>2, 139:0>1.
Arthroleptella hewitti 31:0>1, 129:2>1, 142:0>1, 149:2>1.
Arthroleptella lightfooti 31:0>1, 81:1>2.
Arthroleptides martiensseni 18:1>0, 48:0>1, 121:0>1, 142:0>4, 149:1>0, 161:0>1, 181:0>1.
Arthroleptis 6:0>1, 30:1>0, 63:1>0, 121:1>0, 129:2>1, 167:1>2, 168:0>1.
Arthroleptis variabilis 2:0>1, 41:0>1, 60:0>2, 128:0>1, 130:0>3.
Astylosternus diadematus 0:0>1, 16:2>0, 22:0>1, 51:1>0, 61:1>0, 84:1>0, 102:0>1, 155:0>1, 188:0>1.
Aubria subsigillata 38:2>1, 151:0>2, 186:1>2.
Batrachylodes vertebralis 1:1>0, 16:0>1, 36:1>0, 42:1>0, 52:1>2, 69:0>1, 77:1>2, 100:0>1, 108:0>1, 111:0>1, 120:1>0, 136:1>0, 139:0>1, 146:0>3, 151:0>1, 170:0>1, 177:0>1, 182:0>1, 183:0>1, 187:1>0.
Brevicipinae 0:0>1, 5:0>1, 22:1>2, 29:0>1, 30:0>2, 32:2>0, 65:0>1, 80:2>0, 100:0>1, 171:0>1, 178:3>2.
Cacosternum boettgeri 50:1>3, 66:0>1, 87:0>1, 115:0>1, 116:0>1, 117:0>3, 123:2>0.
Cacosternum capense 96:1>0.
Cacosternum namaquense 66:0>1, 87:0>2, 88:0>2, 116:0>1, 140:1>0.
Cacosternum nanum parvum 60:0>1, 62:0>1, 80:1>2, 84:1>0, 178:2>1.
Cardioglossa 38:0>1, 42:1>0, 49:0>1, 51:1>0, 52:1>0, 59:1>0, 60:0>1, 96:0>1, 104:0>1, 105:0>1, 106:1>0, 155:0>1, 178:1>2, 186:0>2.
Chiromantis xerampelina 6:1>0, 20:2>1, 78:0>1, 91:0>1, 120:0>1, 122:0>1, 124:1>0, 142:1>2.
Colostethus 35:1>6, 105:0>1, 115:0>1.
Conraua crassipes 48:0>1, 99:0>2.
Conraua goliath 146:0>2, 156:1>0.
Dimorphognathus africanus 112:1>0, 142:1>0, 147:2>3.
Discodeles bufoniformis 110:0>1, 111:0>1, 124:1>2, 149:1>2, 177:0>1.
Ericabatrachus baleensis 4:1>0, 13:1>0, 24:1>2, 29:1>0, 30:1>0, 32:2>1, 33:1>0, 39:0>1, 50:3>1, 60:0>1, 80:1>2, 87:0>3, 91:2>0, 96:1>0, 112:0>1, 113:3>5, 119:0>1, 130:4>3, 151:0>1, 160:0>1, 167:2>1, 168:1>0.
Euphlyctis cyanophlyctis 0:1>0, 20:2>1, 26:3>1, 50:1>2, 89:0>1, 112:0>1, 135:2>1.
Hemisus marmoratus 4:2>1, 14:0>1, 20:0>1, 21:0>1, 33:0>2, 69:0>1, 77:1>2, 87:01>2, 88:0>2, 97:0>2, 112:0>1, 113:4>5, 115:0>1, 157:1>0, 176:1>2, 184:0>1, 186:0>1.
Hildebrandtia ornata 44:0>2, 74:0>1, 128:2>1, 129:3>2, 158:0>1, 163:0>1, 170:0>2, 172:1>0.
Hoplobatrachus occipitalis 38:0>1, 44:0>1, 53:1>0, 59:0>1, 108:0>1, 184:0>1.
Hydrophylax galamensis 89:0>1, 110:0>1, 173:0>2.
Hyperolius marmoratus 37:0>1, 41:0>1, 65:0>2, 87:0>3, 94:1>0, 122:0>1, 128:0>1, 158:2>0, 169:1>0, 173:0>1, 181:1>2.
Kassina 14:2>0, 15:1>0, 42:1>0, 45:0>1, 50:1>0, 51:1>0, 53:0>1, 59:1>2, 60:0>2, 69:0>1, 78:0>2, 129:5>1, 157:1>0, 167:1>2, 168:0>1, 171:0>1.
Leptodactylon 7:1>0, 35:8>4, 44:0>1, 58:0>1, 70:1>2, 122:0>1, 123:0>1, 127:3>0, 129:6>2, 144:0>1, 146:0>1, 152:2>1, 162:0>1, 185:0>1.
Leptodactylus 4:0>1, 11:0>2, 20:0>1, 21:0>1, 33:0>1, 44:0>1, 45:0>1, 65:0>2, 69:0>1, 74:0>1, 79:0>1, 91:0>2, 98:0>1, 115:0>1, 123:0>1, 127:3>2, 128:0>2, 129:0>3, 142:0>4, 155:0>1, 161:0>1, 167:1>2, 168:0>1, 172:0>1, 190:0>2.

Leptopelis vermiculatus 2:0>1, 21:0>1, 35:8>7, 36:0>2, 38:0>2, 50:1>0, 56:1>0, 58:0>1, 64:1>0, 78:0>1, 83:0>1, 93:1>0, 101:1>0, 106:1>0, 110:0>1, 114:0>2, 122:0>1, 124:1>0, 125:0>1, 147:2>4, 155:0>1, 156:0>1, 181:1>2, 183:0>1.
Limnonectes blythii 16:1>0, 50:1>2, 54:0>1, 71:0>1, 73:0>2, 74:0>1, 81:0>1, 84:1>0, 107:0>1, 162:0>1, 173:2>1, 177:0>1.
Mannophryne trinitatis 14:2>1, 50:1>0.
Mantella aurantiaca 1:1>0, 11:0>1, 20:2>1, 22:0>1, 36:1>0, 42:1>0, 49:0>1, 51:1>0, 52:1>0, 60:2>0, 61:1>0, 62:0>1, 63:1>0, 64:0>1, 66:0>1, 85:0>2, 117:0>2, 158:0>2, 186:0>1.
Mantidactylus femoralis 44:0>1, 45:0>2, 55:0>1, 72:1>0, 80:2>1, 91:0>1, 138:0>1, 173:0>2, 175:0>1.
Microbatrachella capensis 28:0>2, 31:0>1, 32:2>1, 37:0>1, 59:1>2, 62:0>1, 66:0>1, 100:0>1, 108:0>1, 158:2>0, 169:1>0.
Nannophrys ceylonensis 0:1>0, 4:0>1, 6:1>0, 15:1>0, 16:0>2, 20:2>0, 24:0>1, 26:1>3, 32:2>1, 52:1>2, 54:0>3, 55:0>1, 67:0>1, 106:2>0, 112:1>0, 128:0>1, 135:2>1, 146:0>1, 151:0>1, 157:1>0, 158:0>2, 169:0>1, 177:1>2, 181:1>0, 183:0>1, 184:0>1.
Nanorana 10:1>0, 11:0>2, 12:1>0, 14:2>1, 16:1>2, 19:2>1, 42:1>0, 60:2>0, 68:0>1, 75:0>1, 76:2>3, 78:0>2, 80:0>1, 113:3>4, 126:0>1, 127:3>0, 150:1>0, 154:0>1, 172:1>0, 188:0>3.
Natalobatrachus bonebergi 1:1>0, 2:0>1, 52:1>0, 92:1>0, 107:1>0, 116:0>1, 117:0>2, 119:0>1, 126:0>1, 155:0>1, 169:1>0, 178:2>1.
Nothophryne broadleyi 3:0>1, 34:1>0, 35:6>2, 71:2>0, 79:0>1, 101:1>2, 122:0>1, 130:4>3, 141:1>0.
Nyctibates corrugatus 23:0>2, 27:2>3, 58:0>1, 76:2>1, 85:1>0, 102:0>2, 129:6>2, 171:0>1, 186:1>0.
Pantherana pipiens 6:1>0, 107:1>0.
Petropedetes cameronensis 5:0>1, 7:1>0, 11:0>2, 45:0>2, 135:2>0, 158:2>1, 183:0>1.
Petropedetes natator 11:0>2, 24:0>1, 30:1>0, 54:0>2, 86:0>1, 135:2>0, 138:0>1, 177:0>1, 178:1>2, 187:1>0.
Petropedetes newtoni 26:1>3, 107:1>0, 110:0>1, 143:0>1.
Petropedetes parkeri 68:1>0, 143:0>1, 149:1>0, 161:0>1, 181:0>1.
Philautus 5:0>1, 11:0>2, 24:0>1, 36:1>0, 45:0>2, 55:0>1, 60:2>0, 68:0>1, 84:1>0, 182:0>1.
Phrynobatrachus acridoides 40:0>1, 65:2>0, 110:1>0, 151:1>0, 154:0>1, 155:0>1, 172:2>0, 187:1>0.
Phrynobatrachus cricogaster 38:0>1, 40:0>1, 68:0>1, 185:0>5.
Phrynobatrachus dendrobates 69:0>1, 108:0>1.
Phrynobatrachus krefftii 1:1>0, 50:1>2, 51:0>1, 133:0>1, 169:1>0, 179:0>1.
Phrynobatrachus natalensis 18:0>1, 86:1>0, 89:0>1, 107:0>1, 167:1>2, 168:0>1, 189:1>0.
Phrynobatrachus plicatus 115:0>1, 138:0>1, 155:0>1, 156:0>1, 169:1>0, 175:1>0.
Phrynobatrachus versicolor 5:0>1, 16:0>1.
Phrynodon sandersoni 4:1>0, 21:1>0, 35:3>1, 68:0>1, 79:0>1, 81:0>1, 85:0>1, 108:0>1, 179:0>1, 189:1>0.
Phrynoglossus laevis 4:0>1, 11:0>2, 16:1>2, 48:0>1, 50:1>3, 52:1>0, 57:0>1, 58:0>1, 59:0>3, 63:1>0, 72:0>1, 75:0>1, 78:0>2, 136:1>0, 154:0>1, 176:1>2.
Phrynomantis bifasciatus 12:0>1, 24:0>2, 32:2>3, 37:0>1, 59:0>3,65:0>2, 77:1>0, 92:0>1, 107:0>1, 114:0>1, 135:1>0, 157:1>2, 188:0>1.
Platymantis 2:0>1, 10:1>0, 78:0>1, 80:0>2, 86:0>1, 96:0>1, 104:0>1, 105:0>1, 121:1>0, 155:0>1, 158:0>2, 162:0>1, 175:0>2, 178:1>2, 182:0>1.
Poyntonia paludicola 18:1>0, 31:0>1, 51:1>0, 52:1>0, 56:1>0, 58:0>1, 62:0>1, 121:0>1, 136:1>0, 170:0>2, 188:0>4.
Ptychadena anchietae 56:0>1, 181:0>1.
Ptychadena 0:1>0, 115:0>1.
Pyxicephalus adspersus 78:0>3, 158:0>1, 169:0>1, 170:0>2, 172:1>0, 173:2>0, 190:0>1.
Scotobleps gabonicus 0:0>1, 27:2>3, 70:1>0, 151:0>1, 152:2>0, 171:0>1.
Sooglossidae 4:0>1, 22:0>2, 69:0>1, 76:2>1, 88:0>2, 91:0>1, 119:0>1, 128:0>2, 129:0>2, 152:2>1, 170:0>1, 180:0>1.

Staurois natator 21:0>1, 30:1>0, 35:16>7, 81:0>2, 100:0>1, 102:0>2, 103:1>2, 107:0>2, 113:3>4, 114:2>0, 122:0>4, 123:0>1, 124:1>2, 126:0>1, 129:4>0, 131:0>1, 138:0>1, 152:2>1, 155:0>1, 167:1>0, 170:0>1.

Strongylopus grayii 4:0>1, 5:0>1, 26:3>1, 34:0>1, 42:1>0, 52:1>0, 68:0>1, 70:0>2, 154:0>1, 158:0>2, 166:1>0, 169:0>1, 181:0>1.

Tomopterna marmorata 1:1>0, 16:0>2, 158:0>1, 175:0>1.

Tomopterna tandyi 31:0>1, 48:1>0, 165:0>1.

Trichobatrachus robustus 38:0>2, 44:0>1, 70:1>0, 123:0>1, 127:3>0, 135:0>1, 144:0>1, 146:0>1, 162:0>1.

Node 0 (basal node, all taxa excluding *Heleophryne*) 3:0>1, 9:0>1, 14:0>2, 15:0>1, 16:0>2, 19:0>1, 42:0>1, 76:0>2, 77:0>1, 84:0>1, 94:0>1, 106:0>2, 124:0>1, 127:0>3, 135:0>1, 147:0>2, 149:0>1, 152:0>2, 154:0>1, 157:0>1, 158:0>2, 167:0>1, 169:0>1, 176:0>1, 178:0>3, 187:0>1.

Node 1 (dendrobatids + sooglossids) 36:0>1, 40:0>2, 46:0>1, 50:0>1, 70:0>1, 81:0>1, 86:0>1, 96:0>1, 110:0>1.

Node 2 (dendrobatids) 20:0>2, 25:0>2, 26:0>1, 27:0>2, 29:0>1, 57:0>1, 62:0>1, 84:1>2, 85:0>2, 97:0>1, 101:0>2, 106:2>1, 138:0>1, 155:0>2, 160:0>1, 172:0>2, 173:0>2, 174:0>1, 191:0>2.

Node 3 (*Dendrobates* species) 10:0>1, 16:2>1, 22:0>1, 30:0>1, 49:0>1, 53:0>1, 100:0>1, 116:0>1.

Node 4 (*Colostethus* + *Mannophryne*) 17:0>1, 18:0>1, 24:0>1, 40:2>1, 52:0>1, 89:0>1, 161:0>1.

Node 5 (*Leptodactylus* (Ranoidea + Microhyloidea)) 1:0>1, 17:0>1, 121:0>1, 136:0>1, 191:0>5.

Node 6 (Ranoidea + Microhyloidea) 13:0>1, 25:0>2, 26:0>3, 27:0>2, 61:0>1.

Node 7 (Microhylidae including *Hemisus*) 4:0>2, 14:2>0, 15:1>0, 22:0>1, 40:0>2, 46:0>1, 49:0>1, 66:0>1, 70:0>2, 75:0>1, 81:0>2, 91:0>4, 96:0>1, 109:0>1, 137:0>1, 152:2>1, 170:0>2.

Node 8 (Brevicipinae + *Hemisus*) 9:1>0, 42:1>0, 62:0>1, 82:0>1, 94:1>0, 98:0>1, 99:0>1, 116:0>1, 124:1>0, 128:0>1, 129:0>2, 136:1>0, 161:0>1, 163:0>1, 167:1>2, 168:0>1.

Node 9 (Ranoidea) 20:0>2, 50:0>1, 93:0>1.

Node 10 (arthroleptids and hyperoliids) 59:0>1, 70:0>1, 100:0>1, 101:0>1, 102:0>1, 106:2>1, 129:0>5.

Node 11 (*Hyperolius* + *Kassina*) 4:0>1, 20:2>1, 66:0>1, 83:0>1, 84:1>0, 89:0>1, 97:0>1, 110:0>1, 114:0>2, 125:0>1, 147:2>0, 148:0>1, 176:1>3.

Node 13 (Arthroleptinae) 43:0>1, 61:1>0, 81:0>1, 92:0>1, 129:5>2, 162:0>2, 163:0>1.

Node 14 (*Arthroleptis* species) 11:0>2, 35:8>1, 46:0>1, 55:0>1, 86:0>1, 87:0>3, 113:0>1, 152:2>0, 183:0>1.

Node 15 (Astylosterninae + *Leptopelis*) 41:0>1, 45:0>1, 48:1>0, 62:0>2, 79:0>1, 80:2>1, 128:0>1, 157:1>0.

Node 16 (Astylosterninae) 52:1>0, 87:0>3, 100:1>0, 102:1>0, 129:5>6, 176:1>0, 186:0>1.

Node 18 (*Astylosternus* (*Nyctibates* + *Trichobatrachus*)) 60:0>2, 64:1>0.

Node 19 (*Nyctibates* + *Trichobatrachus*) 77:4>2, 173:0>1.

Node 20 (Ranidae) 33:0>1, 60:0>2, 140:0>2, 158:2>0, 179:0>1.

Node 21 (mantellids + rhacophorids) 39:0>1, 43:0>1, 86:0>1, 97:0>1, 114:0>2, 129:0>4, 191:5>3.

Node 22 (*Mantella* (*Staurois* + rhacophorids) 112:0>1.

Node 23 (*Staurois* + rhacophorids) 2:0>1, 7:1>0, 70:0>2, 77:1>0, 121:1>0, 142:0>1, 187:1>0.

Node 24 (rhacophorids) 34:1>2, 39:1>0, 43:1>0, 48:1>0, 50:1>3, 59:0>1, 86:1>0, 93:1>0, 106:2>0, 125:0>1, 135:1>0, 173:0>2, 178:1>4, 181:0>2.

Node 25 (Ranidae excluding rhacophorids and mantellids) 107:0>1, 167:1>02.

Node 26 (Tomopterninae (*Batrachylodes* (phrynobatrachids + cacosternids))) 92:0>1, 110:0>1, 178:1>2.