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A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data

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Abstract

During the last two decades, major taxonomic rearrangements were instituted in the anuran family Ranidae. Most of these changes were not based on phylogenetic analysis, and many are controversial. Addressing the phylogeny of Ranidae requires broader taxon sampling within the superfamily Ranoidea, the phylogenetic relationships and higher classification of which are also in a state of flux. No comprehensive attempt has yet been made to reconstruct ranid phylogeny using both morphological and molecular data. In the present contribution, data from 178 organismal characters were collated for 74 exemplar species representing the families Arthroleptidae, Hemisotidae, Hyperoliidae, Mantellidae Microhylidae, Petropedetidae, Rhacophoridae, Sooglossidae, and most subfamilies of Ranidae. These were combined with ~1 kb of DNA sequence from the mitochondrial 12S rDNA and 16S rDNA gene regions in a simultaneous parsimony analysis with direct optimization. Results support the classification of *Hemisus* with the brevicipitine microhylids, confirm that Arthroleptidae (and its two component subfamilies Astylosterninae and Arthroleptinae) are monophyletic, and advocate the recognition of Leptopelidae. Monophyly of Ranidae is compromised by recognition of Petropedetidae, Rhacophoridae and Mantellidae, which should be recognized as subfamilies of Ranidae at present. Furthermore, Petropedetidae was found to be grossly paraphyletic, comprising three clades which are all considered separate subfamilies of Ranidae, i.e., Petropedetinae, Phrynobatrachinae and Cacosterninae. Three well defined subfamilies of Ranidae were consistently retrieved as monophyletic in a sensitivity analysis, i.e., Tomopterninae, Ptychadeninae and Pyxicephalinae. However, Ptychadeninae and Pyxicephalinae were embedded in Raninae and Dicroglossinae, respectively. Ceratobatrachinae is removed from Dicroglossinae. Dicroglossinae is synonymized with Pyxicephalinae. A new subfamily Strongylopinae is proposed. Raninae should be conservatively treated as a "metataxon" (*sensu* Ford and Cannatella, 1993) until such time as it is fully revised. Tomopterninae is removed from synonymy with Cacosterninae. Morphological synapomorphies are reported for major monophyletic clades retrieved in the simultaneous analysis with equal weights. The present study found that many Old World clades appear to contain both African and Asian taxa, contrary to the findings of some recent biogeographical analyses. This study demonstrates the value of broad taxonomic sampling in ranid phylogeny, and highlights the immense contribution that can be made from detailed morphological data.

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The anuran superfamily Ranoidea (*sensu* Ford and Cannatella, 1993) comprises a large group of predominantly Old World Neobatrachia, viz., Arthroleptidae, Hemisotidae, Hyperoliidae, Mantellidae, Microhylidae, Petropedetidae, Rhacophoridae and Ranidae. In the early 20th century, most of these taxa were placed in the poorly defined family Ranidae, but many groups were subsequently split off into new families. Some of these (e.g., Hyperoliidae, Rhacophoridae) have been recognized as separate families for decades, and are widely accepted. The elevation of others to the rank of family may have been premature, however, as the phylogenetic relationships among the major clades of Ranoidea remain unclear (Ford and Cannatella, 1993; Hedges and Maxson, 1993; Ruvinsky and Maxson,

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1996; Grant et al., 1997; Vences, 1999; Emerson et al., 2000a).

The taxa that remain as the core of Ranidae comprise just under a quarter of all extant frog species (~700 species). Ranidae are considered one of the most systematically neglected of the larger frog families (Ford and Cannatella, 1993). The simplest and oldest taxonomic scheme for the family is essentially based on Noble (1931), with minor alterations. This scheme, expressed in Frost (1985), and hereafter referred to as Ranidae s.l., represents a traditional view of Ranidae. Three subfamilies (Raninae, Mantellinae and Petropedetinae) were recognized according to this, although Raninae paraphyly was subsequently demonstrated (Ford, 1990; Ford and Cannatella, 1993), and Petropedetinae paraphyly suspected (Ford, 1990).

Dubois (1987, 1992) instituted major taxonomic rearrangements within Ranidae, most of which are reflected in Duellman's (1993) additions and corrections to Frost's (1985) catalog. Dubois' (1987, 1992) classification recognized six subfamilies in Ranidae, and excluded mantellines and petropedetines, which were elevated to familial status (Dubois, 1992). This action, together with the continued recognition of Rhacophoridae, rendered Ranidae paraphyletic (Laurent, 1951; Emerson et al., 2000a; Scott, 2002). Three new subfamilies were erected by Dubois (1987, 1992), and two others resurrected, all from within what was previously regarded as Raninae. Evidence for the monophyly of some of these, e.g., Ptychadeninae and Pyxicephalinae, exists in the literature (e.g., Clarke, 1981, 1983; Ohler, 1996), but is lacking for others, e.g., Dicroglossinae and Raninae, recognition of which may render other taxa paraphyletic (Ford, 1990; Scott, 2002). Dubois' (1987, 1992) changes, not based on phylogenetic analysis, are controversial (Inger, 1996). At least five further new subfamilies of Ranidae have also been proposed in the last two decades, all of uncertain validity. The suprageneric classification of Ranidae is thus in a state of flux, due, in part, to instability in the higher classification of ranoid families, but also to the recognition of various combinations of subfamilies within Ranidae.

Further complicating matters, a suite of new ranid genera and subgenera have recently been created, mostly by Dubois (1992). The family currently contains 45 genera and 43 subgenera, with just under a third of all ranid species being placed in the nominate and paraphyletic genus *Rana*, currently containing 32 new or recently resurrected subgenera (Dubois, 1987, 1992). Although none of these taxonomic emendations have been critically evaluated in a phylogenetic analysis (Inger, 1996), these taxa have been uncritically accepted as a basic assumption by many recent molecular phylogenetic and biogeographical contributions (e.g., Bossuyt and Milinkovitch, 2000, 2001; Marmayou et al., 2000; Kosuch et al., 2001).

The taxonomic changes of Dubois (1987, 1992) are based principally on an authoritarian assessment of overall similarity, do not attempt to separate synapomorphy from symplesiomorphy, and rely on a limited set of mostly external morphological features to define groups, and literature data of variable reliability. Despite these shortcomings, Dubois' scheme imparted a measure of order to the taxonomic chaos that was Ranidae. Importantly, it has provided testable hypotheses of relationship (Inger, 1996). Drawing attention to aberrant groups, in order to prompt further study thereof, is reported to be one of the primary objectives of the new classification, which is expected to be "temporary" and subject to major amendments in future (A. Dubois, pers. comm.). Nevertheless, a phylogenetic approach to the higher classification of Ranidae would be preferable.

Unfortunately, no comprehensive phylogenetic analysis of ranid relationships exists. Clarke's (1981) study of the osteology of African Raninae remains the only detailed morphological study on the group (Sanchez, 1998), but is limited by being restricted to African taxa and in assuming the monophyly of Raninae *a priori*. The taxonomy of the Asian ranids recently received some attention from molecular systematists, but this work was conducted predominantly at lower systematic levels, or focused on geographically and taxonomically restricted subsets of Ranidae (e.g., Tanaka et al., 1996; Tanaka-Ueno et al., 1998a,b; Emerson et al., 2000b; Marmayou et al., 2000; Richards et al., 2000; Jiang and Zhou, 2001a,b; Kosuch et al., 2001). Some molecular studies on the higher level phylogeny of ranids have been published (Emerson et al., 2000a; Bossuyt and Milinkovitch, 2000), and at least four higher-level molecular studies including ranids are currently underway.

In light of these recent molecular studies, and unpublished data, Dubois (2003; pers. comm.) amended his older classification, shuffling genera within tribes of Dicroglossinae, and returning clades that had been previously removed from Ranidae back into the family. Although this improved the classification dramatically, the content of the major clades of Ranidae and the phylogenetic relationships among these remain uncertain, hindering efforts to identify their appropriate ranks.

The present study does not claim to be a comprehensive phylogeny of Ranidae but, by its content and scope, provides a minimal test of the monophyly and content of many of the traditional and recently proposed ranid clades, while elucidating some of their morphological synapomorphies. The intention here is to lay the foundation for future large-scale detailed comparative morphological studies of Ranidae, which will incorporate all putative clades from all geographic regions, as well as additional data sets. The resulting hypothesis of ranid phylogeny will facilitate future revisions of, and emendations to, the classification, in turn assisting future ecological, developmental and biogeographical research on Ranidae.

Materials and methods

Classification of Ranidae

Many of the newly erected genera and subgenera, particularly those within the large genus *Rana*, appear to be well founded and are likely to stand up to rigorous phylogenetic testing. Local workers (e.g., Channing, 1979, 2001; Passmore and Carruthers, 1995; Kosuch et al., 2001) consider the African subgenera of *Rana* (e.g., *Afrana*, *Strongylopus* and *Amietia*) to be generically distinct from *Rana*, as represented by its type species, *R. temporaria* Linnaeus, 1758. Many of Dubois' other subgenera, particularly those pertaining to well-studied species from North America and Europe, are contentious (D. Frost, pers. comm.). However, within the relatively understudied African and Asian taxa, the majority of these subgeneric names will probably be recognized as valid genera and accepted in the future, given the tremendous diversity present in these Old World ranids. The genus *Rana* is undoubtedly paraphyletic. All validly published and unrefuted subgeneric names of Dubois (1987, 1992) are therefore used as substitute generic names in the present study. This usage does not, however, constitute a formal nomenclatural act, nor is it an endorsement of these subgenera, but is merely operational. The subfamilial classification of Ranidae, *sensu* Dubois (1987, 1992), is generally followed in this contribution, as listed in Table 1. The elevation of some clades to the rank of family (e.g., Petropedetidae) is rejected, on the grounds that these decisions were not based on phylogenetic analyses. The more recent emendations of Dubois (2003) are discussed in retrospect in the appropriate section of the discussion and conclusions.

Taxonomic sampling

The present investigation was undertaken using an exemplar approach, with individual species used as terminals (Yeates, 1995; Wiens, 1998; Prendini, 2001).

Table 1
Classification of family Ranidae Rafinesque-Schmaltz, 1814, compiled from Duellman (1993), Dubois (1987, 1992) and Frost (2004). Familial rank for petropedetines rejected, following Scott (2002). Subgenera are indicated in brackets, where applicable. Taxa represented by at least one exemplar species in the present study are underlined

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Subfamily Dicroglossinae Anderson, 1871

Tribe Ceratobatrachini Boulenger, 1884: *Ceratobatrachus* Boulenger, 1884; *Discodeles* Boulenger, 1881; *Ingerana* Dubois, 1987; *Palmatorappia* Ahl, 1927; *Platymantis* Günther, 1859; *Taylorana* Dubois, 1987.

Tribe Conrauini Dubois, 1992: *Conraua* Nieden, 1908.

Tribe Dicroglossini Anderson, 1871: *Euphlyctis* Fitzinger, 1843; *Occidozyga* Kuhl & Van Hasselt, 1822; *Phrynoglossus* Peters, 1867.

Tribe Limnonectini Dubois, 1992: *Hoplobatrachus* Peters, 1863; *Limnonectes* Fitzinger, 1843 [3 subgenera: *Bourretia* Dubois, 1987; *Fejervarya* Bolkay, 1915; *Limnonectes* Fitzinger, 1843]; *Sphaerotheca* Günther, 1859.

Subfamily Petropedetinae Noble, 1931

Anhydrophryne Hewitt, 1919; *Arthroleptella* Hewitt, 1926; *Arthroleptides* Nieden, 1910; *Cacosternum* Boulenger, 1887; *Dimorphognathus* Boulenger, 1906; *Ericabatrachus* Largen, 1991; *Microbatrachella* Hewitt, 1926; *Natalobatrachus* Hewitt & Methuen, 1913; *Nothophryne* Poynton, 1963; *Petropedetes* Reichenow, 1874; *Phrynobatrachus* Günther, 1862; *Phrynodon* Parker, 1935; *Poyntonia* Channing & Boycott, 1989.

Subfamily Ptychadeninae Dubois, 1987

Hildebrandtia Nieden, 1907; *Lanzarana* Clarke, 1983; *Ptychadena* Boulenger, 1917 [2 subgenera: *Ptychadena* Boulenger, 1917; *Parkerana* Dubois, 1984].

Subfamily Pyxicephalinae Bonaparte, 1850

Aubria Boulenger, 1917; *Pyxicephalus* Tschudi, 1838.

Subfamily Raninae Rafinesque-Schmaltz, 1814

Amolops Cope, 1865 [4 subgenera: *Amolops* Cope, 1865; *Huia* Yang, 1991; *Meristogenys* Yang, 1991; *Amo* Dubois, 1992]; *Batrachylodes* Boulenger, 1887; *Chaparana* Bourret, 1939; *Micrixalus* Boulenger, 1888; *Nanorana* Günther, 1896 [2 subgenera: *Altirana* Stejneger, 1927; *Nanorana* Günther, 1896]; *Paa* Dubois, 1975 [4 subgenera: *Eripaa* Dubois, 1992; *Gynandropaa* Dubois, 1992; *Paa* Dubois, 1975; *Quasipaa* Dubois, 1992]; *Rana* Linnaeus, 1758 [32 subgenera: *Afrana* Dubois, 1992; *Amerana* Dubois, 1992; *Amietia* Dubois, 1987; *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.

Subfamily Ranixalinae Dubois, 1987

Indirana Laurent, 1986; *Nannophrys* Günther, 1869; *Nyctibatrachus* Boulenger, 1882.

Subfamily Tomopterninae Dubois, 1987

Tomopterna Duméril & Bibron, 1841; *Sphaerotheca* Günther, 1859; *Laliostoma* Glaw, Vences & Böhme, 1998.

Table 2
Classification of other ranoid and hyloid taxa represented by at least one morphological exemplar in the phylogenetic analysis of Ranidae presented here

Family Arthroleptidae Mivart, 1869
Subfamily Arthroleptinae Mivart, 1869:
Arthroleptis Smith, 1849; *Cardioglossa* Boulenger, 1900; *Schoutedenella* Witte, 1921.
Subfamily Astylosterninae Noble, 1927:
Astylosternus Werner, 1898; *Leptodactylodon* Andersson, 1903; *Nyctibates* Boulenger, 1904; *Scotobleps* Boulenger, 1900; *Trichobatrachus* Boulenger, 1900.
Family Mantellidae Laurent, 1946
Mantella Boulenger, 1882; *Mantidactylus* Boulenger, 1895.
Family Heleophrynidae Noble, 1931
Heleophryne Sclater, 1899.
Family Hemisotidae Cope, 1867
Hemisus Günther, 1859.
Family Hyperoliidae Laurent, 1943
Subfamily Hyperoliinae Laurent, 1943:
Afrixalus Laurent, 1944; *Hyperolius* Rapp, 1842.
Subfamily Kassininae Laurent, 1972:
Kassina Girard, 1853.
Subfamily Leptopelinae Laurent, 1972:
Leptopelis Günther, 1859.
Family Microhylidae Günther, 1858
Subfamily Brevicipitinae Bonaparte, 1850:
Breviceps Merrem, 1820.
Subfamily Phrynomerinae Noble, 1931:
Phrynomantis Peters, 1867.
Family Rhacophoridae Hoffman, 1932
Subfamily Rhacophorinae Hoffman, 1932:
Chiromantis Peters, 1855; *Philautus* Gistel, 1848.
Family Sooglossidae Noble, 1931
Sooglossus Boulenger, 1906.

The aim of the exemplar approach is to test, not assume, the monophyly of particular higher taxa. An attempt was made to include exemplars of all putative ranoid families and subfamilies to resolve the base of the tree, as no *a priori* knowledge of the relationships of any of these groups can be assumed in the absence of a large-scale phylogenetic analysis.

All previously conducted phylogenetic analyses either failed to adequately resolve the basal node of Ranoidea, or obtained conflicting results (Ford, 1990; Hedges and Maxson, 1993; Hay et al., 1995; Ruvinsky and Maxson, 1996; Emerson et al., 2000a). Consequently, the choice of a primary outgroup from within this group may have led to erroneous polarities. Although its monophyly is contentious (Haas, 2003) and remains untested, superfamily Hyloidea Rafinesque, 1815 is widely considered to fall outside the boundaries of Ranoidea (Hedges and Maxson, 1993; Hay et al., 1995; Ruvinsky and Maxson, 1996). The African heleophrynid *Heleophryne* was therefore chosen from this superfamily as the primary outgroup. Sooglossidae have been variously regarded as hyloids, a "transitional" family (*sensu* Lynch, 1973) or putatively associated with Ranoidea (Noble, 1926, 1931; Griffiths, 1959a,b; Lynch, 1971, 1973; Savage, 1973; Ford, 1990; Hillis et al., 1993; Ruvinsky and Maxson, 1996). Microhylidae are also widely held to be basal within, or sister to Ranoidea. The above taxa were included to assist in resolving relationships at the base of the tree, as their exclusion could potentially compromise the elucidation of correct basal relationships.

Exemplars of all major families of Ranoidea were included. Hemisotidae were represented by a single species. In order to represent Arthroleptidae, whose monophyly has not previously been tested, each of the five genera of Astylosterninae was represented by one species, and the three genera of Arthroleptinae by five species. Hyperoliidae, thought to be closely related to Arthroleptidae by Laurent (1951, 1973, 1986), were represented by five species. The familial status of rhacophorines and mantellines, as separate from Ranidae s.l. (*sensu* Frost, 1985), was recently refuted, as these were found to be sister taxa embedded within Ranidae s.l. (Emerson et al., 2000a). Rhacophoridae and Mantellidae were thus each included in the present study by two maximally divergent exemplars. With the exception of Arthroleptidae s.l., 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* Boulenger, 1919).

All currently recognized monotypic genera of the ranid subfamily Petropedetinae were also included, as part of a more detailed investigation into their phylogenetic relationships (Scott, 2002). More than one species of each petropedetine genus was included where possible, as a minimal test of generic monophyly, as the monophyly of this group is untested. An attempt was made to include exemplar species of all hypothesized subfamilies of Ranidae, following the classification of Dubois (1987). The monotypic subfamilies Lankanectinae (raised from within Dicroglossinae), Nyctibatrachinae and Micrixalinae (raised from within Ranixalinae), *sensu* Dubois (2003), were not described or constituted in their current form at the initiation of this research. As such, they were not explicitly targeted for inclusion in this research, and are not represented here. Emphasis was placed on including all African genera of Ranidae s.l. The choice of exemplars was determined by the availability of specimens for examination and skeletal preparation, and tissues for DNA extraction. Some potentially important taxa were represented solely by morphological data, such as *Batrachylodes*. Genera of Ranidae represented in the present study are underlined in Table 1; other ranoid and outgroup taxa included are indicated in Table 2.

Morphological data

Details of the taxa included and voucher specimens examined for this study are provided in Appendix 1. The osteology of *Sooglossus* was scored entirely from the literature (Griffiths, 1959a; Lynch, 1973; Wu, 1994), as no skeletal preparations of this taxon were examined. Character states were scored preferentially from adult males, unless another semaphoront is specified. Minimal dissections were performed on whole specimens. Dissections usually involved 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 cutaneus pectoris*. All osteological material examined was double-stained (alizarin red and alcian blue) and enzymatically cleared. Skeletons were prepared using the method of Dingerkus and 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. Some large or old specimens were difficult to clear enzymatically, the latter due to dehydration or alteration of the tissue composition with time, necessitating an increase in the length of time spent in the KOH: glycerine steps, increased maximally up to two months. Disarticulation occurred in some older specimens as a result, but if the tissue failed to clear, the usefulness of the preparation could be drastically reduced, whereas osteological information was still obtainable from disarticulated specimens. Specimens were not disarticulated for scoring, except for occasional removal of the entire pectoral girdle and lower jaw.

Rare taxa and additional specimens of some species were X-rayed onto Ilford Pan FP4 black and white 9 × 11.5 cm film using a dental X-ray apparatus (25 kV, 4 mA), with the assistance of D.E. van Dijk. Exposure times varied according to the size of the specimen. These were developed using Agfa Rodinal© developer and printed onto black and white high contrast film. X-rays were digitally scanned and processed using Corel Photo Paint version 10 (Corel Corporation Ltd). Digital images will be deposited in the collection of the CAS and AMNH.

Morphological specimens were examined, and illustrations prepared using a Wild Stereomicroscope with a *camera lucida*.

A total of 178 morphological characters were examined from the following sources: 49 from osteology of the skull, 11 from osteology of the vertebral column, 14 from osteology of the pectoral girdle, 8 from osteology of the pelvic girdle, 18 from osteology of the limbs, 20 from the hyolaryngeal apparatus, 41 from external morphology, 12 sexually dimorphic characteristics from osteology or external morphology, three characters of breeding behavior, one muscular character and one karyological character. Ninety-two of the characters were binary and 86 were multistate. Composite coding (*sensu* Maddison, 1993; Strong and Lipscomb, 1999) was used in preference to binary coding where possible in order to minimize the occurrence of inapplicable or missing entries (Maddison, 1993; Pleijel, 1995; Wilkinson, 1995; Lee and Bryant, 1999; Strong and Lipscomb, 1999). Terminology generally follows the two most recent comparable works dealing with Ranoidea, viz., Ford (1990) and Wu (1994). Criteria for recognizing the 178 morphological characters used in the analysis and definitions of the character states are discussed in Appendix 2. The order of appearance of the characters in the matrix is functional, facilitating future data addition, with minimal handling of delicate skeletal preparations being the primary consideration. Sections follow the general body region in dorsal or ventral aspects.

Many of the characters used are well known in anuran systematics. Only new characters or those considered to have been inadequately explained in previous works are illustrated or explained in detail in Appendix 2. Most characters were modified in some way from previous contributions. The process of primary homology assessment inherently contains an element of subjectivity because different researchers may perceive character states differently (Hawkins et al., 1997; Hawkins, 2000; Wiens, 2001). The chronological history of usage of each character in previous phylogenetic analyses is fully referenced in Appendix 3, to facilitate detailed comparisons with the findings of previous researchers.

Mineralization is defined following Fabrezi (2001), or recognized as a disorganized, bubbly textured calcification (L. Trueb, pers. comm.). The presence of a suture was assessed using the criteria of Kaplan (2000). Digits of the manus are numbered in accordance with the interpretation of digit ontogeny outlined by Fabrezi and Alberch (1996), viz., the innermost finger is termed Digit II, considering the first digit to have been lost and not homologous with the prepollex.

Characters were assumed to be logically independent, even if they may not be so biologically. Character polarities were determined via outgroup comparison (Farris, 1982; Nixon and Carpenter, 1993) with reference to *Heleophryne purcelli*, consistently scored zero to facilitate the interpretation of states determined to be plesiomorphic by the analysis. All multistate characters were treated non-additively, i.e., unordered (Fitch, 1971), thereby preventing unfalsifiable hypotheses of character state order from being incorporated *a priori*, and instead allowing character congruence to determine the order (Hauser and Presch, 1991; Slowinski, 1993; Hormiga, 1994).

Unknown determinations of the true state, or missing data, are represented in the matrix by a "?". Primary causes of missing data include character states not being visible on the material available, often due to incomplete clearing of the surrounding tissue, breakage of the structure concerned, or the failure of tissues to adequately take up the stain due to dehydration or decalcification. In some cases, specimens were assessed to be subadult from the incomplete ossification of the diapophyses of long bones and phalanges. In such cases, character states well known to be influenced by the extent of ossification were scored as unknown. Occasionally, specimens that were examined during visits to particular collections were unavailable for subsequent loan. Characters added after their initial examination therefore had to be scored unknown. Characters that were logically impossible to score (or inapplicable) for particular taxa were scored with a "–", for example characteristics of the medial lingual process (characters 121–124), which is absent in most taxa examined. Minimal polymorphism was encountered in the morphological data set (12 entries), and in all cases this was between state 0 and 1, scored as "A" in Appendix 4. The data set is only minimally affected by inapplicable (403 entries, or 3% of the matrix) and unknown (389 entries, or 2.9% of the matrix) entries.

Molecular data

Muscle tissues, either frozen or preserved in 96% ethanol, were predominantly used for sequencing. Liver tissues, preserved in 20% dimethyl-sulfoxide (DMSO) in saturated saline, were used occasionally. Whole genomic DNA was isolated via the phenol–chloroform extraction method (Maniatis et al., 1982; Hillis et al., 1996), or using hexadecyltrimethylammonium bromide (CTAB) digestion buffer and excluding the phenol steps (Corach, 1991).

The choice of gene loci is a crucial factor determining the level of insight that can potentially be obtained from a molecular phylogenetic study (Brower and DeSalle, 1994). Two gene loci were used in the present study, i.e., partial 12S and 16S rDNA. Both of these regions have been widely used in anuran systematics above the species level (Hedges and Maxson, 1993; Hay et al., 1995; Richards and Moore, 1996, 1998; Ruvinsky and Maxson, 1996; Emerson and Ward, 1998; Vences, 1999; Bossuyt and Milinkovitch, 2000; Clough and Summers, 2000; Emerson et al., 2000a,b; Richards et al., 2000; Vences et al., 2000a,b; Wieczorek et al., 2000; Kosuch et al., 2001). Widespread usage does not necessarily mean that a particular gene region is suitable for phylogenetic studies at a particular level (Brower and DeSalle, 1994). These regions have both demonstrated their utility at and just above the species level in the Anura, although they may fail at much higher phylogenetic levels, particularly due to difficulties in alignment (Hertwig et al., 2004). Inclusion of the hypervariable partial sequence of 16S, which may contain many saturated positions, is justified here because it nevertheless represents variation which may be useful in resolving terminal relationships, as demonstrated for third codon positions by Vrana et al. (1994) and Källersjö et al. (1999).

The 12S rDNA fragment was amplified using the 12Sa (L2519) and 12Sb (H2916) primer pair of Simon et al. (1994), and the 16S rDNA fragment was amplified using the 16Sar-L (LR-N-13398) and 16Sbr-H (LR-J-12887) primer pair of Simon et al. (1994). PCR reactions were conducted according to standard methods, using concentrations in the final reaction of 10% PCR buffer, 1–4 mM $MgCl_2$, 0.2 mM dNTPs, 0.12 mM of each primer, to which approximately 100 ng of DNA template and 0.5 units of *Taq* polymerase were added. 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 to amplify the 12S rDNA: 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 held there. Similar protocols were used to amplify the 16S rDNA: 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 held there. The 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.). The 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. Most samples were sequenced on an ABI 377 automatic sequencer (Applied Biosystems Inc.), but some were generated manually, as in Dawood and Channing (2000). Chromatogram files were manually checked for correct base-calling from the peaks, using Sequence Navigator version 1.0.1. (Applied Biosystems Inc.). Table 3 lists samples sequenced in the present study, their localities and sequence accession numbers. The accession numbers of additional sequences obtained from the EMBL/GenBank Data Libraries, http://www.ncbi.nlm.nih.gov, are listed in Table 4.

Composite terminals

Taxa for which one or both of the molecular data sets were missing could affect the analysis by increasing the number of most parsimonious trees, due to the "wild card" or "joker" effect. This increases the instability of the result to the addition of new data (Nixon and Carpenter, 1996). In a few cases, it was possible to combine the morphological data of one exemplar species with sequence data from GenBank for one or both gene

Table 3
GenBank accession numbers for new 12S rDNA and 16S rDNA sequences produced for this study, listing 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 (†). Samples with only a collector acronym (listed in Appendix 1) were obtained from that collector. Where no voucher exists but a prior determination was made, the collector acronym of the person responsible for that determination is listed after "det"

Species	12S rDNA	16S rDNA	Voucher	Locality
Afrana angolensis	DQ022316	DQ022350	RDS 926	Muzambai, Tanzania
Amnirana albolabris	DQ022317†	DQ022351	TMSA 84177	Nguti, Cameroon
Arthroleptides martiensseni	DQ022320	–	TMSA 84077	Armani, Tanzania
Arthroleptis stenodactylus	–	DQ022343	AC 1422	Penhalonga, South Africa
Arthroleptis tanneri	DQ022308	–	Det AC	Armani, Tanzania
Anhydrophryne rattrayi	DQ022319	–	AC 1206	Hogsback, South Africa
Astylosternus diadematus	DQ022309†	–	TMSA 84311	Nguti, Cameroon
Cacosternum boettgeri	DQ022322	–	ES 262	Weenen, South Africa
Cacosternum boettgeri	–	DQ022352	ES 745	Kenilworth, South Africa
Cacosternum capense	DQ022323	DQ022354	TMSA 84242	Klipheuwel, South Africa
Cacosternum nanum	DQ022321	–	ES 342	Boston, South Africa
Cacosternum nanum	–	DQ022353	TMSA 83951	Swaziland
Cardioglossa gracilis	DQ022310†	DQ022345	TMSA 84165	Nguti, Cameroon
Cardioglossa leucomystax	–	DQ022344	HD2	Haute Dodo, Ivory Coast
Conraua crassipes	DQ022324	DQ022355	ZFMK 69355	Mt. Nlonako, Cameroon
Conraua goliath	DQ022325*	–	MV	Cameroon
Dimorphognathus africanus	DQ022326†	DQ022356	TMSA 84170	Nguti, Cameroon
Hildebrandtia ornata	DQ022327	–	AC 1110	Beira, Mozambique
Hoplobatrachus occipitalis	DQ022328	–	AC 1321	Kampala, Uganda
Hydrophylax galamensis	DQ022318	–	AC 1105	Beira, Mozambique
Leptodactylodon cf. *mertensi*	DQ022311	DQ022346	MV	Nlonako, Cameroon
Leptopelis vermiculatus	DQ022312	DQ022347	TMSA 84038	Armani, Tanzania
Microbatrachella capensis	DQ022329	–	TMSA 84315	Hermanus, South Africa
Microbatrachella capensis	–	DQ022357	CDNEC 6698	Aghulhas Plain, South Africa
Nyctibates corrugatus	DQ022313†	–	TMSA 84312	Nguti, Cameroon
Nyctibates corrugatus	–	DQ022348	MV	Edib, Cameroon
Petropedetes cameronensis	DQ022335†	DQ022363	LM 24	Nguti, Cameroon
Petropedetes newtoni	DQ022334	–	ZFMK 75590	Mt. Kupe, Nyasoso, Cameroon
Petropedetes parkeri	DQ022336	DQ022364	LM 3	Nguti, Cameroon
Phrynobatrachus acridoides	DQ022330†	DQ022358	AC 1251	Mafia Island, Mozambique
Phrynobatrachus auritus	DQ022333	DQ022362	TMSA 84101	Nguti, Cameroon
Phrynobatrachus cricogaster	DQ022331	DQ022359	MV	Nlonako, Cameroon
Phrynobatrachus krefftii	–	DQ022360	TMSA 84038	Muzambai, Tanzania
Phrynobatrachus natalensis	DQ022332†	DQ022361	AC 1118	Beira, Mozambique
Phrynodon sp.	DQ022337†	–	ZFMK 69283	Mt. Nlonako, Cameroon
Poyntonia paludicola	DQ022338	DQ022365	ES 175	Steenbras, South Africa
Ptychadena mascareniensis	DQ022339	–	Det AC	Beira, Mozambique
Pyxicephalus adspersus	DQ022340	–	Det ES	Midrand, South Africa
Pyxicephalus cf. *edulis*	–	DQ022366	AC 1147	Bloemfontein, South Africa
Pyxicephalus edulis	DQ022341	–	Det AC	Beira, Mozambique
Schoutedenella sylvatica	DQ022314	DQ022349	TMSA 84161	Nguti, Cameroon
Scotobleps gabonicus	DQ022315†	–	TMSA 84313	Nguti, Cameroon
Strongylopus grayii	DQ022342†	–	MA 10	Stellenbosch, South Africa
Strongylopus grayii	–	DQ022367	TMSA 84854	Sjonajona, South Africa

loci of a congeneric or putatively close relative, to form a composite terminal. Available phylogenetic information was used to avoid the generation of non-monophyletic terminals, at least to the level of resolution required in this analysis. Composite terminals were labeled at the highest inclusive taxonomic level. For example, the morphological data of *Breviceps rosei* were combined with data from both gene loci for *Callulina kreffti*, creating a composite terminal named Brevicipitinae. This approach depends on correctly identified sequences, which unfortunately cannot be verified unless a specimen voucher is included in the GenBank accession information, as is seldom the case (Table 4). Composite terminals are listed in Table 5.

Phylogenetic analysis

The choice of a single analysis algorithm should be made beforehand on philosophical grounds, and justified accordingly. Parsimony analysis (Kluge and Farris, 1969; Farris, 1983) using all available data (Kluge, 1989) is here considered the best method available (in terms of information content, robustness and accuracy), for analyzing morphological and molecular data simulta-

Table 4
Accession numbers of 12S rDNA and 16S rDNA sequences obtained from GenBank data libraries for inclusion in this study, and specimen voucher number, if available

Species	12S rDNA	Voucher	16S rDNA	Voucher
Afrana fuscigula	AF371231.1	MA 12	AY255096.1	MA 12
Afrixalus fornasinii	U22071.1	–	–	–
Afrixalus knysnae	–	–	AF215429.1	–
Amnirana galamensis	–	–	AY322303.1	–
Amolops cf. *ricketti*	AF205557.1	KR-2003	AF315149.1	–
Anhydrophryne rattrayi	–	–	AF215504.1	AC 1206
Arthroleptella landdrosia	AF330244.1	AC 1204	AY205276.1	AC 1204
Arthroleptides martiensseni	–	–	AF026373.1	–
Arthroleptis variablis	AF095343.1	–	AY322301.1	–
Astylosternus diadematus	–	–	AY341723.1	–
Aubria subsigillata	–	–	Y11975.1	MIAS16S
Cacosternum boettgeri	–	–	AF215414	–
Callulina kreffti	AY326068.1	TNHC 62491	AY326068.1	TNHC 62491
Chiromantis rufescens	AY341622.1	–	–	–
Chiromantis xerampelina	–	–	AF215348.1	–
Conraua goliath	–	–	AF215388.1	–
Euphlyctis cyanophlyctis	AF249015.1	–	AY014366.1	–
Heleophryne purcelli	AY364356.1	–	AF432230.1	–
Hemisus marmoratus	AY326070.1	TNHC 62489	AY326070.1	TNHC 62489
Hildebrandtia ornata	–	–	AF215402.1	–
Hoplobatrachus occipitalis	–	–	AF261263.1	–
Hyperolius marmoratus	U22064.1	–	AF215441.1	–
Kassina senegalensis	U22073.1	–	AF215445.1	–
Leptopelis natalensis	AY341626.1	–	AF215448.1	–
Limnonectes blythii	U66130.1	–	U66115.1	–
Mantella aurantiaca	X86243.1	–	AF215299.1	–
Mantidactylus femoralis	AF261238.1	–	AY324818.1	Ambre 929
Nannophrys ceylonensis	AF249016.1	–	AF215394.1	–
Nanorana parkeri	AF206110.1	JF 037	AY322283.1	–
Natalobatrachus bonebergi	AF215198.1	ZFMK 66443	AF215396.1	ZFMK 66443
Nesomantis thomasseti	X86254.1	–	AY330889.1	–
Pantherana pipiens	Y10945.1	–	Y10945.1	–
Philautus petersi	AF026349.1	–	–	–
Philautus surdus	–	–	AF458138.1	–
Phrynodon sp.	–	–	AF215400.1	–
Phrynoglossus laevis	U66138.1	–	AF215401.1	–
Phrynomantis sp.	AY326065.1	TNHC 61077	AY326065.1	TNHC 61077
Platymantis sp.	AY326061.1	JF 0131	–	–
Platymantis vitiensis	–	–	Y11978.1	–
Ptychadena anchiete	AF261249.1	–	AY517610.1	SL1 02
Ptychadena mascareniensis	–	–	AF215407.1	–
Pyxicephalus adspersus	–	–	AF215505.1	–
Scotobleps gabonicus	–	–	AF215341.1	–
Staurois latopalmatus	AY322327.1	–	AY322290.1	–
Tomopterna marmorata	AF371204.1	AC 1534	AY255084.1	AC 1534
Tomopterna tandyi	AF371162.1	AC 2006	AF436071.2	AC 2006
Trichobatrachus robustus	AY322304.1	–	AY322274.1	–

neously. The present study incorporates three different data sets: morphology and two gene regions. There are advantages and disadvantages of combining data sets obtained from different sources for analysis (Kluge, 1989; Bull et al., 1993; De Queiroz, 1993; Eernisse and Kluge, 1993; Kluge and Wolf, 1993; Chippindale and Wiens, 1994; De Queiroz et al., 1995; Miyamoto and Fitch, 1995; Huelsenbeck et al., 1996; Nixon and Carpenter, 1996; Page, 1996). However, the method of "total evidence" or "simultaneous analysis" is given primacy in this contribution on the grounds that it maximizes explanatory power, in addition to allowing the emergence of secondary signals (Kluge, 1989; Kluge and Wolf, 1993; Chippindale and Wiens, 1994; Nixon and Carpenter, 1996; Cognato and Vogler, 2001).

Sequence alignment is a problematic procedure, both philosophically and empirically (Wheeler, 1994; Wheeler et al., 1995; Lutzoni et al., 2000; Hertwig et al., 2004). Substantial length variation was found to occur in unaligned sequences of the chosen gene loci across

Table 5

Data sets used to construct composite terminals when data could not be obtained from all three data sources for the same species. Terminals are labeled at the most inclusive taxonomic level, assuming monophyly thereof, and contingent on correct identification of GenBank sequences. *Phrybat.* = *Phrynobatrachus*.

Terminal taxon	Morphology	12S rDNA	16S rDNA
Afrixalus	*A. fornasinii* Bianconi, 1849	*A. fornasinii* Bianconi, 1849	*A. knysnae* (Loveridge, 1954)
Arthroleptis	*A. stenodactylus* Pfeffer, 1893	*A. tanneri* Grandison, 1983	*A. stenodactylus* Grandison, 1983
Brevicipitinae	*Breviceps rosei* Power, 1926	*Callulina kreffti* Neiden, 1911	*Callulina kreffti* Neiden, 1911
Cardioglossa	*C. escalaerae* (Boulenger, 1903)	*C. leucomystax* (Boulenger, 1903)	*C. leucomystax* (Boulenger, 1903)
Chiromantis	*C. xerampelina* Peters, 1854	*C. rufescens* (Günther, 1869)	*C. xerampelina* Peters, 1854
Leptodactylodon	*L. ventrimarmoratus* (Boulenger, 1904)	*L. mertensi* Perret, 1959	*L. mertensi* Perret, 1959
Leptopelis	*L. mossambicus* Poynton, 1985	*L. natalensis* (Smith, 1849)	*L. natalensis* (Smith, 1849)
Philautus	*P. surdus* (Peters, 1863)	*P. petersi* (Boulenger, 1900)	*P. surdus* (Peters, 1863)
Phrybat. plicatus	*P. plicatus* Günther, 1858	*P. auritus* Boulenger, 1900	*P. auritus* Boulenger, 1900
Phrynodon	*P. sandersoni* Parker, 1935	*Phrynodon* sp.	*Phrynodon* sp.
Phrynomantis	*P. bifasciatus* (Smith, 1847)	*Phrynomantis* sp.	*Phrynomantis* sp.
Platymantis	*P. corrugatus* (A. Duméril, 1853)	*Platymantis* sp.	*P. vitiensis* (Girard, 1853)
Schoutedenella	*S. taeniata* Boulenger, 1906	*S. sylvatica* Laurent, 1954	*S. sylvatica* Laurent, 1954
Sooglossidae	*Sooglossus sechellensis* (Boettger, 1896)	*Nesomantis thomasseti* Blgr., 1909	*Nesomantis thomasseti* Blgr., 1909
Staurois	*S. natator* (Günther, 1859)	*S. latopalmatus* (Boulenger, 1887)	*S. latopalmatus* (Boulenger, 1887)

Ranoidea, greatly reducing the confidence that can be placed in the homology statements inferred from fixed multiple alignments of these data. The conventional approach to this problem is to exclude such variable regions, which constitutes a loss of phylogenetic information, as well as being arbitrary and unscientific (Gatesy et al., 1993). An alternative to fixed alignments, used here, is the direct optimization (DO) method of Wheeler (1996).

Sensitivity analysis

Character weighting remains controversial. Many phylogenetic practitioners adopt the position that all characters should be weighted equally in phylogenetic analysis, as this is the least assumption-laden approach (Kluge, 1989, 1997; Siebert, 1992; Brower, 2000). Differential weighting, involving the use of multiple cost ratios (parameter sets) can, however, be used to assess the extent to which different analysis parameters affect phylogenetic conclusions, termed "sensitivity analysis" (*sensu* Fitch and Smith, 1983; Wheeler, 1995). Perturbing the data by weighting facilitates the differentiation of robust relationships, supported under a range of parameter values, from unstable relationships, which appear only in association with particular values. This approach is widely considered an essential part of phylogenetic reconstruction, insofar as it avoids the adoption of hypotheses supported only by unique combinations of parameter values (Giribet and Wheeler, 1999; Giribet and Ribera, 2000; Hertwig et al., 2004), but has been criticized on philosophical grounds (Grant and Kluge, 2003). In the present study, the result of simultaneous analysis with equal weights was adopted as the preferred topology, as it contains the fewest assumptions. However, the effects of differential weighting were also explored, to assess whether it is possible, under any different analysis parameter sets, to obtain the hypothesized clades represented in the new classification of Dubois (1987, 1992). If the various clades present in the new classification appear under few or none of the analysis parameters assessed, then their validity can be doubted in light of the data presented in this study.

For the sensitivity analyses conducted here, a parameter space of two analytical variables was explored, viz., insertion: deletion cost ratio (gap cost, G), and transition: transversion cost ratio (change cost, C), as in Wheeler (1995) and Giribet and Ribera (2000). When the transition to transversion cost ratio was set to a value other than unity, the insertion to deletion cost ratio was set according to the cost of transversions. When the costs of gaps to transversions to transitions are set to unity, the analyses are equivalent to those conduced under equal weights. Weighting was implemented by invoking Sankoff-style step-matrices (Sankoff, 1975). In total, 12 parameter sets were analyzed, 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. These parameter sets were analyzed 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 (C), or equal to the gap cost (G). Twenty simultaneous analyses of molecular and morphological data were conducted, as four analyses use the same parameter values, in POY version 3.0.11 (Wheeler et al., 2003).

The morphological data were analyzed separately, merely to indicate what relationships are suggested by the morphological data set in isolation. Two analyses were conducted, the first implementing the parsimony ratchet (Nixon, 1999) in NONA version 2.0. (Goloboff, 1999), with all characters weighted equally. Secondly, morphological data were subjected to implied weighting, using the mildest standard concavity function of 6, in PIWE (Goloboff, 1993). Branch support, or decay indices (Bremer, 1988, 1994; Donoghue et al., 1992) up to 30 steps, were calculated in NONA for the simultaneous analysis with equal weights, and for the separate analysis of morphological data under equal weights. Jackknife resampling for the simultaneous analysis with equal weights was performed in TNT (Goloboff et al., 2004).

Character optimization

Characters were optimized onto the topology obtained from the simultaneous analysis with equal weights, using WinClada version 1.00.08 (Nixon, 2002). Only unambiguously optimized characters are discussed. In the present study, a distinction is recognized between synapomorphies that occur only once in the tree, in a single clade only, termed "unique" here, and those that occur in more than one clade in the tree, termed "non-unique", in order to provide more information regarding their relative homoplasy in the discussion. However, stating that a character state is unique to a clade does not imply that it occurs in all taxa, as reversals and transformations to other states may be present within that clade, as in the usage by Kluge and Farris (1969). All synapomorphic character states that support a clade are reported, regardless of their tendency for reversal or transformation within that clade. Terminology regarding characters and their states follows Ford (1990), e.g., c2:1 refers to state 1 of character 2.

Results

The morphological data matrix collated in this study is presented in Appendix 4. The single most parsimonious tree obtained from a separate analysis of the morphological data with equal weights is presented in Fig. 1. This tree is well resolved, but contains some questionable groupings. For example, Mantellidae is non-monophyletic, and *Batrachylodes* is isolated from other ranids. Some questionable placements might be expected in any large phylogenetic analysis where sampling is incomplete, because particular taxa required to stabilize relationships may be missing.

Cacosterninae are identified as the basal clade of Ranoidea in this topology, more distal from Ranidae than the hyperoliid–arthroleptid lineage, with *Ericabatrachus* as the basal cacosternine. This may reflect the high proportion of plesiomorphic and loss character states present in the morphology of this group. The single tree topology obtained by analysis of the separate morphological data under implied weighting and using the weakest standard concavity function of 6, is presented in Fig. 2. In this topology, Cacosterninae are placed as sister to Phrynobatrachinae, in turn forming a sister clade to the remaining ranids.

The results of the sensitivity analyses of the morphological and molecular data sets analyzed simultaneously varied according to the analysis parameters used, although the content of major clades retrieved was fairly consistent and generally congruent with that supported by the separate analyses of morphology. This was especially evident in well-sampled taxonomic groups, such as the petropedetines. The most commonly retrieved relationships concern pairs of sister species, or individual clades, such as Phrynobatrachinae or Hyperoliidae. However, there was much variation between the relative placements of these major clades.

A graphical summary of the results of the sensitivity analyses is presented in the gallery of analysis space plots (Fig. 3). This demonstrates the retrieval of putative clades, as advocated in the current classification or previous literature, as monophyletic or not, under particular analysis parameters. Clades or subfamilies that were consistently retrieved as monophyletic (Ptychadeninae, Tomopterninae, Rhacophoridae) are not illustrated in Fig. 3, which visually differentiates groups retrieved as monophyletic only under particular parameter sets from those retrieved as monophyletic more generally. Individual results of each of the 20 sensitivity analyses have been supplied as Supplementary material. See http://www.blackwell-synergy.com, or contact the author.

The topology obtained from the simultaneous analysis of molecular and morphological data with equal weights (111) is presented in Fig. 4. This topology is more similar to the result of the separate analysis of morphology under weak implied weighting (Fig. 2) than it is to the analysis of morphology under equal weights (Fig. 1), and does not displays the questionable relationships mentioned above for the equal weights morphology analysis (Fig. 1). This may be interpreted as demonstrating the positive synergistic effect of analyzing both datatypes simultaneously. Lack of resolution of the molecular phylogeny in isolation (results not shown) may partly be due to the choice of gene loci used (e.g., Hertwig et al., 2004). The small quantity of molecular data included (~1 kb), although insufficient to adequately resolve relationships between the disparate ranoid taxa included here in isolation, appears to have been important for placing individual morphologically divergent taxa, which sometimes displayed questionable placements based on the analysis of morphological data alone, e.g., the two included Mantellidae, Ptychadeninae and *Strongylopus*.

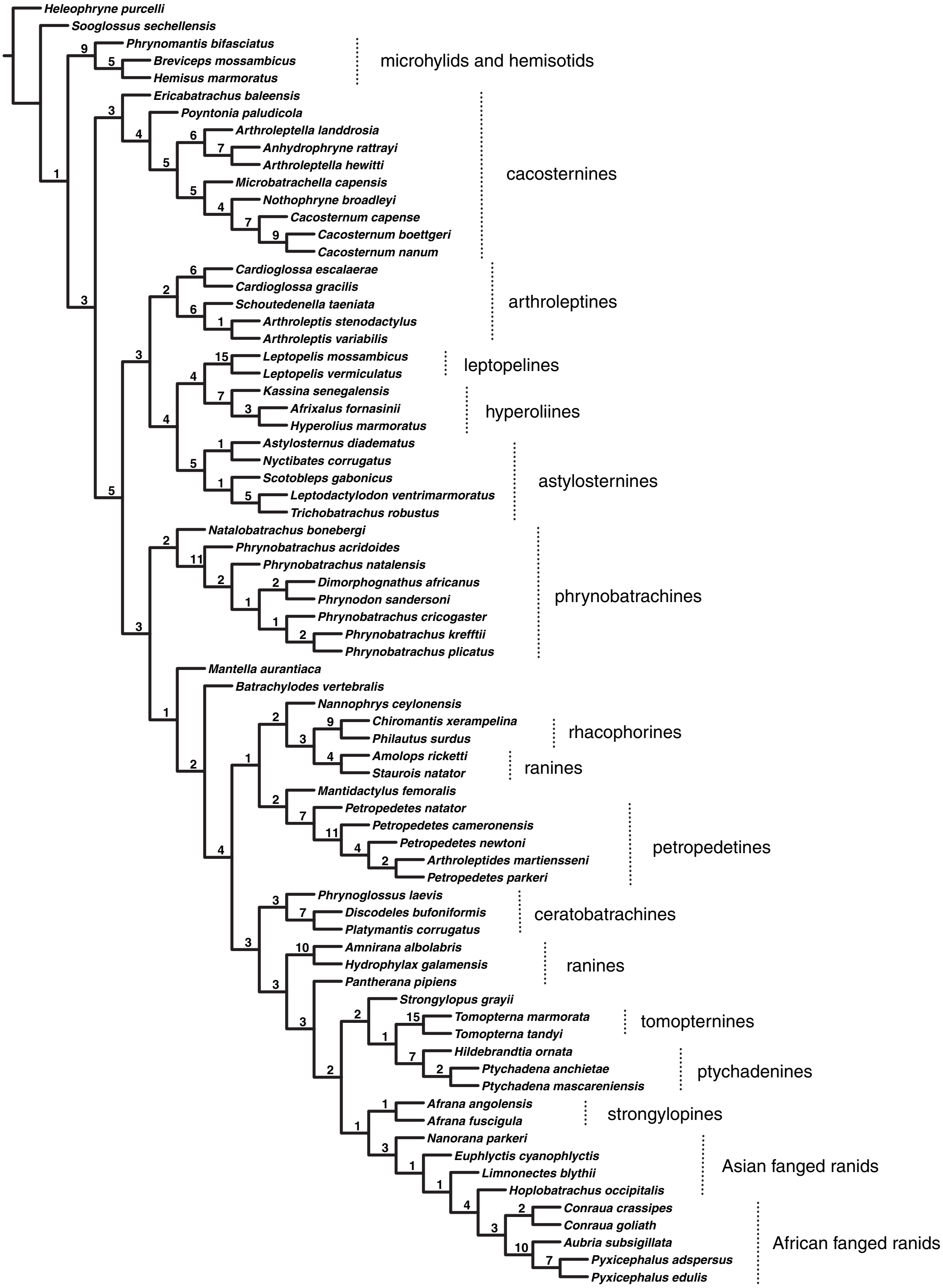

Fig. 1. Single most parsimonious tree obtained from separate analysis of morphological data, under equal weights. Length = 1433 steps, CI = 0.21, RI = 0.62. Branch support values provided to the left of each node.

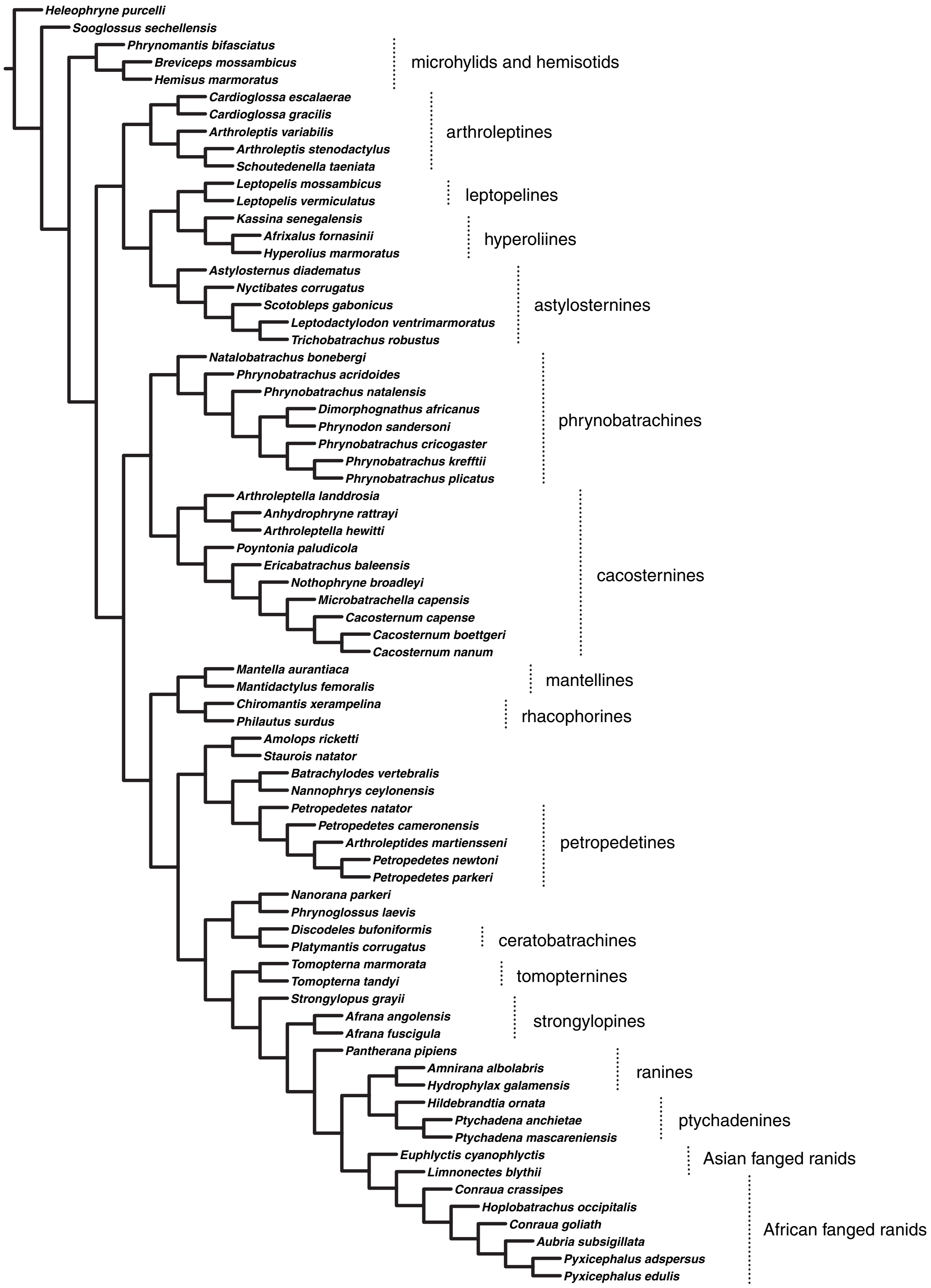

Fig. 2. Single most parsimonious tree obtained from separate analysis of morphological data, under implied weights with a concavity function (k) of 6. Total fit = 1002.1 (33%).

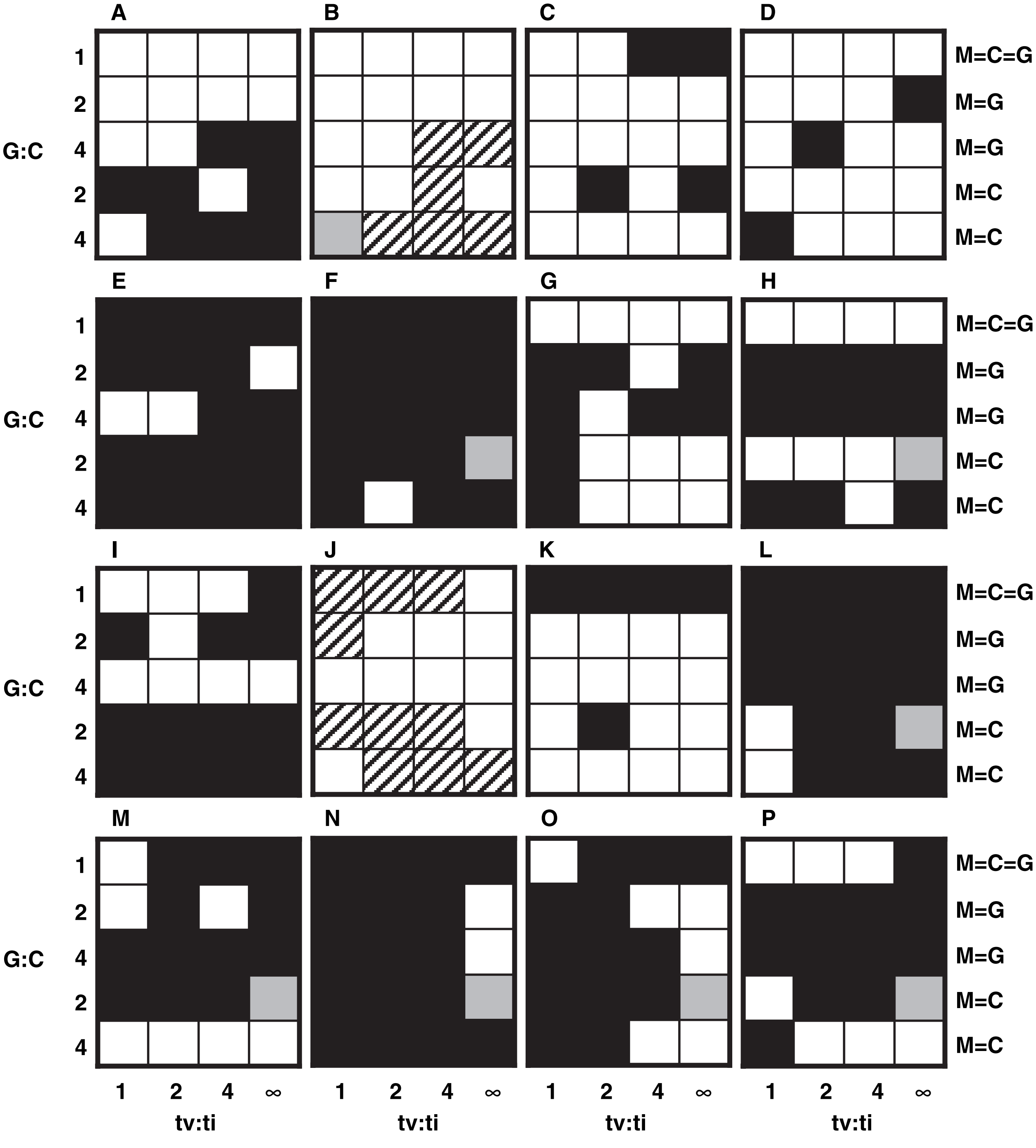

Fig. 3. Gallery of analysis space plots for selected groups proposed in the literature, as reflected in the sensitivity analyses conducted in the present study. White = monophyletic, gray = unresolved, black = non-monophyletic, shaded = minor alternative rearrangements as specified below. Consistently monophyletic and consistently paraphyletic groups not illustrated. M = morphology, C = change cost, G = gap cost, tv = transversions, ti = transitions, ∞ represents infinity. (A) *Hemisus* within monophyletic Microhylidae clade. (B) (Brevicipitinae + *Hemisus*); in all shaded cells (Sooglossidae + *Hemisus*) was retrieved within the clade containing all included microhylids. (C) All included Hyperoliidae and Arthroleptidae. (D) (Astylosterninae + Arthroleptinae), i.e., Arthroleptidae s.l. (E) (((Hyperoliinae + Leptopelinae) Astylosterninae) Arthroleptinae). (F) Ranidae excluding Mantellinae and Rhacophorinae. (G) (Mantellinae + Rhacophorinae). (H) (*Amnirana* + *Hydrophylax*), *Pantherana* and (*Amolops* + *Staurois*). (I) (*Phrynoglossus* (*Discodeles* + *Platymantis*)). (J) Fanged ranids, i.e., (*Pyxicephalus*, *Aubria*, *Conraua*, *Limnonectes*, *Euphlyctis*, *Hoplobatrachus*, *Nanorana* and *Nannophrys*); shaded cells denote the same clade excluding *Nannophrys* as monophyletic. (K) (*Pantherana* (*Amnirana* + *Hydrophylax*)). (L) “Petropedetidae”. (M) (Phrynobatrachinae + Cacosterninae). (N) (Tomopterninae + Cacosterninae). (O) (Cacosterninae + Tomopterninae + Phrynobatrachinae). (P) African clade, i.e., ((*Strongylopus* + *Afrana*) + Tomopterninae + Cacosterninae + Phrynobatrachinae).

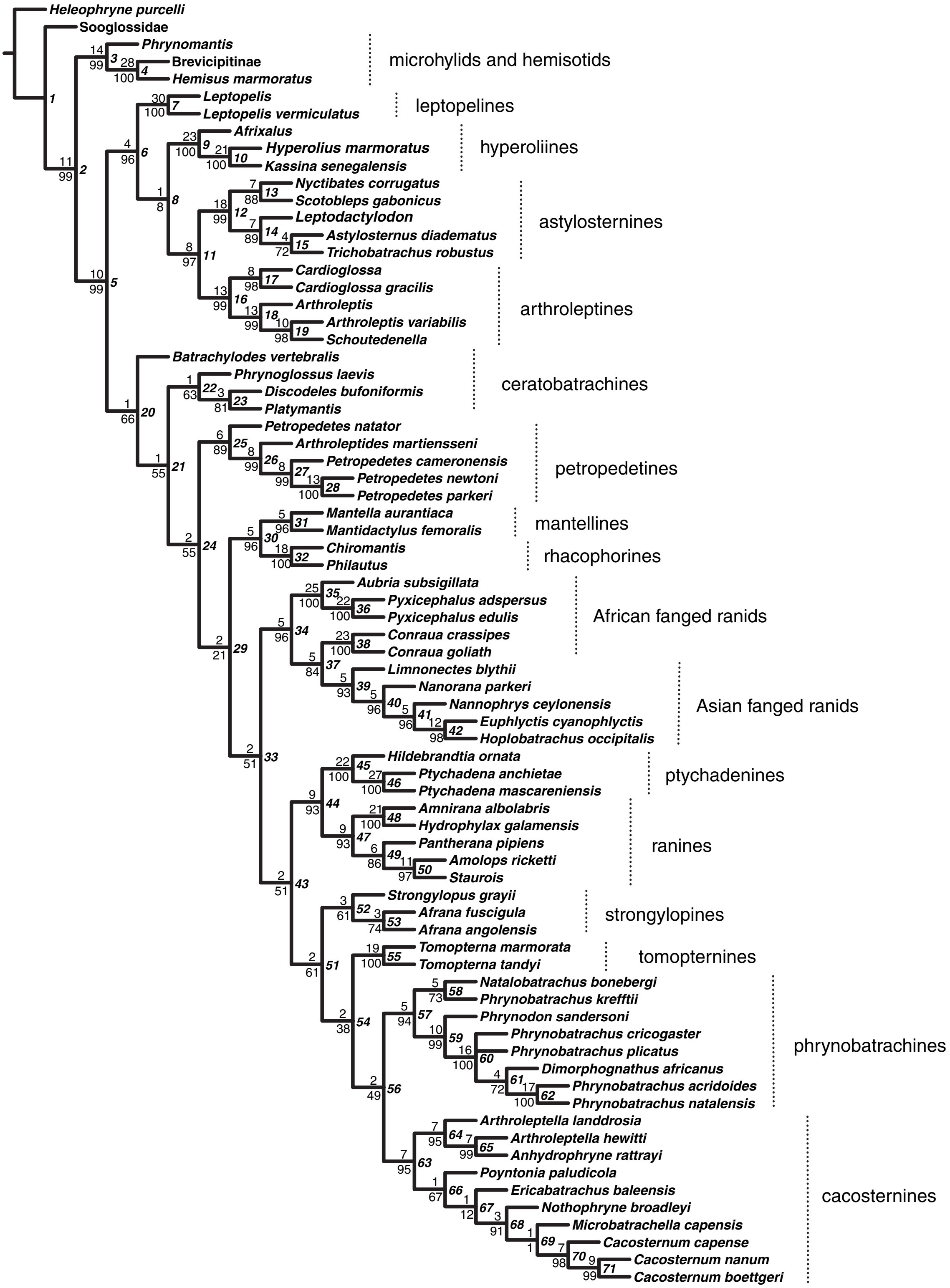

Fig. 4. Strict consensus of two equally parsimonious trees obtained from the simultaneous analysis of all morphological and molecular data, utilizing direct optimization under parameter set 111, representing an equally weighted total evidence hypothesis. Total length: 11 894 steps, morphological matrix length: 1550, CI = 0.24, RI = 0.51. Node numbers, provided to the right of each node in bold italic, correspond to the apomorphy list (Appendix 5). Branch support indices provided to the left of and above each node, whereas jackknife percentage provided to the left of and below each node.

Figure 4 demonstrates that while the major clades are reasonably strongly supported, as indicated by their relatively high branch support values and jackknife percentages, internal nodes of the tree (between clades) within Ranidae are generally weakly supported, suggesting that more taxa should be included in future studies.

The discussion that follows focuses on each clade in turn, and highlights novel placements obtained in the analyses. A brief summary of the taxonomic history, focusing particularly on the putative relationships in each group, is also presented. Unique morphological synapomorphies identified in the simultaneous analysis with equal weights (Fig. 4) are also discussed for each major clade. All unambiguously optimized apomorphic character states present in the strict consensus tree are listed in Appendix 5. These may reverse in the clade in question, and may also be present in other clades. Taxonomic emendations are implemented where the supporting evidence is discussed, and summarized in Appendix 6. An updated classification of Ranidae, incorporating changes made in the present study and those made by Dubois (2003), is provided in Appendix 7.

Discussion

Microhylidae and Hemisotidae

The microhylid lineage was placed basal in the topology obtained by simultaneous analysis with equal weights, and strongly supported (node 3 on Fig. 4, jackknife percentage of 99, branch support of 14). This placement is consistent with the views of Laurent (1940) regarding its position in Ranoidea, and with the perception of superfamily Microhyloidea by Dubois (1987). Little else can be deduced from the analysis regarding this diverse lineage, on account of the limited taxonomic sample. Nevertheless, the analysis does shed light on the phylogenetic position of *Hemisus*.

Noble (1931) regarded *Hemisus* as a microhylid, but Parker (1934) excluded *Hemisus* from his seminal monograph of the family Microhylidae, as De Villiers, 1933, p. 257) had pronounced it "quite definitely a terrestrial Ranid", without presenting supporting arguments. Laurent (1980) subsequently elevated Hemisotidae to the rank of family. Recent molecular and morphological work (Blommers-Schlösser, 1993; Wu, 1994; Emerson et al., 2000a) suggested that *Hemisus* should be regarded as a brevicipitine microhylid, a group which Wu (1994) considered worthy of familial status as "Brevicipitidae". Channing (1995) and Van Dijk (2001) were unconvinced that *Hemisus* should be classified with Microhylidae.

Hemisotidae were also recently allied to Hyperoliidae. In an analysis of partial 16S rDNA sequence data Vences (1999) found *Hemisus* to be more closely related to Astylosterninae and Hyperoliidae than to Microhylidae. Recently, Haas (2003) found *Hemisus* to be sister to Hyperoliidae on the basis of predominantly larval characters, with Microhylidae sister to (*Hemisus* + Hyperoliidae). Chromosome data from Morescalchi (1973, 1981) and Bogart and Tandy (1981) show that *Breviceps*, *Hemisus* and many Hyperoliidae have 12 pairs of chromosomes ($2n = 24$), whereas the arthroleptid lineage shows many presumably derived states (see Character 177), thus offering no further clarification of this point.

Representatives of the above-mentioned clades, all previously suggested to be related to *Hemisus*, were included in the present study. The results of the present analysis are unequivocal on this issue: the microhylid lineage (*Phrynomantis* (*Hemisus* + Brevicipitinae)) was retrieved under the majority of analytical parameters (Fig. 3A). When this microhylid lineage was not retrieved, this was due to *Phrynomantis* failing to group as sister to (*Hemisus* + Brevicipitinae), as in Fig. 3A, or Sooglossidae moving deep into the microhylid clade, as sister to *Hemisus* (all non-monophyletic shaded occurrences in Fig. 3B). Interestingly, the position of *Hemisus* as sister to Sooglossidae is the exact phylogenetic position postulated by Biju and Bossuyt (2003) for their new genus *Nasikabatrachus* Biju and Bossuyt (2003). On the grounds of its phylogenetic placement next to the enigmatic Sooglossidae, these authors erected a new "family" Nasikabatrachidae Biju and Bossuyt (2003) to accommodate this genus. However, the limited morphological data presented in their contribution strongly suggests that *Nasikabatrachus* is possibly a new Indian genus of hemisotid. Additional specimens of *Nasikabatrachus*, besides the single female holotype, are needed to clarify its phylogenetic position and taxonomic status as a monotypic family.

The exact phylogenetic relationship of *Hemisus* to the microhylids in general, as depicted in Fig. 4, may not be strictly correct, due to the sparse taxon sampling of this diverse lineage. If brevicipitine microhylids are not monophyletic with the remaining microhylids (as initially suggested by Wu (1994) and retrieved here in sensitivity analyses in which *Phrynomantis* did not group with Brevicipitines and *Hemisus*), then the above discussion pertaining to the putative microhylid–*Hemisus* relationship would refer specifically to a brevicipitine–*Hemisus* relationship. None of the sensitivity analyses presented in the present study retrieved any relationship between *Hemisus* and either Arthroleptidae or Hyperoliidae.

Among the diverse sample of ranoids examined in the present study, four unique morphological synapomorphies supported the placement of *Hemisus* with the microhylids: the presence of posterior palatial folds (Character 127: 1); well developed lateral processes of the mentomeckelian bone (Character 53: 2); absence of the median branch of the anterior process of the hyale

(Character 83: 4); and long bronchial processes of the cricoid, ramifying through the lungs (Character 100: 1). Other non-unique synapomorphies of this clade include: acutely anterolaterally oriented transverse processes of the eighth vertebra (Character 3: 2, which transforms in *Hemisus*); laterally oriented sacral diapophyses (Character 16: 1, reversing in *Breviceps*); absence of maxillary and premaxillary teeth (Character 45: 1); short or reduced parasphenoid alae (Character 60: 1, also occurring in Hyperoliidae and some Cacosterninae); small, thin, triangular or club-shaped nasals (Character 64: 2); forward angling of the *crista parotica* (Character 68: 1); reduced or absent *pars facialis* of the maxilla (Character 74: 2); absence of the esophageal process of the cricoid (Character 99: 1); and absence of the *cartilago sesamoides* (Character 110: 1). Many of these non-unique synapomorphies also occur in some Hyperoliidae and Arthroleptidae. Regardless of how convincing the above-mentioned unique synapomorphies may seem in allying the microhylids and *Hemisus*, Haas (2003) also found convincing synapomorphies from larval morphology that rather group Hyperoliidae and *Hemisus*. However, many of these character states were also found in the microhylids in Haas' study. Furthermore, Haas scored the gular gland as present in *Hemisus* (see discussion of Character 136 in Appendix 2), which would have strongly influenced the outcome of his analysis towards (*Hemisus* + Hyperoliidae). This state is here scored as unique to Hyperoliidae.

Van Dijk (2001) argued that the many morphological differences between *Hemisus* and *Breviceps* preclude a relationship between these taxa. This argument is based on the presence of many individually aberrant states in each genus, both of which burrow, but in distinctly different ways. In *Hemisus*, burrowing is effected forwards using the snout, whereas in *Breviceps*, burrowing is effected backwards using the feet (Wager, 1965; Van Dijk, 1971). Most of the divergent features mentioned by Van Dijk (2001) were examined as potential character states in the present study, but found to be autapomorphic for either *Hemisus* or *Breviceps*, and therefore uninformative regarding the relationships of either.

The absence of a microhylid-type tadpole (Orton's (1957) Type II) in *Hemisus* must be viewed as an unlikely reversal, according to the present hypothesis of relationship. However, if brevicipitines are not sister to all other microhylids and *Hemisus* is sister to brevicipitines, then the absence of an Orton Type II tadpole in *Hemisus* does not require special explanation. Rather, it would suggest that the "microhylid" tadpole may have evolved at least twice, once in brevicipitines and once in the rest of the microhylids. These questions can only be addressed by developmental studies of microhylid-type larvae. Tadpole characters were not included in the present study, nor was adult osteology included in Haas' (2003) work. Furthermore, Haas' study was conducted at the level of Anura, whereas the present study was conducted at the level of Ranoidea, so there is a vast disparity in the taxon sets examined, preventing direct comparison between the results of these two studies. The inclusion of larval characters could potentially place *Hemisus* at the base of the microhylid clade, or even outside it altogether. Combining the osteological, morphological, larval and sequence data sets accumulated to date may finally determine the true affinities of *Hemisus*, perhaps also of *Nasikabatrachus*.

There is no doubt that Hyperoliidae and Arthroleptidae, with which *Hemisus* has been allied by Vences (1999) and Haas (2003), are all relatively basal in the ranoid lineage as a whole, as are the microhylids. As in the analysis of Ford (1990), no Astylosterninae were included in Haas' (2003) analysis. Relationships at the base of Ranoidea remain uncertain, but an association between the brevicipitine microhylids, *Hemisus* and the hyperoliid–arthroleptid lineage appears probable. However, a close relationship between other non-brevicipitine microhylids and the arthroleptids cannot at present be dismissed, nor can the possibility that all of these taxa form one major lineage, referable to as superfamily Microhyloidea.

Arthroleptidae and Hyperoliidae

Dubois (1981) reinstated the family Arthroleptidae to accommodate two subfamilies, Astylosterninae and Arthroleptinae, historically placed in either Ranidae or Hyperoliidae. Dubois (1987) subsequently expanded the family by transferring the hyperoliids to Arthroleptidae, which has nomenclatural priority over Hyperoliidae. Dubois (1992) again revised his opinion, elevating Arthroleptidae, Astylosternidae and Hyperoliidae to family rank, perhaps to avoid the problems associated with possible paraphyly of Astylosterninae (Frost, 2004). Whereas most workers accept the status of Hyperoliidae, the status of Arthroleptidae is highly contentious. Many workers disagree regarding familial status for even a conservative Arthroleptidae, containing Astylosterninae as a subfamily. For example, J.D. Lynch (in Frost, 1985, p. 14) commented that, "the recognition of this family is premature given that no phylogenetic justification or diagnosis has been presented". Ford and Cannatella (1993) treated Arthroleptidae as a "metataxon", as no unique synapomorphies of the group had been identified at the time. Grant et al. (1997, p. 16) stated 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) consistently rejected the inclusion of the petropedetines with the arthroleptids.

Laurent's views were vindicated by the sensitivity analyses presented here, none of which suggested a close relationship between any of the three identified clades of Petropedetinae with either Arthroleptinae or Astylosterninae. Furthermore, none of the sensitivity analyses retrieved a sister-group relationship between Hyperoliidae and *Hemisus* (cf. Vences, 1999; Haas, 2003; discussed in the section on the microhylids and *Hemisus* above). Hyperoliidae were instead found to be closely related to Arthroleptidae.

Only four out of 20 sets of analysis parameters investigated failed to retrieve a monophyletic clade containing all included arthroleptines, astylosternines, leptopelines and hyperoliines (Fig. 3C). In all four cases, two clades were retrieved, viz., (Hyperoliinae + Leptopelinae) and (Arthroleptidae + Astylosterninae), and placed in a pectinate arrangement at the base of Ranoidea, with Arthroleptidae s.l. placed sister to Ranidae, in turn forming a sister group to (Hyperoliinae + Leptopelinae).

Laurent (1951) noted that *Leptopelis* has affinities with Astylosterninae. However, in no cases did the two exemplars of *Leptopelis* group inside Astylosterninae, suggesting that these are separate clades. In all sensitivity analyses, both arthroleptid subfamilies were found to be monophyletic and mutually exclusive, not containing *Leptopelis* or other genera therein. Seventeen of the 20 sensitivity analyses could not refute monophyly of (Arthroleptinae + Astylosterninae) either (Fig. 3D). In the three analyses that did, this was caused by the inclusion of (Hyperoliinae + Leptopelinae) therein, as sister to Astylosterninae (Fig. 3E).

Recent molecular studies placed *Leptopelis* outside Hyperoliidae (Vences, 1999; Emerson et al., 2000a). However, in the present study, *Leptopelis* was placed sister to the other included Hyperoliinae in the separate analyses of morphology, and in all except one of the sensitivity analyses. The exception was the simultaneous analysis with equal weights (Fig. 4), which placed *Leptopelis* basal to the entire hyperoliid–arthroleptid lineage, as sister-group of the remaining hyperoliid and arthroleptid clade, although this was weakly supported. This result implies that if *Leptopelis* is retained as a hyperoliid, then Arthroleptidae is embedded in Hyperoliidae, and this monophyletic clade should take the older familial name Arthroleptidae (as advocated by Dubois, 1987). However, an equally plausible and, indeed, preferable alternative is to elevate Leptopelidae **New Rank**. In so doing, Hyperoliidae can be retained as distinct from Arthroleptidae s.l., because each of these lineages is monophyletic. However, further analysis of this issue, based on morphological and molecular data, and including a more representative sample of hyperoliid taxa, is required before deciding on the appropriate rank of Astylosterninae, which are presently retained as a subfamily of Arthroleptidae s.l.

Past studies of Hyperoliidae and Arthroleptidae (Liem, 1970; Laurent, 1980, 1986; Drewes, 1984; Channing, 1989) suggested the following synapomorphies for Hyperoliidae (Ford and Cannatella, 1993): presence of the *musculus dentomentalis*, claw-shaped terminal phalanges, vertical pupils and a cartilaginous sternum; and absence of nuptial pads and the posterolateral process of the hyoid. Muscular characters have not been examined for Arthroleptinae or Astylosterninae, but it is likely that some of the reported muscular synapomorphies of Hyperoliidae may occur more widely in Arthroleptidae. The absence of nuptial pads (Character 132: 0) and presence of a cartilaginous metasternum (Character 30: 0) were both shown to be plesiomorphic states in the present analysis. Carpal (Character 102) and tarsal (Character 103) states, postulated to be synapomorphic for some of these taxa (Laurent, 1986), were found to be more variable in these groups than previously thought, and their significance could not be adequately determined. Claw-shaped terminal phalanges (Character 118: 2 and Character 119: 3) also occur in many Raninae. Indeed, the only state of this phalangeal character unique to this lineage is that in which the tip is detached from the body of the terminal phalanx and curves sharply downwards (Character 119: 6). This state occurs in only three Astylosterninae, and is distinctly different from the "claw shaped" protruding phalanges recorded in the literature for *Ptychadena* (Parker, 1936; Perret, 1966). As noted by Ford and Cannatella (1993), the definition of this character is notoriously difficult, has varied widely in the literature, and requires standardization.

One unique morphological synapomorphy for the hyperoliid–arthroleptid lineage (node 6 on Fig. 4) was identified in this analysis, i.e., the absence of posterior lateral processes of the hyoid (Character 93: 2), although these processes are present in most Astylosterninae (absent only in *Astylosternus* and reduced in *Nyctibates*) and variable among other Hyperoliidae not included here (Drewes, 1984). The condition of vertical pupils (Character 146: 3), is almost unique (occurring elsewhere in *Hemisus*), but does not occur in Arthroleptinae or *Hyperolius*.

Traditional Ranidae, including Mantellinae and Rhacophorinae

The ranks of the mantelline and rhacophorine lineages are contentious. Both groups have repeatedly been recognized as separate families, or as subfamilies of traditional Ranidae. Laurent (1951) suggested that rhacophorines were ranids, and objected to their recognition at family rank. The osteological work of Ford (1990) demonstrated that recognition of either Mantellidae or Rhacophoridae renders Ranidae paraphyletic. Blommers-Schlösser and Blanc (1991) recognized both Rhacophoridae and Mantellidae. Duellman (1993) followed Dubois (1992) in recognizing Mantellidae at family level, but not Dubois (1987) in returning Rhacophoridae to a subfamily of traditional Ranidae. Duellman (1993) followed Channing (1989) instead, who recognized Rhacophoridae. Blommers-Schlösser (1993) returned the mantellines and rhacophorines to subfamilies of Ranidae s.l. More recently, Emerson et al. (2000a) demonstrated that Rhacophorinae and Mantellinae are sister taxa, embedded in Ranidae s.l., but both taxa continue to be recognized at familial level (e.g., Wilkinson and Drewes, 2000; Channing, 2001; Dubois, 2003; Frost, 2004).

In the present sensitivity analyses, Ranidae, defined to exclude rhacophorines and mantellines (but including petropedetines), was found to be paraphyletic in all but two analyses where these taxa grouped sister to Ranidae (Fig. 3F). Ranidae s.l., defined to include both groups (plus petropedetines), was always monophyletic (not shown in Fig. 3). These analyses again vindicate Laurent's (1951) contention that rhacophorines should be treated as a subfamily of Ranidae, and they are henceforth considered as such.

Laurent (1980, 1986) characterized Ranidae s.l. on the presence of a bony sternal style, the second distal carpal fused to other carpals, the second distal tarsal fused to other tarsals and the tongue notched posteriorly. Tyler (1971) suggested the presence of the *musculus cutaneus pectoris* as a possible synapomorphy of Ranidae s.l. Ford and Cannatella (1993) dismissed Laurent's (1986) tarsal and carpal characteristics, concluding that only the bony sternal style and notched tongue were synapomorphic for Ranidae s.l., but noted that the *musculus cutaneus pectoris* could be synapomorphic for the family. The simultaneous analysis with equal weights presented here demonstrated that the presence of the *musculus cutaneus pectoris* (Character 130: 2) is a unique morphological synapomorphy for Ranidae s.l. (node 20 on Fig. 4). This muscle is present in Mantellinae, although it is absent in Rhacophorinae and one species of *Phrynobatrachus* examined here. The metasternum as a narrow or broad bony stylus (Character 30: 1) is synapomorphic for Ranidae s.l. A narrower medial than lateral palatine process of the premaxilla (Character 46: 2 and state 3 derived from that) is a non-unique synapomorphy for Ranidae s.l., because state 2 also occurs in Arthroleptidae. The anterior margin of Presacral V being parallel to the posterior margins of this vertebra (Character 5: 1), which reverses in some African ranines, is another non-unique synapomorphy. A notched tongue (Character 126: 1) also occurs in Arthroleptidae, Hyperoliidae and *Phrynomantis*, and is not synapomorphic for Ranidae s.l.

Mantellinae and Rhacophorinae

A sister-group relationship between the Rhacophorinae and Mantellinae, previously demonstrated by Ford (1990), Blommers-Schlösser (1993) and Emerson et al. (2000a), was also retrieved in the present analysis (node 30 on Fig. 4). The two rhacophorine exemplars, *Chiromantis* and *Philautus*, formed a monophyletic group in all analyses. The two exemplar mantellines, *Mantidactylus* and *Mantella*, however, did not group together in the separate analysis of morphology with equal weights (Fig. 1), but did in all sensitivity analyses, which included molecular data. The monophyly of Mantellinae was previously questioned on the basis of morphological data (Daly et al., 1996), and it is debatable whether this has been satisfactorily demonstrated for the entire clade by published molecular studies (e.g., Richards and Moore, 1998; Richards et al., 2000).

The failure to consistently retrieve (Mantellinae + Rhacophorinae) in the sensitivity analyses presented here (Fig. 3G) was predominantly due to the movement of Rhacophorinae together with (*Amolops* + *Staurois*) under some extreme weighting parameters, or due to the affinity of Mantellinae for *Batrachylodes*, a taxon lacking molecular data in this study. The separation of Mantellinae from Rhacophorinae is probably an artifact of sampling too few exemplar taxa from these clades. The morphological data, analyzed separately, appear to be insufficient to unite (Mantellinae + Rhacophorinae), which were consistently retrieved as a clade only after the inclusion of sequence data. Clearly, Mantellinae and Rhacophorinae are both nested within Ranidae s.l.

Ford and Cannatella (1993) stated that if Hyperoliidae are not the sister-group of Rhacophorinae, as demonstrated in the present analyses, then the presence of the intercalary element must be synapomorphic for (Mantellinae + Rhacophorinae). Blommers-Schlösser (1993) and Glaw et al. (1998) identified two other potential synapomorphies of Mantellinae: presence of Y-shaped terminal phalanges and absence of a strong amplexus during mating (Duellman and Trueb, 1986). Y-shaped terminal phalanges, qualified by noting the presence of flattened oval flanges on the branches of the arms (Character 119: 4), were found to be uniquely synapomorphic for (Mantellinae + Rhacophorinae) in the present study. Weak amplexus (Character 174: 3) united the two mantelline exemplars included here, but has been justifiably criticized as a potential synapomorphy, because it requires a more precise definition (Daly et al., 1996). Other non-unique morphological synapomorphies for (Mantellinae + Rhacophorinae) identified here include: ilial crest 1/2 to 1 times the height of the ilium (Character 13: 1); roughly cylindrical sacral diapophyses (Character 15: 1); neopalatines touching the sphenethmoid but not meeting medially (Character

37: 0); zygomatic ramus of squamosal shorter than the otic ramus (Character 73: 2); and short posterolateral processes of the hyoid (Character 94: 1). However, all of these character states occur sporadically in many other clades in the present analysis, some reversing within (Mantellinae + Rhacophorinae). As such, none can be used to define (Mantellinae + Rhacophorinae). Further research must be conducted in order to identify morphological synapomorphies of this group.

Although a sister-group relationship between Mantellinae and Rhacophorinae has gained widespread acceptance, the relationship of this clade to other ranid taxa remains obscure. The sensitivity analyses presented here suggest that within Ranidae, the Asian genera *Batrachylodes*, *Nannophrys*, (*Platymantis* + *Discodeles*) and/or (*Amolops* + *Staurois*) are possibly the closest relatives to (Mantellinae + Rhacophorinae), from within the present taxon sample.

Dicroglossinae and Pyxicephalinae

Emerson and Berrigan (1993) and Emerson et al. (2000b), in their work on fanged ranid phylogeny, demonstrated that phylogenetic relationships in Dicroglossinae contradict the classification of Dubois (1987, 1992). Dicroglossinae was recently extensively modified by Dubois (2003), resulting in a more evolutionarily meaningful tribal classification. Many genera were transferred among the tribes, altering original assignments that rendered Dicroglossinae paraphyletic. In the new scheme, tribe Paini was transferred from Raninae to Dicroglossinae, and the former ranine genus *Chaparana* was assimilated into it, joining *Paa* and its subgenera. The former ranixaline genus *Nannophrys* was transferred to tribe Dicroglossini by Dubois (2003), a decision supported by a published molecular study (Kosuch et al., 2001). In addition, Occidozyginae was removed from Dicroglossinae.

Eight taxa included in Dicroglossinae (*sensu* Dubois, 1987, 1992) were included in the present study, viz., *Conraua*, *Discodeles*, *Euphlyctis*, *Hoplobatrachus*, *Limnonectes*, *Phrynoglossus* and *Platymantis*. Despite the recent improvements to its classification, the sensitivity analyses presented here still did not retrieve this newly construed Dicroglossinae (*sensu* Dubois, 2003) as monophyletic under any of the 20 analysis parameter sets investigated. In each analysis, Dicroglossinae comprised between two and three clades, due to the consistent inclusion of *Nanorana*, the consistent exclusion of the ceratobatrachine genera *Discodeles* and *Platymantis*, the exclusion of *Nannophrys* or the inclusion of the occidozygine genus *Phrynoglossus*, and finally, the inclusion of Pyxicephalinae.

The consistent inclusion of *Nanorana* in this clade necessitates the transfer of *Nanorana* to Dicroglossinae. The ceratobatrachine genera (*Platymantis* + *Discodeles*), were in no cases found to be related to the main dicroglossine clade, resulting in dicroglossine paraphyly in all sensitivity analyses. Either *Batrachylodes* or *Phrynoglossus* (the latter recently placed in Occidozyginae by Dubois, 2003) were usually placed sister to (*Platymantis* + *Discodeles*), as shown in (Fig. 3I), with *Nannophrys* frequently found to be the sister to these three taxa (five of the 10 instances shaded in Fig. 3J, when *Nannophrys* did not group with the main dicroglossine clade). In sensitivity analyses where (*Batrachylodes* (*Discodeles* + *Platymantis*)) was retrieved (11 out of 20 sensitivity analyses), *Phrynoglossus* usually grouped with the main clade of dicroglossines. However, when (*Phrynoglossus* (*Discodeles* + *Platymantis*)) was retrieved, *Batrachylodes* was usually placed nearby (with or without *Nannophrys*) or, rarely, isolated elsewhere in the topology (three instances), but never near the main clade of fanged ranids.

Nannophrys was excluded from Dicroglossinae in three of 20 sensitivity analyses, grouping instead with (*Amolops* + *Staurois*). In a further six of 20 sensitivity analyses, *Nannophrys* grouped with the ceratobatrachines (*Platymantis* + *Discodeles*) and *Batrachylodes*; occasionally this clade also included *Phrynoglossus*. Thus, in approximately half of all sensitivity analyses, *Nannophrys* did not group with the taxa with which it is currently classified, viz., (*Hoplobatrachus* + *Euphlyctis*). The simultaneous analysis with equal weights (Fig. 4) supports the conclusion that *Nannophrys* is indeed related to Dicroglossini ranids. However, it is notable that *Nannophrys* lacks the unique shared derived morphological character states of fanged ranids, as discussed later.

The uncertainty in the relative placement of these Asian ranid exemplars indicates a need to sample more extensively within these lineages. However, it is clear that Dicroglossinae (*sensu* Dubois, 2003) contains at least two unrelated clades. Although the results presented here indicate that ceratobatrachines may be relatively basal in traditional Ranidae, the main dicroglossine clade is unlikely to be basal (cf. Marmayou et al., 2000). Ceratobatrachini are therefore elevated to their own subfamily, Ceratobatrachinae Boulenger, 1884 **New Rank**.

The third major cause of Dicroglossinae paraphyly was the position of subfamily Pyxicephalinae, comprising (*Pyxicephalus* + *Aubria*). Pyxicephalinae were nested inside Dicroglossinae, comprising *Conraua*, *Euphlyctis*, *Hoplobatrachus*, *Limnonectes*, *Nannophrys* and *Nanorana* (Fig. 3J), in 15 of 20 sensitivity analyses. Pyxicephalinae grouped sister to Dicroglossinae in the remaining analyses. Pyxicephalinae were never associated with ranid clades other than Dicroglossinae, for example, grouping near the "African clade" (described and discussed later), as recently suggested by Van der Meijden et al. (2005). In all cases where (*Pyxicephalus* + *Aubria*) was embedded inside Dicroglossinae, the clade was placed sister to the African dicroglossine tribe Conrauini (genus *Conraua*). Four sensitivity analyses, including the simultaneous analysis with equal weights (Fig. 4), placed *Conraua* in a pectinate relationship between (*Euphlyctis*, *Hoplobatrachus*, *Limnonectes*, *Nannophrys*, *Nanorana*) and (*Pyxicephalus* + *Aubria*).

It is clear that the Asian fanged ranids are closely related to the African fanged ranids, and surprising, in retrospect, that this relationship has not been seriously considered in recent classifications, as it was strongly suggested by Clarke (1981), over two decades ago. Pyxicephalinae also display the specialized morphology and behavior noted by Emerson and Ward (1998) and Emerson et al. (2000b) to be characteristic of the southeast Asian fanged ranids, such as reversed sexual dimorphism, male territoriality and parental care, large bony odontoids on the lower jaw, and enlarged heads. Emerson et al. (2000b, p. 136) state that their "molecular analysis fully supports the finding from the previous morphological study [Emerson and Berrigan, 1993] that the fanged frogs constitute a monophyletic group". However, the sampling of Emerson and Berrigan (1993) and Emerson et al. (2000b) was insufficient to demonstrate this with respect to the African Pyxicephalinae. Similarly, Kosuch et al. (2001) retrieved a sister group relationship between *Conraua* and *Limnonectes* in their Neighbor Joining analysis of 16S rDNA, and a sister genus relationship between *Pyxicephalus* and *Limnonectes* in a similar analysis of 16S rDNA and 12S rDNA, yet disregarded these findings and invoked intercontinental dispersal to explain the distribution of African *Hoplobatrachus*. Haas (2003) also demonstrated a close relationship between *Pyxicephalus* and *Limnonectes*, based on larval characters. The present study suggests that a monophyletic clade of "fanged" ranids (*sensu* Emerson and Ward, 1998) exists, but that it includes both African and Asian members.

It is inconsistent to place (*Pyxicephalus* + *Aubria*) in a separate subfamily, Pyxicephalinae, from the Asian fanged ranids, Dicroglossinae, given that both subfamilies form part of the same monophyletic lineage, sharing many morphological and behavioral synapomorphies, and Pyxicephalinae is probably embedded in Dicroglossinae. In view of the fact that Pyxicephalinae is the older name, and Dicroglossinae is not firmly established in the literature, Dicroglossinae is hereby synonymized with Pyxicephalinae: Dicroglossinae Anderson, 1871 = Pyxicephalinae Bonaparte, 1850 **New Synonym**. The tribal structure of the former Dicroglossinae is retained under this new conception of Pyxicephalinae, pending further morphological investigation, and tribe Pyxicephalini Bonaparte, 1850 is resurrected to accommodate *Pyxicephalus* and *Aubria*.

The redefined Pyxicephalinae is strongly supported (node 34 on Fig. 4, jackknife percentage of 96, branch support of 5). Two morphological synapomorphies are unique to Pyxicephalinae: the presence of large mandibular odontoids (Character 50: 1, absent in *Nanorana* and *Nannophrys*); and overlap of all or most of the *crista parotica* and 1/4 to 1/2 of the prootic by the otic plate of the squamosal (Character 65: 1, transforming to state 2 in *Nanorana* and reversing to state 0 in *Nannophrys*). A predominantly ossified *crista parotica* (Character 67: 1, reversing in *Nannophrys*) is almost unique to Pyxicephalinae, but also occurs in the burrowing genus *Hildebrandtia*. Non-unique synapomorphies for the subfamily include: clavicle not touching the coracoid, separated by a long procoracoid cartilage (Character 22: 0, changing to small point contact, state 2, in some Asian taxa); a long anterior process of the vomer (Character 39: 1, which reverses independently to 0 in *Conraua goliath*, *Nanorana* and *Euphlyctis*); center, medial and lateral edges of the frontoparietal extending forward to a similar extent (Character 70: 1); stalk of the alary process of the hyale thickened and rounded (Character 84: 1); femoral granules absent or extremely faint (Character 141: 1); and basal row of subarticular tubercles of feet small, sharply defined, rounded to conical (Character 160: 2). A detailed study of the morphology of additional taxa of fanged ranids and characters not included in the present study, many of which are mentioned in Appendix 2, needs to be conducted. In particular, discovering the exact phylogenetic position of *Nannophrys* and *Phrynoglossus* relative to Pyxicephalinae and Ceratobatrachinae, and elucidating the exact content of the tribes within the newly construed Pyxicephalinae, requires further investigation. In the interim, caution should be exercised when sampling taxa from within this lineage for phylogenetic studies.

Ptychadeninae

The monophyly of Ptychadeninae, i.e., (*Hildebrandtia* + *Ptychadena*), was strongly supported (node 45 on Fig. 4, jackknife percentage of 100, branch support of 22) and not falsified by any sensitivity analyses in the present study. Some confidence can therefore be placed in the validity of this clade (Bogart and Tandy, 1981; Clarke, 1981), which also includes *Lanzarana*. Results of the sensitivity analysis also show that the Ptychadeninae may be embedded in subfamily Raninae, basal in Ranidae s.l., or may be closely related to some taxa in Raninae with two lateral external vocal sacs, such as (*Hydrophylax* + *Amnirana*), which appear, in turn, to be putatively allied to the North American genus *Pantherana*, and the Asian genera (*Amolops* + *Staurois*) (Fig. 3H). More taxa from these lineages should be included in future analyses to test the affinities of Ptychadeninae.

Ptychadeninae appears to represent a classic "long branch" among the taxa included in the present study, displaying numerous apomorphic morphological character states. Ptychadeninae also display highly divergent sequence data from the remaining ranids, as noted by Richards and Moore (1998). Four unique non-homoplastic morphological synapomorphies of Ptychadeninae were found in the present study, including: fusion of Presacral VIII and the sacral vertebra (Character 7: 1); clavicles descending and fused to the coracoids (Character 22: 2); long anterior ramus of the pterygoid curving medially away from the maxilla (Character 49: 2); and velvety nuptial pads on the inner three digits, i.e., fingers two, three and four (Character 132: 3). Non-unique synapomorphies of this lineage include: short, rectangular Presacral Vertebrae V to VIII (Character 4: 1); absence of neopalatines (Character 36: 2); width of the base of the alary processes equal to that of their stalks (Character 85: 0); laterally angled stalks of the alary processes (Character 87: 1); and Digit II not reaching the tip of Digit III of the hand (Character 149: 0).

Raninae

Subfamily Raninae of Ranidae s.l. has long been a "catch all" group containing the problematic taxa that cannot readily be accommodated in any of the other supposedly better-defined subfamilies. Dubois (1987, 1992) elevated many groups formerly placed in Raninae to subfamilies, without presenting phylogenetic evidence. The topology obtained from the simultaneous analysis with equal weights conducted here (Fig. 4) retrieved four clades for the 10 exemplars of Raninae that were included. The transferal of *Nanorana* to Pyxicephalinae reduces the number to three.

The sensitivity analyses failed to retrieve a monophyletic Raninae under any analysis parameter set utilized here. Instead, each analysis obtained between three and five clades for these exemplars. None of the sensitivity analyses retrieved a relationship between *Batrachylodes* and the main clade of Raninae. *Batrachylodes* was usually placed near the ceratobatrachines (*Platymantis* + *Discodeles*). *Batrachylodes* exhibits direct development, which was used to define Ceratobatrachini (*sensu* Dubois, 1992). *Batrachylodes* is thus formally transferred to Ceratobatrachinae on the basis of the results of the sensitivity analyses presented here. The removal of *Batrachylodes* from Raninae removes another source of paraphyly for the subfamily. No sensitivity analysis falsified a sister-group relationship between *Amolops* and *Staurois*. Accordingly, *Staurois* is hereby transferred from tribe Ranini to tribe Amolopini, thereby restricting Ranini to the nominate genus *Rana* and its numerous subgenera, which are in all probability still not monophyletic (see Appendices 6 and 7).

The clade (*Pantherana* (*Amnirana* + *Hydrophylax*)) was retrieved in most of the sensitivity analyses (Fig. 3K), and placed sister to Ptychadeninae or to (*Amolops* + *Staurois*). The clade (*Amnirana*, *Hydrophylax*, *Pantherana*, *Amolops* and *Staurois*), illustrated in Fig. 3H, was strongly supported on the simultaneous analysis with equal weights (node 47 on Fig. 4, jackknife percentage of 93, branch support of 9). Were the validity of this clade to be confirmed by future studies, it would be intriguing on biogeographical grounds. Although most members of the Hylarana clade are Asian, the lineage contains a few African members (e.g., the species of *Amnirana* and *Hydrophylax* included in the present study), as do the Rhacophorinae (e.g., *Chiromantis*) and the fanged ranids (*Aubria*, *Conraua*, *Hoplobatrachus*, *Pyxicephalus*). The clade (*Amnirana*, *Hydrophylax*, *Pantherana*, *Amolops* and *Staurois*) could potentially also demonstrate biogeographical links between the Asian and North American ranids. Ptychadeninae are strongly supported as sister to this assemblage on the simultaneous analysis with equal weights (node 44 on Fig. 4, jackknife percentage of 93, branch support of 9).

A third clade appeared repeatedly in the sensitivity analyses and compounds ranine paraphyly. This clade (*Strongylopus* + *Afrana*), seldom grouped with the major clade of ranines, instead usually occupying a position intermediate between (Tomopterninae, Phrynobatrachinae, Cacosterninae) and (Raninae, Ptychadeninae, Pyxicephalinae).

Unpublished molecular evidence allegedly placing *Strongylopus* and *Tomopterna* near Cacosterninae prompted Dubois (2003) to transfer these genera, without discussion, to Cacosterninae. In the same contribution, Cacosterninae was removed from synonymy with Petropedetinae and reinstated, while Petropedetinae was returned to a subfamily of Ranidae, again without any discussion whatsoever of the supporting evidence prompting these emendations. This putative "African clade" was falsified in two-thirds of the sensitivity analyses presented here (Fig. 3P), and was weakly supported in the simultaneous analysis with equal weights (node 51 on Fig. 4, jackknife percentage of 65, branch support of 2). Furthermore, this relationship was supported exclusively by molecular data (Appendix 5, node 51). This clade was most often absent from sensitivity analyses in which the Rhacophorinae, Mantellinae and Ceratobatrachinae were placed more basally in Ranidae, and the constituent clades (Cacosterninae + Phrynobatrachinae) separated from Tomopterninae and (*Strongylopus* + *Afrana*), the latter two clades usually grouped in a pectinate arrangement closer to the main ranine clade in these sensitivity analyses. Results of the sensitivity analyses conducted here suggest that, as with Tomopterninae, (*Strongylopus* + *Afrana*) are more distantly related to other ranines than are Ptychadeninae, but also that their placement nearer to (Cacosterninae + Phrynobatrachinae) could be a sampling artifact.

In spite of recent molecular efforts, the relationships between major ranid clades remain to be definitively resolved. The transferal of *Strongylopus* and *Tomopterna* to Cacosterninae was premature and unjustifiable on morphological grounds. *Strongylopus* shares none of the morphological synapomorphies of Cacosterninae (discussed in detail under Cacosterninae). Its transferal to Cacosterninae by Dubois (2003) neglects the demonstrated relationship of *Strongylopus* with *Afrana* (the latter inexplicably retained as a subgenus of *Rana* in tribe Ranini by Dubois, 2003), and contradicts the evidence of a closer relationship between Phrynobatrachinae and Cacosterninae than between *Strongylopus* and the latter.

The appropriate course of corrective action is to remove *Strongylopus*, and its sister genus *Afrana* **New Rank** from Cacosterninae and Raninae, respectively, and place them into a separate subfamily, Strongylopinae **New Subfamily**. This clade was demonstrated to be more closely related to Tomopterninae, Cacosterninae and Phrynobatrachinae than to other ranines in the present study, even if it appears superficially to be more similar to the latter. Synapomorphic character states supporting Strongylopinae include: cylindrical sacral diapophyses (Character 15: 0); posterodorsal orientation of the *pars facialis* of premaxilla (Character 78: 1); shape of the terminal phalanx of Digit IV of hand sharply pointed and slightly elongated (Character 118: 2); and tarsal fold present the entire length of the tarsus (Character 156: 1). There are also four molecular synapomorphies for this clade. Although the abovementioned morphological synapomorphies are not unique to Strongylopinae, occurring in many Raninae, the formal recognition of this new subfamily is required to preserve the monophyly of other subfamilies as currently defined. It is likely that subgenus *Amietia*, from southern Africa, is also a member of Strongylopinae. However, there is currently no evidence to support this transferal, since *Amietia* has not actually been included in any published analyses to date. The transferal of this subgenus to Strongylopinae, in the absence of supporting data, would be speculative and thus unscientific, and is not conducted here. Much work remains to be done pertaining to relationships of taxa currently classified as Raninae.

Tomopterninae

On the basis of osteological evidence, Clarke (1981) considered *Tomopterna* to be isolated within "Raninae" as he recognized it. The main character on which this was based was the presence of a spike-like ilial process, combined with the absence 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. *Tomopterna* was placed basal to the main clade of Raninae, possibly a sampling artifact, due to the exclusion of this genus' closest relatives. Clarke's findings appear to have subsequently been used by Dubois (1987) as justification to raise a new subfamily of Ranidae, Tomopterninae. This subfamily was subsequently demonstrated to be polyphyletic (Vences et al., 2000a). *Tomopterna*, the sole genus included in this subfamily, was found to comprise three distinct clades currently regarded as separate genera. The Indian *Sphaerotheca* has been suggested to be related to the dicroglossine *Fejervarya*, the Malagasy *Laliostoma* to the enigmatic *Aglyptodactylus*, and the nominate African genus *Tomopterna* to *Cacosternum* (Vences et al., 2000a). Recognition of Tomopterninae, as originally construed, thus rendered Dicroglossinae and Rhacophorinae or Mantellinae paraphyletic, the latter depending on the placement of *Aglyptodactylus* (see Blommers-Schlösser and Blanc, 1991; Glaw et al., 1998; Emerson et al., 2000a; for discussion).

Dubois (2003) recently synonymized Tomopterninae with Cacosterninae, without presenting supporting evidence or justification. This move contradicts the findings of the present study (Fig. 3N, Appendix 4). In the sensitivity analyses (Cacosterninae + Tomopterninae) was refuted under 85% of the parameter sets, and retrieved under only two parameter sets. This was predominantly due to Phrynobatrachinae being retrieved as the sister-group to Cacosterninae (Fig. 3M). *Tomopterna* was, instead, suggested to be the sister-group of (Cacosterninae + Phrynobatrachinae), as in Fig. 3O, occupying the position between this clade and Strongylopinae, collectively all forming the "African clade" (Fig. 3P). However, relative branch support and jackknife percentages for all of these relationships are weak (Fig. 4).

The geographic range of *Tomopterna*, i.e., its "arid corridor" distribution (*sensu* Van Zinderen Bakker, 1967; De Winter, 1971; Poynton, 1995) and ability to survive in arid ecosystems of southern and eastern Africa, are indeed shared with some *Cacosternum* species (Van Dijk, 1971, 1977). Strong ecological constraints on the external morphology of *Tomopterna*, selected for by its burrowing habit, may indeed have obscured the resolution of its phylogenetic position. Indeed, African *Tomopterna* were classified in *Pyxicephalus* for many years, as both are fossorial genera, superficially similar in external appearance. However, their internal morphology tells a different story, as *Pyxicephalus* and *Tomopterna* differ substantially in their osteology (Appendices 2, 4 and 5). Similarly, both Cacosterninae and Tomopterninae are extremely well-defined morphologically, and differ considerably.

It is incomprehensible, from a morphological standpoint, as to why *Tomopterna* should be considered part of the morphologically well-defined Cacosterninae (e.g., Dubois, 2003), even if this clade were the sister-group of the latter. This observation is reinforced if one considers the plethora of monotypic subfamilies recently erected by Dubois and collaborators for the Asian ranids, e.g., Lankanectinae, Micrixalinae, Nyctibatrachinae and Ranixalinae. It is inconsistent to recognize each of these monotypic Asian subfamilies, yet lump many of the hyper-diverse African lineages into a single subfamily, given the morphological divergence among African taxa detailed in this contribution, which greatly exceeds that reported for the Asian taxa in question. The list of morphological synapomorphies for Tomopterninae (node 55 in Appendix 5) is certainly more extensive than a similar list, if compiled, would be for other currently recognized monotypic subfamilies of Ranidae. The relationships among these Asian subfamilies are poorly known, but most are probably closely related to one another, and to other previously named clades, given their evident morphological similarity. For example, *Indirana* is, inexplicably, still currently placed in its own unique subfamily, Ranixalinae, despite molecular evidence that this taxon is closely related to Asian Fanged ranids (Vences, 1999; Van der Meijden et al., 2005). Lankanectinae and Nyctibatrachinae are apparently sister groups, according to Van der Meijden et al. (2005), but these are each recognized at subfamilial rank. Subsuming Tomopterninae into Cacosterninae is unfounded on morphological grounds, and rejected accordingly. Given the synapomorphies of Tomopterninae listed below, its monophyly and position within the lineage, as well as the implied requirement for equivalency of ranks, Tomopterninae **New Rank** is hereby resurrected.

Two unique morphological synapomorphies were identified here for Tomopterninae (node 55 on Fig. 4), i.e., the neural spine of Presacral Vertebra I and Presacral Vertebra II overlapping but not fused (Character 1: 2), and the presence of a free flange or projection centrally on the hyale, facing towards the jaw (Character 82: 1). The carpus of Tomopterninae probably represents a unique and derived morphology, requiring further evaluation. Additional tomopternine synapomorphies occurring in only a few other taxa include: a heart-shaped frontoparietal arrangement (Character 70: 3), occurring elsewhere only in *Nanorana*, and frontoparietals that are wider posteriorly than anteriorly (Character 71: 2), occurring elsewhere in some Cacosterninae, microhylids and a few other taxa. The simultaneous analysis with equal weights identified seven additional synapomorphies uniting the two exemplars of *Tomopterna* (node 55 in Appendix 5).

"Petropedetidae"

It is difficult to determine how the assemblage of taxa termed "Petropedetidae" (*sensu* Frost, 2004) came to be considered related to one another. Parker (1935), while describing *Phrynodon*, linked it and *Dimorphognathus* to *Petropedetes* and *Arthroleptides*, primarily due to the presence of mandibular pseudo-teeth (Character 51: 1 here) and femoral glands (Character 140: 1 here). The *Phrynobatrachus* lineage was subsequently considered related to *Petropedetes* by Laurent (1941a). Poynton (1964) amalgamated Cacosterninae with these genera, perhaps because *Arthroleptella* was already considered part of Phrynobatrachinae by Laurent (1941a), along with various "*Arthroleptis*" species, some of which are probably species of *Phrynobatrachus*. The latter two genera remain mutually confused in many large museum collections to this day.

Ford (1990) concluded that taxa from the ranid subfamilies Raninae and Petropedetinae were probably each para- or polyphyletic with respect to the other. "Phrynobatrachidae" was subsequently elevated to family by Dubois (1992), and later ruled to be a junior synonym of Petropedetidae (Anon, 1999). Dubois (2003) revoked his earlier decision to elevate this paraphyletic assemblage to the rank of family. This example underscores the need for a rigorous hypothesis of relationship, based on synapomorphy and monophyly, as a prerequisite for changing ranks in the taxonomic hierarchy.

The sensitivity analyses conducted here could not retrieve a monophyletic "Petropedetidae" except in two instances under severe weighting (Fig. 3L). Instead, three distinct monophyletic clades, comprising genera formerly included in "Petropedetidae", were identified, the recognition of any of which at familial level would render Ranidae paraphyletic. *Petropedetes* and *Arthroleptides* are not closely related to the other African taxa with which they are classified, but rather to some Asian ranids. All three clades of "Petropedetidae" must therefore be reduced to subfamilies of Ranidae. Dubois (2003) implemented this taxonomic emendation, again without evidence or justification, recognizing two clades at subfamilial rank, Petropedetinae Noble (1931) and Cacosterninae Noble (1931). However, Phrynobatrachinae Laurent, 1941 **New Rank** also requires recognition as distinct from Petropedetinae, as demonstrated with supporting evidence by Scott (2002).

The character states previously used to justify the grouping of the cacosternines, phrynobatrachines and petropedetines were found in the present analysis to be either plesiomorphic or homoplastic. Some of these are known to be correlated to particular ecological strategies and occur in many different groups of frogs. Examples can be found in Blommers-Schlösser's (1993) analysis of ranid relationships, in which 15 morphological characters (excluding the autapomorphies) were used to determine the relationships among all firmisternal frogs, and seven characters were separately used to determine the relationships among Ranidae, Rhacophoridae and Mantellinae. Remarkably, given the paucity of the data set, Blommers-Schlösser (1993) concluded that Petropedetinae was paraphyletic, although the analysis that led to this conclusion was not presented, nor were the specific terminal taxa used in each of the two analyses explicitly stated. Blommers-Schlösser (1993) considered Cacosterninae to comprise *Cacosternum*, *Microbatrachella*, *Anhydrophryne*, *Nothophryne*, *Arthroleptella* and the Sri Lankan ranid *Nannophrys* (at the time placed in Ranixalinae, but recently transferred to Dicroglossinae, which is synonymized with Pyxicephalinae in this study). 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 present many subtly diverse forms (Emerson, 1979; the present study Characters 14–16), occur in many Neobatrachia (Lynch, 1973), and have previously even been used to ally Cacosterninae and Microhylidae (Noble, 1931). Reduced ossification of the omosternum and procoracoid-clavicular bar is known to be correlated to small size (Trueb, 1973), and also occurs in many disparate ranids. Both characters are widespread and cannot therefore be used in isolation to determine the contents of Cacosterninae with respect to the Asian taxa in question. All sensitivity analyses presented here refuted Blommers-Schlösser's (1993) transferal of *Nannophrys* to Cacosterninae.

Blommers-Schlösser's (1993) concept of Petropedetinae comprised the genera *Arthroleptides*, *Dimorphognathus*, *Natalobatrachus*, *Petropedetes*, *Phrynobatrachus* (in part, but which part was not explicitly stated), *Phrynodon*, as well as assorted Asian genera (*Staurois*, *Batrachylodes*, *Palmatorappia*, *Platymantis*, *Ceratobatrachus*, *Discodeles*, and tentatively *Micrixalus*, *Occidozyga* [including *Phrynoglossus*] and *Elachyglossa* Anderson, 1916). This group was based on the plesiomorphic character states of widely separated atlantal cotyls (Character 19: 0), and on two correlated characters, i.e., T-shaped terminal phalanges (Character 119: 0) and expanded digital pads with circum-marginal grooves (Character 152: 0). 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 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, each of which was subsequently placed in different subfamilies of Ranidae s.l.

The tendency towards terrestrial breeding noted by Blommers-Schlösser (1993) as evident in some petropedetine genera is, in reality, a complex suite of characters, manifesting themselves at various levels of specialization. Although these breeding characters were not included in the present study due to lack of explicit data, they are unlikely to be synapomorphic for "Petropedetidae", given the diversity of breeding strategies employed by the taxa concerned. Egg-laying out of water is a common anti-predation strategy, whereas guarding of egg clutches by either parent is similarly widespread and probably linked to desiccation avoidance associated with the former strategy (Amiet, 1981, 1991). The femoral glands (Character 140: 1) and medial lingual process (Characters 120–124) alluded to by Parker (1935) are widespread in Ranoidea (Grant et al., 1997; Glaw et al., 2000) and absent in many taxa traditionally assigned to Petropedetinae. Absence of vomerine teeth (Character 44: 1) occurs sporadically in many ranids (Lynch, 1973), and is not synapomorphic for "Petropedetidae". Vomerine teeth are present in the type genus *Petropedetes* (Noble, 1931), and may even vary intragenerically, e.g., in *Tomopterna.* Mandibular tooth-like tusks (Character 51: 1) occur only in males of *Phrynodon sandersoni*, *Dimorphognathus africanus* and *Petropedetes natator*, but the simultaneous analysis with equal weights demonstrates that they are not synapomorphic for these taxa, as was assumed by Parker (1935) when he united these taxa into Petropedetinae. The similar morphology of tooth-like tusks in these three species is peculiar (as is the general distribution of the medial lingual process and femoral glands in Ranoidea), but tooth-like tusks are clearly associated with male combat (Amiet, 1981). The present analysis revealed that such tooth-like tusks evolved convergently in *Petropedetes* and Phrynobatrachinae. Detailed species-level studies of *Phrynobatrachus* currently underway may indeed confirm a sister group relationship between *Dimorphognathus* and *Phrynodon*, as depicted in Figs 1 and 2, contrary to the results obtained in Fig. 4. No analyses supported Dubois' (2003) concept of Petropedetinae, viz., phrynobatrachines and petropedetines in the same clade. The analyses could not refute the notion of Cacosterninae and Phrynobatrachinae as closely related, if not monophyletic (Fig. 3M). Although the simultaneous analysis with equal weights (Fig. 4) suggested that Cacosterninae and Phrynobatrachinae are sister taxa, no unique morphological synapomorphies supported this clade and it is weakly supported (node 56 in Appendix 5, jackknife percentage of 49, branch support of 2). Five of the eight non-unique synapomorphies of this clade are reversals to the plesiomorphic state, also shared by other ranoid clades. The remainder are unconvincing: absence of the posterior process of the vomer (Character 42: 1); large, rectangular to round nasals (Character 64: 1, changing to state 2 in most Cacosterninae); and a haploid chromosome complement of $n = 12$ (Character 177: 2, which is only scored as such for two taxa in this clade).

Phrynobatrachinae

Phrynobatrachinae, viz., *Phrynobatrachus*, *Natalobatrachus*, *Dimorphognathus* and *Phrynodon*, were consistently retrieved as a well-supported monophyletic clade (node 57 on Fig. 4, jackknife percentage of 94, branch support of 5). Inclusion in the present study of five *Phrynobatrachus* species, and all three monotypic "minor" phrynobatrachine genera, demonstrated a remarkably tight cohesion among the members of this clade on morphological grounds. This is in sharp contrast to the findings of Van der Meijden et al. (2005), who placed *Natalobatrachus* in their "African Clade", and *Phrynobatrachus* (represented by a single species) sister to *Ptychadena*. The latter finding, and that of paraphyly of Phrynobatrachinae as defined here, must be viewed as a spurious result, given the morphological synapomorphies uniting these taxa, as detailed in the present study. *Phrynobatrachus* contains approximately 68 species, 15 known only from the type locality, and many of which may not be valid. Some indication of the diversity of *Phrynobatrachus* is obtained from evidence that three different chromosome numbers were found in the genus when six species were examined (Bogart and Tandy, 1981), whereas at least two different carpal arrangements (Laurent and Fabrezi, 1990) and two distinct morphologies of the medial lingual process (Grant et al., 1997) have been documented in the genus.

In the present analyses, the monophyly of *Phrynobatrachus* was compromised only by the placement of *Dimorphognathus* and *Phrynodon*. *Dimorphognathus* was found to be closely related to the southern African *Phrynobatrachus natalensis* and *P. acridoides*, all with 18 chromosomes (Bogart and Tandy, 1981). The South African *Natalobatrachus* was placed basal to the entire phrynobatrachine clade in all but two of the sensitivity analyses (including the simultaneous analysis with equal weights presented in Fig. 4), where it grouped sister to *P. krefftii*, which together were placed sister to remaining phrynobatrachines. The monotypic *Natalobatrachus* lacks many defining morphological features of *Phrynobatrachus*, and its basal position within the lineage sanctions the continued recognition of *Natalobatrachus* as distinct from *Phrynobatrachus*. This is not the case with *Phrynodon* and *Dimorphognathus*, however, both of which were consistently embedded within *Phrynobatrachus* in the sensitivity analyses. A recent paper describing a new reproductive mode in *Phrynobatrachus alticola* Guibé and Lamotte, 1962 (Rödel and Ernst, 2002) demonstrated that the strategy of *Phrynodon* (detailed in Amiet, 1981) may not be unique, but may be synapomorphic for the two taxa. The diversity of the *Phrynobatrachus* clade is poorly understood, and there are no gross morphological differences between *Phrynodon*, *Dimorphognathus* and *Phrynobatrachus*. Autapomorphic character states from breeding biology, the basis for the diagnoses of the two monotypic genera, require further investigation in other *Phrynobatrachus* species, in order to place them in the correct context. To restore the monophyly of *Phrynobatrachus*, the following synonymies are proposed: *Phrynodon* Parker, 1935 = *Phrynobatrachus* Günther, 1862 **New Synonym**. *Dimorphognathus* Boulenger, 1906 = *Phrynobatrachus* Günther, 1862 **New Synonym**. *Phrynobatrachus* requires a thorough revision, incorporating data from conventional morphological sources as well as from life history, behavior, advertisement calls and DNA sequence data. *Phrynobatrachus* may ultimately be split into several genera, in which case *Dimorphognathus* and *Phrynodon* would be available names, but would be unlikely to remain monotypic.

Chevron-shaped glands in the scapular region (Character 173: 4) represent a unique morphological synapomorphy of Phrynobatrachinae, although these glands are absent in two exemplar species examined for the present study. A small round heel tubercle (Character 159: 1) is restricted to Phrynobatrachinae, but also occurs in *Mantidactylus* and one species of *Tomopterna*. Other non-unique synapomorphies identified for Phrynobatrachinae (node 57 on Fig. 4) include: laterally positioned vomers (Character 38: 1); alary process of the premaxilla inclined laterally outwards in the transverse plane (Character 79: 1); terminal phalanx of Digit IV of hand with bifurcate tip (Character 118: 0); terminal phalanx of Digit IV of foot with bifurcate tip (Character 119: 1); terminal phalanx of Digit IV of foot expanded with a circum-marginal groove (Character 152: 0); and a wedge-shaped snout (Character 128: 1). Phrynobatrachinae also display a distinctive indel in their mitochondrial 16S rDNA sequences.

Cacosterninae

The monophyly of a group comprising *Cacosternum*, *Ericabatrachus*, *Nothophryne*, *Microbatrachella*, *Poyntonia* and the terrestrial breeding *Anhydrophryne* and *Arthroleptella*, was not refuted by any of the sensitivity analyses conducted in the present study. This clade is here referred to as Cacosterninae. Poynton (1964, p. 137) postulated that Cacosterninae are derived from "a primitive *Phrynobatrachus* stock", and therefore synonymized Cacosterninae with Phrynobatrachinae. No discussion or evidence was presented to support this synonymy. The analyses presented here suggest that these taxa could be sister lineages, but does not support Poynton's (1964) view of two separate lineages in Cacosterninae, i.e., (*Arthroleptella* + *Anhydrophryne*) and (*Cacosternum* + *Microbatrachella*), due to the variable positions of the more recently described genera *Ericabatrachus*, *Nothophryne* and *Poyntonia*. Poynton (1964) hypothesized that *Arthroleptella* is the sister genus of the monotypic *Anhydrophryne* because both are characterized by a terrestrial breeding system and similarly reduced shoulder girdle architecture. The present analyses, and a more detailed investigation of cacosternine relationships currently underway, suggest that *Arthroleptella hewitti* is the sister taxon of *Anhydrophryne*, and should be transferred to the latter to preserve the monophyly of *Arthroleptella*, as follows: *Anhydrophryne hewitti* (FitzSimons, 1947) **New Combination**.

The present analyses also refute Loveridge's (1957) synonymy of *Microbatrachella* with *Phrynobatrachus*, rejected by subsequent workers, e.g., Poynton (1964), who argued that the synonymy was inadmissible on sternal characteristics alone. The simultaneous analysis with equal weights placed *Microbatrachella* as the sister genus of *Cacosternum*, although half of the sensitivity analyses favored a reversal of the positions of *Nothophryne* and *Microbatrachella*. *Cacosternum* was, in all cases, found to represent the most derived genus in the cacosternie lineage.

Channing and Boycott (1989) postulated that *Poyntonia* is closely related to *Cacosternum* and *Microbatrachella*. Some of the sensitivity analyses indicated that *Ericabatrachus* may be the sister of *Poyntonia*, but most displayed a pectinate relationship in which *Poyntonia* was placed basal to *Ericabatrachus* and the rest of Cacosterninae. These results are difficult to explain on biogeographical grounds. *Poyntonia* (extreme south-western regions of South Africa), *Nothophryne* (Malawi) and *Ericabatrachus* (Ethiopia) appear to be paleoendemics distributed in relictual patches of Afro-montane and Afro-alpine habitat. Other taxa may have existed in this lineage, bridging the morphological disparities between the extant relicts. Another possible explanation is that the exact placement of these three genera is an analysis artifact, caused by the absence of molecular data for both *Ericabatrachus* and *Nothophryne*.

Cacosterninae are strongly supported (node 63 on Fig. 4, jackknife percentage of 95, branch support of 7), and can be defined by one unique morphological synapomorphy, i.e., clavicles narrowing sharply and reaching only half the length of the coracoids (Character 20: 2, transforming to clavicles absent deeper into the clade). However, they are also supported by another three synapomorphies that occur in only a few other taxa. These include the *musculus cutaneus pectoris* present as a thin slip (Character 130: 1, occurring elsewhere only in *Natalobatrachus* and *Staurois*); testes with black pigment (Character 131: 1, occurring elsewhere only in *Ptychadena* and the hyper-pigmented *Phrynobatrachus natalensis*); both the basal and one distal subarticular tubercle present on the third finger (Character 164: 1, occurring also in Sooglossidae and *Afrana angolensis*, and reversing in *Cacosternum*). Other non-unique synapomorphies include: Presacral Vertebrae V to VIII rectangular with a large gap (Character 4: 1); dorsal ridge of urostyle extending only to half the length of urostyle (Character 9: 1); distinctly flattened sacral diapophyses (Character 15: 0); laterally angled anterior margins of sacral diapophyses (Character 16: 1); clavicle-coracoid contact only point via short procoracoid or no contact (Character 22: 3); proximal end of omosternum entire (Character 29: 0); anteriorly reduced *pars facialis* of maxilla (Character 74: 1); absence of nuptial excrescences (Character 132: 0, reversing to present deeper into the clade); and absence of webbing between the toes (Character 147: 2).

The corresponding states for *Strongylopus* are: Characters 20: 0, 130: 2, 131: 0, 164: 0, *4: 1*, 9: 2, *15: 0*, 16: 0, 29: 1, 74: 0, 132: 2 and *147: 2* (states present as in Cacosterninae are italicized). For *Tomopterna*, these are: Characters 20: 0, 130: 2, 131: -, 164: 0, 4: 0, *9: 2*, 15: 1, 16: 0, 29: 1, 74: 0, 132: 2 and 147: 1. Neither the single unique nor three nearly unique synapomorphies of Cacosterninae occur in either *Strongylopus* or *Tomopterna*. The lack of these synapomorphic character states of Cacosterninae confirms that *Strongylopus* and *Tomopterna* cannot be placed in Cacosterninae (as implemented by Dubois, 2003), regardless of whether or not they might be more closely related to Cacosterninae and Phrynobatrachinae than to other Raninae.

According to the simultaneous analysis with equal weights presented here, the *os sesamoides tarsale* (Character 109: 1) was independently acquired in all taxa in which this element occurs, viz., Sooglossidae, *Cacosternum*, *Ericabatrachus* and *Arthroleptella*. Similar protective requirements of the ankle joint in small frogs probably selected for a similar morphology in this sesamoid bone.

The analyses conducted here leave no doubt that the recently described monotypic Ethiopian genus *Ericabatrachus* is a cacosternine, not a petropedetine, as was assumed due to the presence of dorsal digital scutes (Character 148: 1). *Ericabatrachus* is a peculiar genus. Its most notable external character state is a reduction in the first finger relative to the second finger (not coded here, as autapomorphic in this taxon set), which occurs sporadically in certain Microhylidae, ranids and leptodactylids (Myers and Ford, 1986; Wu, 1994; Brown et al., 1997). *Ericabatrachus* displays other aberrant character states. In the simultaneous analysis with equal weights (Fig. 4), 16 apomorphic character state changes occur on the branch leading to *Ericabatrachus*. Seven of these are reversals to the plesiomorphic state and include: laterally oriented transverse processes of the eighth vertebra (Character 3: 0); procoelous centrum of the eighth vertebra (Character 18: 0); undilated medial edges of the coracoids (Character 25: 0); cartilaginous metasternum (Character 30: 0); long, straight and thin medial branch of anterior process of hyale (Character 83: 0); anteriorly angled alary processes of the hyoid (Character 87: 0); and toe tips expanded with a ventral circum-marginal groove (Character 152: 0). The acquisition of molecular data for *Ericabatrachus* would assist in determining its placement within Cacosterninae, although it is probably basal in this enigmatic lineage.

Petropedetinae

Petropedetes and *Arthroleptides* formed a monophyletic clade in all analyses performed here. Petropedetinae were placed relatively basal among ranids in the simultaneous analysis with equal weights (node 25 on Fig. 4). Most sensitivity analyses suggested that these taxa are related to Asian, rather than African ranids, notably Ceratobatrachinae and (*Amolops* + *Staurois*). One non-unique character of Petropedetinae, i.e., the presence of dorsal digital scutes (Character 148: 1), is rare among ranids, occurring elsewhere in this analysis only in *Ericabatrachus*. The large, triangular xiphisternum with a serrated edge (Character 32: 2) occurs elsewhere only in *Nothophryne*. Other non-unique synapomorphies include: short, hourglass-shaped metasternum (Character 31: 0); anterior ramus of the pterygoid separated from the maxilla by cartilage (Character 48: 1); nasals not overlapping sphenethmoid (Character 62: 1); large rectangular to round nasals (Character 64: 1, changing within the clade to state 2); anteriorly reduced *pars facialis* of maxilla (Character 74: 1); distance between thyrohyals approximately one times width of the proximal expansion of thyrohyals apart (Character 98: 1); and femoral glands present in males (Character 140: 1).

In the present analyses, *Petropedetes natator* was always placed as the basal member of Petropedetinae, which in turn formed a homogeneous group. *Arthroleptides* was consistently placed inside the clade of *Petropedetes* species in all sensitivity analyses, rendering *Petropedetes* paraphyletic. Most *Petropedetes* species share unique synapomorphies with *Arthroleptides*, such as the metacarpal spike (Character 117: 1) and tympanic papillae in breeding males (Character 142: 1). *Arthroleptides* and *P. newtoni* share a unique state of the cartilage of the *crista parotica* (Character 66: 3). According to Noble (1931), these two genera differ in size and the absence of vomerine teeth in *Arthroleptides*. The latter character, widely applied to distinguish genera in older literature, was deservedly criticized by Inger (1954). These slight morphological differences do not constitute sufficient evidence for separate generic status. In order to restore the monophyly of *Petropedetes*, the following synonymy is proposed: *Arthroleptides* Nieden, 1910 = *Petropedetes* Reichenow, 1874 **New Synonym**.

Conclusions

As with previous studies of Ranoidea, the present analyses did not unequivocally resolve the basal relationships among the major clades. The basal cladogenic events within the group are ancient, concealed by tens of millions of years of evolutionary change. Some novel insights into ranoid relationships were nonetheless obtained. Foremost among these is the finding that Microhylidae are basal in Ranoidea, consistent with the notion that they could be placed in a separate superfamily, Microhyloidea. However, before this superfamily can be accepted, the phylogenetic position of both the brevicipitine and non-brevicipitine microhylids must be adequately resolved. In the present study, brevicipitine microhylids were placed as sister to hemisotids. Astylosterninae linked Arthroleptinae to Hyperoliidae, together forming a well-supported monophyletic clade. *Leptopelis* is probably basal in the hyperoliid–arthroleptid lineage, or sister to Hyperoliidae, either scenario justifying the recognition of Leptopelidae. Rhacophorinae and Mantellinae are sister taxa, embedded in Ranidae, suggesting that they should be regarded as subfamilies thereof. Neither should be recognized at family level unless Ranidae is completely subdivided.

The monophyly of many ranid subfamilies, genera or subgenera remains to be tested and the classification of Ranidae is likely to remain unstable until this is addressed. The present study demonstrated that Raninae probably contains the monophyletic but highly divergent Ptychadeninae. Ranini was redefined in the present study to include only those taxa remaining in the paraphyletic genus *Rana*, which are in particularly dire need of revision. Raninae should be conservatively treated as a "metataxon" (*sensu* Ford and Cannatella, 1993) until a thorough revision is conducted. A new subfamily, Strongylopinae, was proposed for some African genera formerly contained in Raninae. Dicroglossinae (*sensu* Dubois, 1987, 1992) was subdivided, Ceratobatrachinae raised from within Dicroglossinae, and the remaining fanged ranids of Asia amalgamated with the fanged ranids of Africa, into a redefined subfamily Pyxicephalinae. Petropedetinae was subdivided—each of its component clades recognized as subfamilies of Ranidae. Tomopterninae was removed from recent synonymy with Cacosterninae.

Morphological synapomorphies of the abovementioned clades are described in the present contribution, but it remains imperative that further sources of organismal data be explored, including myology, karyology, visceral anatomy, larval anatomy, behavior and ecology. Such data undoubtedly contain informative new insights into the problem of ranid frog evolution (Haas, 2003), would complement the vast quantity of molecular sequence data currently being generated, and also provide essential characters for diagnosing taxa.

The need for such studies is particularly urgent and relevant at present due to the misguided dismissal of organismal sources of data as uninformative, homoplasious, and convergent in recent molecular studies of Anura (see, e.g., Bossuyt and Milinkovitch, 2000, 2001; Biju and Bossuyt, 2003; Van der Meijden et al., 2005). Such statements are unjustified, given that morphological data have not been examined in sufficient detail for the taxa in question. The present study, and that of Haas (2003), clearly and definitively demonstrated the exact opposite: the morphology of ranid frogs is highly informative, and not as subject to convergence as these recent authors state.

Instead of criticizing traditional sources of evidence, future molecular studies should concentrate on correcting their own shortcomings. For example, the complex and unique problems inherent in ranid taxonomy, as detailed in the present study, need to be acknowledged. Studies that uncritically accept the classification of Dubois (1987, 1992) as an *a priori* assumption (e.g., Bossuyt and Milinkovitch, 2000) suffer on account of the fact that it is largely discordant with the evolutionary history of Ranidae, as demonstrated here. Biogeographical hypotheses promulgated on the basis of the findings of these studies are essentially meaningless as a result.

Of greater concern is the observation that many published molecular analyses include only a limited set of taxa relative to those potentially available in each consecutive analysis. The authors of these studies appear to rely on the mistaken assumption that previous results are "correct" and that their subsequent analyses are impervious to previous sampling problems. This philosophy is evident by the approach of excluding taxa which appeared in small previous analyses, instead of constructing larger and more inclusive datasets with each new acquisition of data and taxa. The studies presented sampled maximally six partial loci, amounting to around 3 kb, typically employed arbitrary and unscientific alignment methodologies, and excluded data (particularly indels) that may contain phylogenetic information (Gatesy et al., 1993; Giribet and Wheeler, 1999; Terry and Whiting, 2005).

The results of such analyses may be viewed with skepticism if they contradict groups that are well-supported by morphological synapomorphies, and accepted only after they have survived rigorous testing in a simultaneous analysis framework. The uncritical acceptance of "unexpected" results may promulgate erroneous conclusions, e.g., insisting that guinea-pigs are not rodents (Graur et al., 1991), that are easily falsified in future analyses including more data and taxa (e.g., Robinson-Rechavi et al., 2000).

It should also be acknowledged that analyses based exclusively on molecular data can never falsify morphological classifications, as they do not include the characters on which these classifications were based, and therefore do not provide a legitimate test of these morphology-based hypotheses. Only a simultaneous analysis of all available data can claim to do so.

Molecular data have, of course, enlightened systematists on many important issues, and the purpose of the above critique is not to belittle the immense contribution to be made by molecular data, but merely to suggest that these data should not be considered *a priori* as inherently superior to morphological data (Freudenstein et al., 2003; Jenner, 2004; Wiens, 2004), a misguided delusion that is severely afflicting the field of ranid frog systematics at present. "Unexpected" molecular findings should reasonably be presented as preliminary, pending further tests and confirmation, and may guide the sampling strategies of more detailed morphological studies, and vice versa.

The hypothesis of ranid relationships presented here, the most comprehensive phylogeny of the group published to date, is still too poorly sampled to be considered definitive. The classification of Ranidae remains in need of refinement but this can only be accomplished once the evolutionary relationships in the group are known with greater confidence. Future research on ranid frogs should avoid focusing exclusively on taxa from restricted geographic regions, as the monophyly of many existing named clades cannot be trusted. A robust hypothesis of ranid relationships, with dense taxon sampling in a single inclusive analysis, incorporating all available sources of data, is required before further taxonomic emendations are made, to avoid the proliferation of para- or polyphyletic higher taxa. This also remains a prerequisite for the formulation of meaningful interpretations of the historical biogeography of ranid frogs.

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Appendix 1

Exemplar species and material examined for morphological data collection. The number of specimens in lots is listed in brackets after the accession number. Superscript ‡ denotes the type species of the genus, † denotes specimens that were subject to X-ray photography, * denotes specimens that were double stained and cleared. Repositories for material examined are abbreviated as follows: AC, Alan Channing (UWC, Bellville, 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); CDNEC, Cape Department of Nature and Environmental Conservation (Jonkershoek, South Africa); ES, Elizabeth Scott (New York, NY); 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 ES); LIVCM, National Museums and Galleries of Merseyside (Liverpool, UK); MB, Marius Burger (at TMSA); MNHNP, Muséum National d'histoire Naturelle (Paris, France); NMBA, National Museum (Bloemfontein, South Africa); NMSA, Natal Museum (Pietermaritzburg, South Africa); PEM, Port Elizabeth Museum (Port Elizabeth, South Africa); RAS, unknown from Malawi (with ES); RMNH, Nationaal Natuurhistorisch Museum, formerly Rijksmuseum van Natuurlijke Historie (Leiden, Netherlands); 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 LM, Les Minter; MA, Marleen Dupreez (neé Adams); MV, Miguel Vences; RDS, Rafael de Sá.

Afrixalus fornasinii Bianconi, 1849: AC 618*. ES 708*. TMSA 84116, 84140. ***Afrana angolensis*** (Bocage, 1866): AC 597*, 1522. CAS 152766*, 201982*. ES 742. TMSA 51868, 51861, 51863, 51864*. ***Afrana fuscigula***‡ (Duméril and Bibron, 1841): CAS-SU 9556*. ES [2, 1*], 735. TMSA 35763, 19629*. ***Amnirana albolabris***

(Hallowell, 1856): CAS 103711–103714, 141603*, 204716, 207656†. TMSA 84176–84177†. ***Amolops ricketti*** (Boulenger, 1899): 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: CAS 156431*, 156437*, 156439*, 156440*. ES 550*, 551*, 552–560. EVD N50280*. NMSA 3497, 3499–3501, 5837 [7]. PEM [1*], 7124*. ***Arthroleptella hewitti*** FitzSimons, 1947: CAS 157244*, 156518*, 157024*. NMSA 993, 1192 [3, 1*], 1246 [5], 1339–1345, 1348, 1350, 1352, 1391, 3442, 3446, 3448, 3449, 3451, 3452, 3454, 3459, 3460, 3462, 3464–3469, 3473, 3485, 3486, 3488, 3490, 3492, 5275, 5276, 6415, 6425 [4], 6431 [2], 6565*, 6567*, 6570–6575, 6741, 6746–6749, 6752. TMSA 36334*. ***Arthroleptella landdrosia*** Dawood and Channing, 2000: AC 1715*. MB 1117–1119. NMSA 3416–3419. ***Arthroleptides martiensseni***‡ Nieden, 1910: CAS 168625–168627†, 168628*, 168629–168633†, 168681, 168682. ES 704*, 723. TMSA 84077. ***Arthroleptis stenodactylus*** Pfeffer, 1893: ES [8, 2*]. JV 4682. TMSA 79814, 84182. ***Arthroleptis variabilis*** Matschie, 1893: BMNH 1975.310*, 1975.352*. CAS 196108, 199162*, 207821, 207822*, 207823–207826. MHNG 1040.006*. TMSA 84163, 84307. ***Astylosternus diadematus***‡ Werner, 1898: TMSA 84311*. ***Aubria subsigillata***‡ (Duméril, 1856): CAS 103804, 113967, 113968, 145276, 144214*, 144215, 146050*. TMSA 84436. ***Batrachylodes vertebralis***‡ Boulenger, 1887: 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: AC 561*, 584*, 586*. TMSA 26662–26664, 84115. ***Cacosternum boettgeri*** (Boulenger, 1882): ES 24*, 31*, 32*, 150*, 152*, 173*, 237*, 299*, 315*. EVD [8*]. NMSA 267, 840, 3305, 3320, 3323–3328, 3342, 3343, 5248, 5814 [14], 5820 [2], 5251, 5245–5247, 6052, 6478, 6479, 5253–5256, 5822 [2], 7513. ***Cacosternum capense*** Hewitt, 1926: AC 791*. CAS 156592*. CAS-SU 9538*. EVD [1*], 15079*, 15179*. NMSA AM110, 3397. PEMA 4974*, 4975*. TMSA 84242. SAMC 46158, 46162, 50063, 50073, 50086, 50088, 50099, 50100, 50103. ***Cacosternum nanum*** Boulenger, 1887: ES 22*, 148*, 237*. NMSA 6426, 7421, 7468–7471, 6576, 6577, 3317, 3319, 748 [8], 749 [9], 6432 [8], 6424 [2], 919, 1156 [9], 1193 [4], 1357, 5252, 3321, 1146, 5339, 5341, 3385–3387, 3388–3393, 3384, 5826 [5], 5830 [2]. LM [6, 2*]. TMSA 84309. ***Cardioglossa escalaerae*** (Boulenger, 1903): BMNH 1979.515*. CAS 103974–103975, 143231, 196115, 196118*. MNHG 1039.028*. MNHNP 1904.0109, 1965.0461. TMSA 84310*. ***Cardioglossa gracilis*** Boulenger, 1900: MNHG 1093.021*. MNHNP 1902.0417, 1907.0213, 1934.0024, 1934.0025. RMNH 4513. TMSA 84165. ***Chiromantis xerampelina***‡ Peters, 1854: AC 599, 600*, 1517, 1518. ES 677*. TMSA 84049–84051. ***Conraua crassipes*** (Buchholz and Peters, 1875): CAS 153623, 153624*, 153625, 103908–103914, 38858, 103805, 103806, 207771. ***Conraua goliath*** (Boulenger, 1906): CAS 103389, 103390, 8396, 153620, 153621, 153622*. ***Dimorphognathus africanus***‡ (Hallowell, 1857): CAS 207779–207782, 207783*, 153801, 153802, 153803*, 199305–199307. TMSA 84170–84171. ***Discodeles bufoniformis*** (Boulenger, 1884): CAS 109887–109891, 109895*. ***Ericabatrachus baleensis***‡ Largen, 1991: LIVCM 1986.212.363†, 1986.212.368†, 1986.212.380*, 1986.212.381*. ***Euphlyctis cyanophlyctis*** (Schneider, 1799): AMNH A-23984, A-45826, A-45834*, A-45845, A-45847, A-67570, A-67572, A-67573, A-77479–A-77484, A-104985. ***Heleophryne purcelli***‡ Sclater, 1899: EVD N55680*. PEM [3], A-4*, A-560, A563, A-2092, A-5057*. ***Hemisus marmoratus*** (Peters, 1854): AC 1520. ES [1*], 659–661. TMSA 84095–84098. ***Hildebrandtia ornata***‡ (Peters, 1878): CAS 154656*, 154657, 154658, 202702, 202703. ES 638*. TMSA 26110, 26373, 60843, 60847, 84437–84438. ***Hoplobatrachus occipitalis*** (Günther, 1858): CAS 135615*, 152599, 202432, 204600. ***Hydrophylax galamensis*** (Duméril and Bibron, 1841): CAS 136117, 151133*, 183788–183790. TMSA 35992. ***Hyperolius marmoratus*** Rapp, 1842: CAS 211611–211613. ES [5*], 351, 411, 412. ***Kassina senegalensis***‡ (Duméril and Bibron, 1841): AC 546, 504–506, 1399, 1411. AMNH A-9354*. ES [2*]. TMSA 84343. ***Leptodactylodon ventrimarmoratus*** (Boulenger, 1904): CAS 153793, 153794. MNHG 1524.91*, 1524.95*. MNHNP 1995.2474. ***Leptopelis mossambicus*** Poynton, 1985: TMSA 79874, 79877*. ***Leptopelis vermiculatus*** (Boulenger, 1909): ES 703*, 717*, 718*. TMSA 84038, 84045–84048. ***Limnonectes blythii*** (Boulenger, 1920): AMNH A-90518, A-90519, A-90520, A-90521, A-90522*, A-90523–A-90525. ***Mantella aurantiaca*** Mocquard, 1900: AMNH A-106561*, A-123695, A-156962–A-156964, A-73447, A-73448. ***Mantidactylus femoralis*** (Boulenger, 1882): AMNH A-50361*, A-50362, A-157116, A-157126. ***Microbatrachella capensis***‡ (Boulenger, 1910): AC 4000*. CAS 154655*, 157015*. CDNEC 6594, 6595, 6598–6600, 6601*, 6602, 6603*, 6691*, 6692–6697, 6698*. ES [1*], 154*, 156*, 159*. EVD [4*]. NMBA 441–446. NMSA 3299, 3300, 3330. TMSA 84315, 84316. ***Nannophrys ceylonensis***‡ Günther, 1869: AMNH A-23825*, A-77467–A-77473, A-74238. ***Nanorana parkeri*** (Steneger, 1927): AMNH A-53178, A-53179*, A-62939–A-62943, A-102782. ***Natalobatrachus bonebergi***‡ Hewitt and Methuen, 1913: ES 546*, 547*, 548, 549. PEMA 4769*, 4848*. NMSA 989, 3279, 3290–3292, 3294, 5854*, 5856, 5860–5862, 5865, 5866, 5868, 5869, 5896, 5900, 6939. TMSA 21466, 21467, 22206, 49971, 51798–51800, 51803. ***Nothophryne broadleyi***‡ Poynton, 1963: AMNH A-95098, A-95099. BMNH 1965.817. CAS 156122*, 156123*, 156124–156127. NMBZ 19360, 25143, 25175*, 25176, 25177, 25179, 25182, 25183, 25189, 25190, 25195, 25273, 25274, 25277–25279, 25286, 25287, 25291, 25293, 25294, 25302.

Nyctibates corrugatus*‡** Boulenger, 1904: CAS 152526*, 153797, 155901, 155902. MNHG 1525.026*. TMSA 84312*. ***Pantherana pipiens*‡** (Schreber, 1782): AMNH A-18807–A-18810, A-96579–A-96582, A-100504, A-100505, A-103207, A-114359*, A-114360*, A-114452, A-125965. ***Petropedetes cameronensis*‡** Reichenow, 1874: BMNH 1969.496*, 1984.377, 1984.38. LM 24. UTACV A-35324, A-35325, A-35329, A-35335, A-35341, A-44398. ***Petropedetes natator Boulenger, 1905: AMNH A-83319, A-83320, A-84604–A-84615. BMNH 1961.1248*, 1964.179†. ***Petropedetes newtoni*** (Bocage, 1895): AMNH A-3138, A-6687, A-14369. CAS 103325, 103326*, 103327, 103349, 125582–125585. UTACV A-35348, A-35350, A-35352, A-35358, A-35360, A-35362. ***Petropedetes parkeri*** Amiet, 1983: BMNH 1936.3.4.112, 1936.3.4.113, 1936.3.4.126, 1984.395*. LM [6†]. UTACV A-44739, A-44740, A-44749, A-44751. ***Phrynoglossus laevis*** (Günther, 1858): CAS-SU 16275*, 16392*, 16395. CAS 124059–124076. ***Philautus surdus*** (Peters, 1863): CAS-SU 20339, 20342–20343, 23343–23345, 23347, 23348. CAS 133163, 133199, 133200, 136862*, 182568, 183204, 210012. ***Phrynobatrachus acridoides*** (Cope, 1867): AMNH A-12667, A-126670, A-12671, A-12673, A-12687, A-12691, A-12696. CAS 148377*, 148384*. ***Phrynobatrachus cricogaster*** Perret, 1957: CAS 158975*, 158976*, 158977*. UTACV A-34596, A-34598, A-34601, 34603–34605, A-34608, A-34608. ***Phrynobatrachus krefftii*** Boulenger, 1909: BMNH 1974.80*. CAS 168512, 168514*, 168530, 168538*, 168547, 168549, 168550, 169380. ES 728*, 733*. TMSA 84038–84044. ***Phrynobatrachus natalensis*‡** (Smith, 1849): AC 515. CAS 141564*, 160639*, 160640*, 211604, 211605, 211592, 211597. ES 283*, 286–288*. EVD [2*], 13176*. TM 84183, 84184, 84187, 84188. ***Phrynobatrachus plicatus*** Günther, 1858: CAS 104017, 104020, 126443–126448, 126451–126454, 136292, 136293, 136294*, 136295–136297, 136298*, 136299–136305, 141769. ***Phrynodon sandersoni*‡** Parker, 1935: CAS 153804, 153805. UTACV A-35065, A-35066, A-35068, A-35069, A-35071, A-35074, A-35076, A-35079, A-35080*, A-35085, A-35103, A-35105, A-35125, A-35127, A-35129, A-35132. ***Phrynomantis bifasciatus*‡** (Smith, 1847): AC 554, 555. ES 668*. ***Platymantis corrugatus*** (A. Duméril, 1853): CAS-SU 19523, 21992, 21999*, 22000–22022, 22032, 22033, 22136*, 24060. ***Poyntonia paludicola*‡** Channing and Boycott, 1989: BMNH 2000.178–2000.184. EVD [1*]. CDNEC 6607, 6625*, 6628, 6630, 6636*, 6637, 6639, 6642*, 6645*, 6680, 6682. MB 1253*. TMSA 84117–84130. ***Ptychadena anchietae*** (Bocage, 1867): CAS 148187*. JPB 140*. TMSA 6434, 6449, 6468, 6476, 6811, 26049, 84052–84057, 84059, 84061. ***Ptychadena mascareniensis*‡** (Duméril and Bibron, 1841): AC 611*, 621*. CAS 131481*, 153558–153562, 165129. JPB 163*, 164*. TMSA 37247, 46056, 46057, 67751. ***Pyxicephalus adspersus*‡** Tschudi, 1838: AMNH A-23621. AC 1484. CAS [2*]. TMSA 14981, 83676, 84440. ***Pyxicephalus edulis*** Peters, 1854: AC 619*. JPB 78. TMSA 84415. ***Schoutedenella taeniata*** Boulenger, 1906: MNHG 1040.041*. MNHNP 1965.0363. ***Scotobleps gabonicus*‡** Boulenger, 1900: MHNG 1524.078*, 1524.073*. CAS 103918, 153579, 153796. RMNH 26896, 26897. TMSA 84313*. ***Sooglossus sechellensis*‡** (Boettger, 1896): BMNH 1906.8.15.6, 1906.8.15.7. CAS 160084, 160085. ***Staurois natator*‡** (Günther, 1859): CAS 61901–61935, CAS-SU 23364*, 23368*. ***Strongylopus grayii*** (Smith, 1849): CAS 211614, 211616. ES 108, 109*, 125*, 322, 698*. TMSA 84193, 84339–84341. ***Tomopterna marmorata*** (Peters, 1854): AMNH A-95116–95119. CAS 130580, 130900, 130901, 130904, 130905, 131559. RAS 73/A.5.1.73*. ***Tomopterna tandyi*** Channing and Bogart, 1996: AC 1171, 1181*, 1553–1555, 1557–1560, 1561*, 1562, 1563, 1568, 1569, 1570*, 1571–1574. ES 182*, 845–850, 884–887. ***Trichobatrachus robustus*‡** Boulenger, 1900: CAS 38843*, 38844, 38845, 54740, 152596. MNHNP 1920.0060, 1920.0061, 1913.0011, 1903.0194, 1997.1038, 1902.0413. SAMC 20522, 20524.

Appendix 2

Morphological character descriptions, arranged in an order conducive to minimal handling of specimens during character scoring.

Osteology: axial skeleton and pectoral girdle, dorsal view

0. Presacral Vertebra I, neural arch ossification: (0) meeting medially (Fig. 5E); (1) failing to meet medially, neural arch chondrification visible dorsally (Fig. 5A). Duellman and Trueb (1986) noted that in poorly ossified species (e.g., *Notaden* Günther, 1873), the ossified halves of the neural arch may fail to unite on the anterior vertebrae. D.E. van Dijk (pers. comm.), in his work on African anuran fossils from the rich Langebaanweg fossil site near Cape Town, noticed that many ranid frogs exhibit an unmineralized furrow on the dorsal surface of the cervical vertebra through which, in extant frogs, a nuchal ligament passes. This character was scored state 1 only in taxa in which it is not ossified in adults, as it is possible that fusion may only be completed upon maturity.

1. Presacral Vertebra I and Presacral Vertebra II: (0) full fusion of neural arches (not centra) present; (1) neural spine of first vertebra flattened and extending posteriorly, overlapping and fused with anterior portion of Presacral II, forming a dorsal bone bridge centrally between first and second presacral vertebrae (Fig. 6A); (2) neural spine of first presacral vertebra strongly overlapping second presacral vertebra, but no fusion evident between neural arches of first and second presacral vertebra; (3) normally ossified and

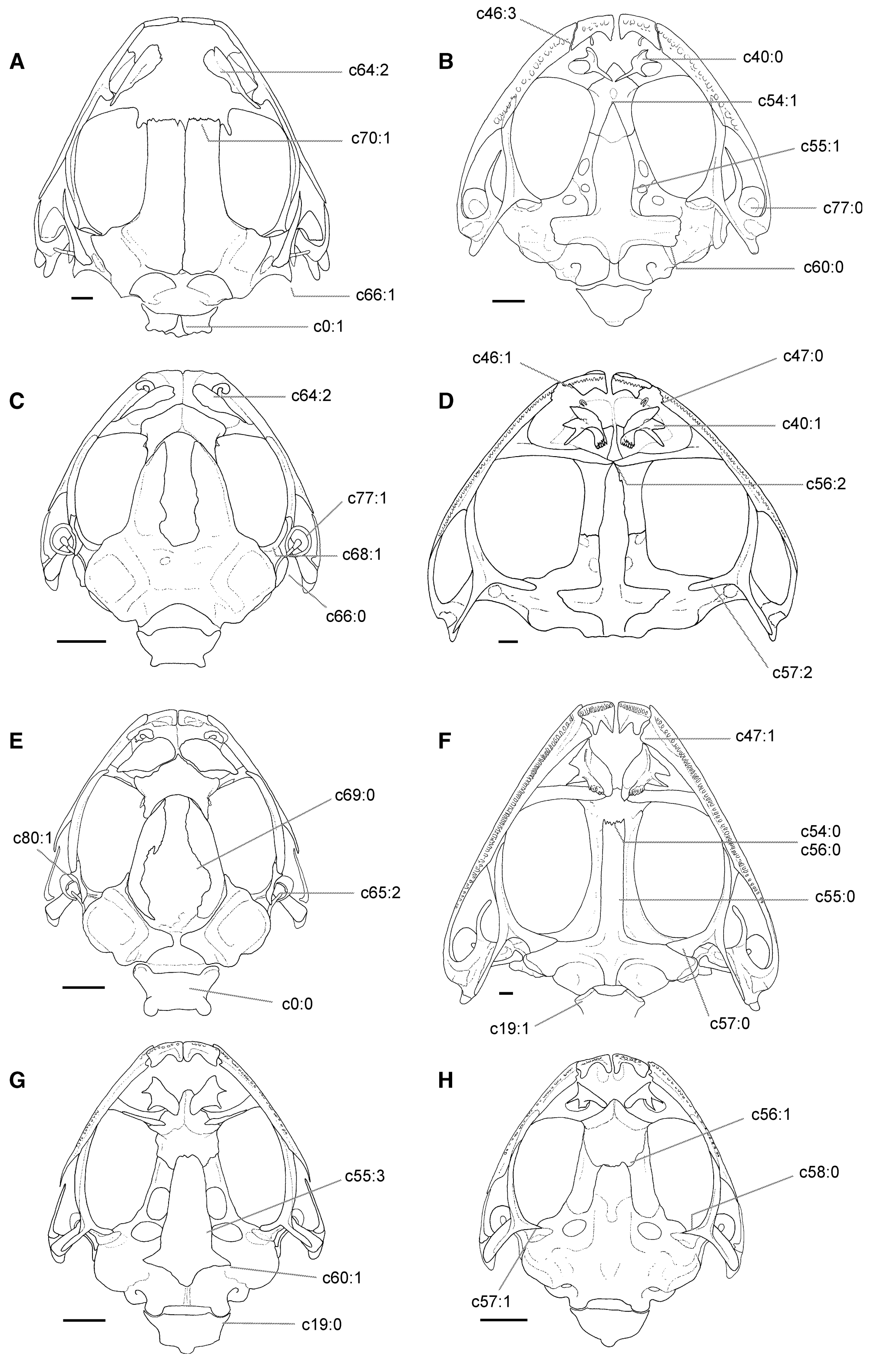

Fig. 5. Skull: (A) *Amnirana albolabris* (CAS 141603), dorsal view. (B) *Poyntonia paludicola* (MB 1254), ventral view. (C) *Cacosternum nanum* (ES 342), dorsal view. (D) *Astylosternus diadematus* (TMSA 84311), ventral view. (E) *Cacosternum boettgeri* (ES 299), dorsal view. (F) *Discodeles bufoniformis* (CAS 109895), ventral view. (G) *Cacosternum boettgeri* (ES 299), ventral view. (H) *Cacosternum nanum* (ES 342), ventral view. Scale bar = 1 mm.

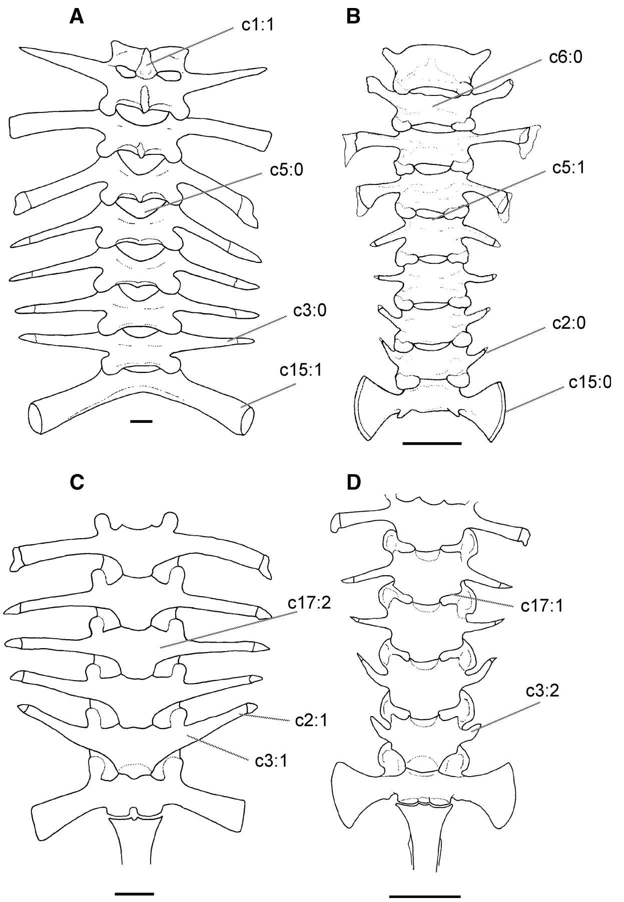

Fig. 6. Vertebral column: (A) *Petropedetes parkeri* (BMNH 1936.3.4.113), dorsal view. (B) *Cacosternum boettgeri* (ES 64), dorsal view. (C) *Phrynobatrachus krefftii* (ES 733), ventral view. (D) *Cacosternum boettgeri* (ES 152), ventral view. Scale bar = 1 mm.

separate. A separate neural spine and bridge (state 1) were not observed in any taxon, suggesting that the bridge is formed by 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 taxa examined that exhibit the bridge. Fusion was assessed by the presence of transverse processes on Presacral Vertebra I, which does not normally bear transverse processes (Trueb, 1973). R.C. Drewes (pers. comm.) observed this condition in various Arthroleptidae. One of the four specimens of *Ericabatrachus baleensis* examined exhibited fused neural arches of Presacral Vertebra I and Presacral Vertebra II, hence this character was scored as polymorphic in this taxon. The general use of "fused" versus "unfused" Presacral Vertebra I and Presacral Vertebra II, as commonly stated in previous studies, confounds two types of fusion of presacrals (L. Trueb, pers. comm.), i.e., partial or total fusion of the neural arches, and fusion of the centra of Presacral Vertebra I and II. The second condition is uncommon, and may be distinguished from the first by the presence, on Presacral Vertebra I + II, of two foramina on each side for the spinal nerves (L. Trueb, pers. comm.). Various degrees of neural arch fusion are common in Anura.

2. Presacral Vertebra VIII, relative length of transverse processes: (0) much shorter than transverse processes of Presacral Vertebra IV (Fig. 6B); (1) roughly equal in length to transverse processes of Presacral Vertebra IV (Fig. 6C).

3. Presacral Vertebra VIII, orientation of transverse processes in frontal plane: (0) oriented laterally, perpendicular to spine (Fig. 6A); (1) slight anterolateral orientation, approximately 20°–30° (Fig. 6C); (2) acute anterolateral orientation, approximately 45° or more (Fig. 6D). Although Lynch (1973) did not consider this character to be independent from the length of the transverse processes (Character 2), the distribution of both characters here suggests that they are. Drewes (1984) noted that the condition of the transverse processes is not related to size, but rather to the degree of lateral movement of the spine. Although Trueb (1977) noted variability in the angle of the transverse processes in *Hyla lanciformis* (Cope, 1870), substantial variation was not found in a sample of 83 skeletal preparations of seven *Cacosternum* species examined for a revision of this genus currently underway. This character was consistent intraspecifically among the taxa examined here, due to the wide range of angle allowed for each state.

4. Presacral Vertebrae V–VIII, shape in dorsal view: (0) square, width approximately equal to length, minimal space between vertebrae; (1) rectangular, length less than width, with gap between vertebrae greater than half their length. This coding substitutes for imbricate versus non-imbricate vertebrae, but does not consider the neural spines. Lynch (1973, 1978) considered the character of imbricate versus non-imbricate vertebrae to primarily reflect the degree of ossification.

5. Presacral V, angle of contact between anterior margins of neural arches in dorsal view: (0) neural arches strongly angled posteriorly, where they join a strong, V-shaped, posteriorly directed indent is evident centrally along the anterior margin of the vertebra, the depth of which is approximately half the length of the vertebra, so that the anterior edge of the vertebra is not parallel to the posterior edge (Fig. 6A; Gaupp, 1896, p. 22, fig. 5); (1) neural arches approach each other approximately in the same plane, where they join, no discernable V-shaped indent is evident in the anterior margin of the vertebra, which is parallel to the posterior margin (Fig. 6B). This character could not be determined for many of the larger ranids due to insufficient clearing of the *fascia dorsalis* (*sensu* Gaupp, 1896). Whether the anterior margin was indented or not did not influence the coding of Character 4. These two characters present fundamentally different distributions among the examined taxa and are considered independent.

6. Presacral Vertebrae II–IV, neural spines: (0) absent (Fig. 6B); (1) present (Fig. 6A). Separation of the characteristics of imbricate versus non-imbricate vertebrae from the features of the neural spine is here similar to that implemented by Wu (1994), since treating these characters together obfuscates the variation.

7. Presacral VIII and sacral vertebra: (0) not fused; (1) fused (Clarke, 1981, p. 324, fig. 14B). Noble (1922) and Laurent (1940) noted that Presacral Vertebra VIII and the sacral vertebra are reportedly fused in *Cardioglossa elegans* Boulenger, 1905, but this was not observed in any Arthroleptidae examined for the present study.

8. Ossification of suprascapular cartilage: (0) limited, only proximal section ossified, forming a Y-shaped flange of mineralization with the cleithrum, with fork facing dorsally (Fig. 7A); (1) heavily ossified, 1/3 to 2/3 of blade, forming one rounded, rectangular or triangular flange with the cleithrum on the antero-proximal surface (Fig. 7B). This character must be assessed from adult specimens.

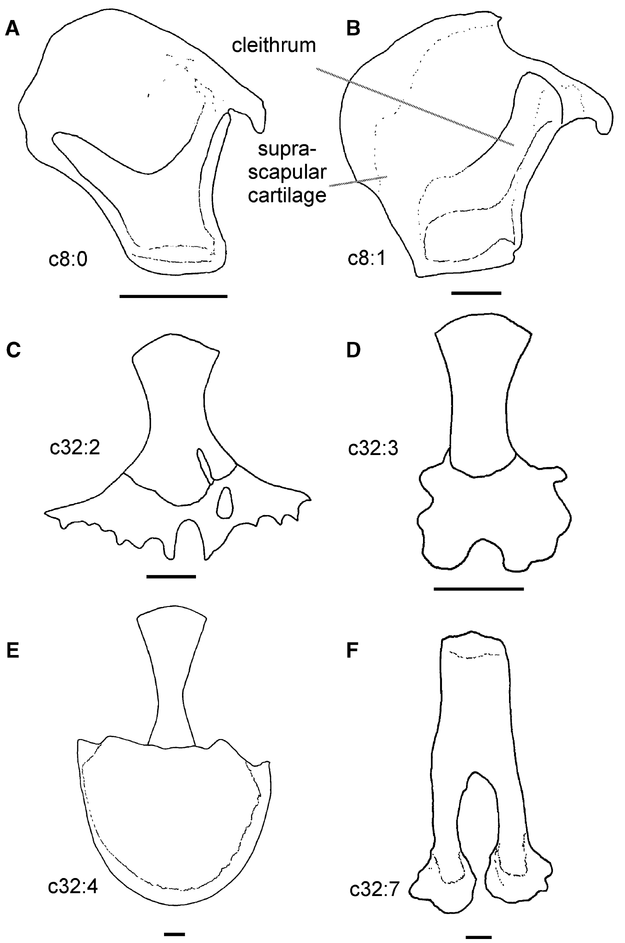

Fig. 7. Suprascapula: (A) *Cacosternum nanum* (ES 95). (B) *Phrynobatrachus krefftii* (CAS 168514). Sternum: (C) *Petropedetes palmipes* Boulenger, 1905 (BMNH 1906.5.28.28). (D) *Phrynobatrachus krefftii* (ES 728). (E) *Aubria subsigillata* (CAS 144214). (F) *Leptopelis vermiculatus* (ES 717). Scale bar = 1 mm.

9. Urostyle, dorsal ridge (or crest, *crista dorsalis sensu* Gaupp, 1896): (0) absent or greatly reduced, extending to less than half length of urostyle; (1) moderately developed, extending to around half length of urostyle; (2) well developed, extending more than half length of urostyle (Gaupp, 1896, p. 25, fig. 6). Trueb (1973) mentioned that in ranids, bufonids and some large species of other families, the urostyle may exhibit a well-developed longitudinal ridge that is largest anteriorly and gradually decreases posteriorly. The length and height of this ridge was found to vary considerably in ranids, with three states being discernible. Most taxa examined displayed a well-developed urostylar ridge (state 2). Absence or extreme reduction of the ridge occurs only in the outgroups, Microhylidae, some Cacosterninae and *Kassina*.

10. Urostyle, anterodorsal process at anterior edge of dorsal ridge: (0) poorly developed, indistinct to absent; (1) strongly developed, large and distinct (Gaupp, 1896, p. 26, fig. 8). Most ranoid taxa display a strongly developed anterodorsal process of the urostyle, but some Microhylidae and Cacosterninae display extreme reduction of this process.

11. Urostyle, transverse processes: (0) present anteriorly, often as small vestiges (Noble, 1931, p. 488, figs 155A, B); (1) absent. The presence of transverse processes on the urostyle is considered to be plesiomorphic (Lynch, 1973; Trueb, 1973), and occurs here in Sooglossidae and *Heleophryne*. Vestigial transverse processes were observed in one of the four specimens of *Ericabatrachus baleensis* examined, but X-rays of two additional specimens did not reveal their presence. Transverse processes were occasionally observed in some species of *Cacosternum*, which were scored as polymorphic.

12. Ilium, dorsal protuberance: (0) oval, inconspicuous (Clarke, 1981, p. 309, fig. 9A); (1) projected laterally and spike-like, to small, sharp and triangular or slightly rounded; (2) large spike- or flange-like, not oval or adpressed to shaft (Clarke, 1981, p. 309, fig. 9B). Large ilial crests obscure the coding of the dorsal protuberance, whereas taxa with reduced or absent crests appear to show well-developed protuberances, sometimes protruding laterally. State 2 is unique to *Tomopterna*.

13. Ilium, height of dorsal crest as measured centrally: (0) absent (Lynch, 1971, p. 61, fig. 36 top; Clarke, 1981, p. 309, fig. 9B); (1) 0.5 to 1 times height of ilium (Lynch, 1971, p. 61, fig. 36 middle); (2) 1.2 to 2.5 times height of ilium, very well developed (Lynch, 1971, p. 63, fig. 39C; Clarke, 1981, p. 309, figs 9A, C). The ilial crests are well developed in most ranids, but reduced in many Cacosterninae and Hyperoliidae.

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

15. Sacral diapophyses, distal ends in lateral view: (0) distinctly flattened (dorsoventrally compressed) (Emerson, 1979, p. 159, fig. 5B; (1) approximately cylindrical (Emerson, 1979, p. 159, fig. 5C). If the diapophyses are dilated, then the distal ends are always distinctly flattened. Undilated diapophyses may be cylindrical or flattened.

16. Sacral diapophyses, orientation of anterior margin: (0) posterolateral (Figs 6A, C); (1) lateral, perpendicular to spine; (2) anterolateral (Figs 6B, D). Expanded diapophyses may point anterolaterally or laterally. In *Nannophrys*, the diapophyses exhibit straight lateral (distal) edges, and the anterior margins point posterolaterally (Clarke, 1983, p. 386, figs 5C, D), unlike in *Cacosternum*, where the lateral (distal) margin is crescent-shaped and the anterior margin points laterally (Fig. 6B). A distinction is recognized between these types of diapophyses using this coding, because if the diapophyses are straight-edged, they are never directed anteriorly in the taxa examined here. Unexpanded diapophyses generally point posterolaterally or laterally. The distribution of states between Characters 14, 15 and 16 suggests that they are independent.

Osteology: axial skeleton and pectoral girdle, ventral view

17. Presacral Vertebrae V–VIII, relative positions and contours of centra and bases of transverse processes: (0) centra cylindrical or subcylindrical, bases of transverse processes not laterally expanded, and not set back entirely against the ventrolateral surface of the dorsal neural arches, but instead positioned laterally and medially of the centra (Noble, 1931, p. 488, fig. 155A; Liem, 1970, p. 32, fig. 22); (1) centra rectangular-shaped in ventral contour, with a distinct small rectangular narrow gap evident ventrolaterally between vertebrae, with the transverse processes narrow basally, and positioned laterally and medially of the centra (Fig. 6D); (2) centra grading gradually into the base of the transverse processes, which are well developed laterally (wider) at their bases. Centra thus have no discernable cylindrical shape nor a distinct boundary with the bases of the transverse processes. As a result of this, there appears to be a triangular-shaped ventrolateral "gap" between the vertebrae, where ossification is reduced, leading to the entire structure having an overall diamond shape in ventral contour (Fig. 6C; Noble, 1931, p. 488, fig. 155B; Liem, 1970, p. 32, fig. 21; Wu, 1994, p. 220, fig. 27); (3) centra clearly distinguishable from bases of transverse processes, which are not strongly laterally expanded, bases of the transverse processes are set back on the extreme ventrolateral surface of the dorsal neural arches, giving centra a sharply cylindrical appearance (Gaupp, 1896, p. 21, fig. 4; Noble, 1931, p. 239, fig. 89C; Liem, 1970, p. 32, fig. 20). Liem (1970), Lynch (1978) and Ford (1990) recognized some of the variation described by the states of this character, but all these authors experienced difficulty in quantifying it, as here. This character requires further examination, as it may incorporate more than the one character as stated here. A. Haas (pers. comm.) mentioned that states 0–2 versus state 3 may partly reflect epichordal versus perichordal centrum development in those types.

18. Presacral Vertebra VIII, centrum: (0) procoelous; (1) amphicoelous. This character was first used in the classification of frogs by Nicholls (1916), and followed by Noble (1922, 1931). Trueb (1973) provided good definitions of this widely used character, the use of which, in the present study, distinguishes only the state of Presacral Vertebra VIII. All specimens of *Leptopelis vermiculatus* examined displayed the procoelous condition. All other species of *Leptopelis* that have been examined are diplasiocoelous (Liem, 1970; Drewes, 1984). However, Ramaswami (1939) noted that some species of *Rhacophorus* are procoelous whereas others are diplasiocoelous. Guibé (1978) also reported that some species of *Mantidactylus* are procoelous, whereas others are diplasiocoelous. *Ericabatrachus baleensis* was the only exemplar of Ranidae s.l. in which the procoelous condition was observed. This was clearly evident in two specimens, obscured by fusion in another and equivocal from the last, assessed using X-ray photography. The fusion of Presacral Vertebra VIII with the sacral vertebra obscures the determination of this character in Ptychadeninae.

19. Atlantal intercotylar distance: (0) widely separated, more than one cotyl's width apart (Lynch's Type I) (Fig. 5G); (1) one cotyl's width distance apart (Fig. 5F); (2) juxtaposed but distinct, very narrowly separated (Lynch's Type II). No taxa were observed to exhibit Lynch's (1973) Type III cervical cotyls (fully confluent without a small gap) in the present study, as expected based on Trueb's (1973) suggestion that Type III cotyls are only found in ceratophrynine leptodactylids and ascaphids. Clarke's (1981) observation that Type III cotyls are the adult state in *Hoplobatrachus occipitalis* were not verified. One subadult and one adult specimen of this taxon were examined and found to exhibit Type II cotyls, in common with most large ranids. However, Drewes (1984) observed Type III cotyls (although Type II condyles) in two subadults of *Lithobates palmipes* (Spix, 1824), a species not examined for this study, suggesting that there may be ontogenetic variation in some ranids.

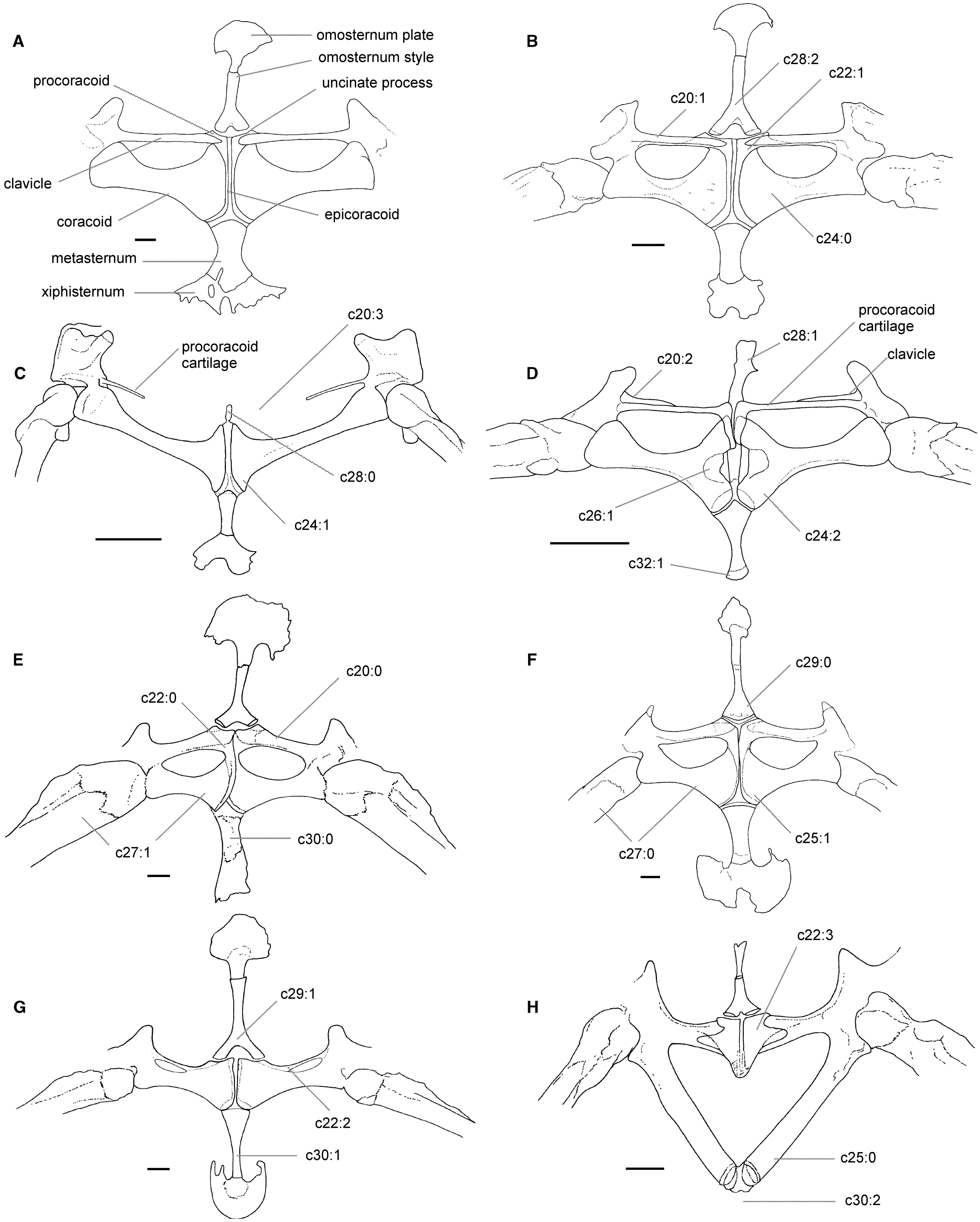

Fig. 8. Pectoral girdle: (A) *Petropedetes palmipes* (BMNH 1906.5.28.28) illustrating nomenclature. (B) *Phrynobatrachus krefftii* (ES 728). (C) *Cacosternum boettgeri* (ES 152). (D) *Microbatrachella capensis* (ES 32). (E) *Astylosternus diadematus* (TMSA 84311). (F) *Afrana fuscigula* (ES). (G) *Ptychadena anchietae* (JPB 163). (H) *Hemisus marmoratus* (ES). Scale bar = 1 mm.

20. Clavicle, thickness: (0) approximately equal in width along entire length, bony and thick, meeting the procoracoid cartilage medially (Fig. 8E); (1) approximately equal in width along entire length, but reduced and proportionately thin, meeting the procoracoid cartilage medially (Fig. 8B; Clarke, 1983, p. 384, fig. 3C); (2) narrowing medially, reduced and thin, not descending towards and fused with the coracoid and not meeting the procoracoid medially (Fig. 8D); (3) clavicle absent (Fig. 8C). Most ranids display the common state 0, whilst state 1 occurs predominantly in Phrynobatrachinae. States 2 and 3 only occur in Cacosterninae and *Phrynomantis*. Scored as inapplicable in Ptychadeninae (Fig. 8G).

21. Clavicle, orientation: (0) strongly or slightly bowed, pointing distinctly anteromedially more than 35°; (1) straight and pointing roughly perpendicular to body axis, not more than 30° angled forwards.

22. Sternum, anteromedial section: (0) long procoracoid cartilage, clavicle separated from coracoid by large gap (Fig. 8E, F; Sheil, 1999, p. 60, fig. 5C); (1) procoracoid and epicoracoid cartilage short but heavily mineralized, coracoids appear "fused" to clavicles by mineralization for approximately 1/5 to 1/4 of the clavicle's length, uncinate process mineralized and strongly developed, the anteromedial edge of coracoid is expanded anteriorly to be somewhat hook- or barb-like (Fig. 8B; Deckert, 1938, pp. 157–158, figs 17, 18); (2) clavicle thin and descends posteromedially, fusing to coracoid at approximately the medial third of its length (Fig. 8G); (3) short procoracoid cartilage, resulting in only point contact between coracoid and clavicle anteromedially, or in aberrant cases, no contact (Fig. 8H). This character is similar to Ford's (1990) character 32, but is more concerned with the extent of mineralization of the procoracoids. Scored only from adult specimens. The "exceptional development of the procoracoid cartilage and … medial divergence of the coracoids and clavicles" mentioned by Dubois (2003, p. 246) as being characteristic of the dicroglossine tribe Conrauini (and the grounds for its recognition by Dubois, 1992), may have been based partly on a statement by Noble (1931, p. 519) that this genus differs from *Rana* "in that the coracoid cartilages ("epicoracoids") anterior to the coracoids are only weakly calcified." This appears to be within the variation observed as state 0 here. In the present study, the procoracoid was not found to be more notable in *Conraua* than in many other dicroglossine taxa examined, and state 0 also occurs in *Afrana*, some Asian ranids, all Astylosterninae and some outgroup taxa. Putative procoracoid differences that uphold the dicroglossine tribe Conrauini thus require further scrutiny. The clavicles are often reduced or relatively thin (Character 20: 1) in taxa exhibiting state 1, e.g., *Philautus*, suggesting a reduction in the required strength of the clavicles. State 1 is common in Dendrobatidae Cope, 1865 (Ford, 1990) and Phrynobatrachinae. State 2 occurs only in Ptychadeninae.

23. Pectoral girdles: (0) epicoracoids elaborated into posterior epicoracoid horns which overlap medially, usually fused in the interclavicle region (arciferal condition); (1) epicoracoids anteriorly fused, posteriorly free and usually overlapping, coracoids slightly angled ventrally, one side overlapping the other medially, the overlapping coracoid usually fenestrated at its medial edge (modified firmisternal condition, or pseudoarciferal condition, or arciferal-like condition) (Deckert, 1938, p. 138, figs 1, 2; Trueb, 1973, p. 96, fig. 2.9F; Duellman and Trueb, 1986, p. 347, fig. 13.36G); (2) epicoracoid cartilage fused medially (firmisternal condition). The terms arciferal, pseudoarciferal and firmisternal were shown to be somewhat misleading by Kaplan (2003), insofar as their historical usage portrays an entire suite of characters. State 1 was discussed in Noble (1926), Clarke (1981) and, in considerable detail, for some large fanged ranids by Kaplan (2000). According to Griffiths (1959a), *Sooglossus* exhibits pseudoarcifery, but Wu (1994) and Kaplan (2000) considered sooglossids to be arciferal, which is followed here. Clarke's (1981) observations of state 1 in *Tomopterna* were not confirmed in an examination of numerous specimens, but a similar state was observed in some *Hildebrandtia* specimens, suggesting that a similar morphology may also occasionally occur in large burrowing forms. Kaplan (2000) presented strong arguments against interpreting state 1 as intermediate between states 0 and 2 (i.e., ordering this character), whereas Kaplan (2003) discussed pseudofirmisterny in detail. In this study, some Astylosterninae appeared to exhibit the arciferal-like condition, but insufficient material was available to confirm this. Astylosternid pectoral girdles require further examination.

24. Coracoid, shape of medial (sternal) edge: (0) trumpet-shaped (Figs 8A, B, E, F, G); (1) T-shaped (Fig. 8C); (2) Y-shaped, broader medially than state 0, and narrowing substantially towards the glenoid edge (Fig. 8D). The reference to Y-shaped in state 2 does not imply bifurcation of the medial ends of the coracoids, but merely that the distension towards the medial edges occurs from a single definable point, and is not a gradual enlargement, as in state 0.

25. Dilation of the coracoid: (0) lateral (glenoid) and medial (sternal) edges of coracoid approximately the same width, with medial edge less than 1.3 times width of lateral edge (Fig. 8H); (1) medial edge of coracoid dilated and distinctly wider than lateral edge, more than 1.4 times its width (Fig. 8F). Within the taxon sample examined, the lateral edge was never observed to be wider than the medial edge.

26. Medial edges of coracoids: (0) both left and right sides always single; (1) both sides often bifurcated or nicked (Fig. 8D). Oxnard (1971) observed that net tension on flat bones can lead to fenestrae and replacement of bone by fibrous material, suggesting that fenestrae are generally associated with loading. Fenestration on a single side, often associated with the pseudoarciferal condition in large ranids (Character 23: 1), was not coded as state 1 for this character, and appears to be consistent with Oxnard's comments. However, the condition in which the left and the right coracoids are both bifurcated is marked in many small species, where general reduction in ossification is observed. This, not tension and loading, is a more probable explanation for this character state.

27. Ventral elements of pectoral girdle: (0) size in normal proportion to rest of body, glenoid fossae widely separated; (1) size proportionally smaller, glenoid fossae narrowly separated (Fig. 8E). Proportional reduction in the clavicle and coracoid was only observed in Astylosterninae. This condition is presumed to impact negatively on the reach of their forelimbs, and therefore on their movement and ecology. The forelimbs would probably be held normally under the body. In Fig. 8E, the proportionally smaller pectoral girdle can be assessed by comparing it with the relative size of the humerus, and comparing this to the relative size of the humerus in other illustrations, e.g., Fig. 8F.

28. Omosternum style: (0) minute vestigial cartilaginous peg or absent (Fig. 8C); (1) present, large and cartilaginous (Fig. 8D); (2) present, large and well ossified (Fig. 8B). Trueb (1973) noted that the omosternum is myocommatous in origin and thus extremely labile in its distribution among taxa. State 2 is the common state in ranids.

29. Omosternum, shape of proximal end (base) that articulates with pectoral girdle: (0) entire (Fig. 8F); (1) bifurcated (Fig. 8G). The nature of the bifurcation varies substantially in traditional Ranidae, from a slightly triangular base of the omosternum with a faint nick, to widely separated arms of a distinct fork. In addition, it may be hypervariable within some species, as illustrated in Deckert (1938, p. 139) fig. 3 for *Tomopterna delalandii* Tschudi, 1838. Nevertheless, this character was included, using a simple coding scheme, because of its historical importance in the literature and because it is one of the primary characters underpinning the subfamilial classification of Dubois (1987, 1992). The resulting distribution of this character on the topology in Fig. 4 confirms that it is highly homoplastic, and less reliance should thus be placed on it as a key indicator of phylogenetic relationship.

30. Metasternum: (0) broad and cartilaginous, sometimes with slight mineralization (Fig. 8E); (1) narrow or broad bony stylus (Fig. 8G); (2) absent (Fig. 8H). The metasternum is heavily mineralized (using the same definition as Fabrezi, 2001) in *Leptopelis*, but still considered cartilaginous.

31. 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. This widely used character is variable between genera, and its usage is therefore simplified here from that of previous authors.

32. Posterior section of sternum, shape: (0) large and round; (1) small peg, usually triangular (Fig. 8D); (2) large and triangular with distinctly serrated posterior edge (Fig. 7C); (3) roughly X-shaped, equally long as wide (Fig. 7D); (4) large inverted U-shaped plate (Fig. 7E); (5) rectangular with a smooth posterior edge; (6) large anchor shape (Fig. 8C); (7) narrow and rectangular, divided with two long projections with distal expansions (Fig. 7F); (8) rectangular with strongly serrated posterior edge (Fig. 8E). Tyson's (1988) character 26 refers to the shape of the posterior margin of the xiphisternal plate as pointed, expanded slightly or expanded greatly, as used in Wu's (1994) character 164.

Osteology: skull, ventral view

33. Sphenethmoid, ventromedial portion: (0) fused, single; (1) paired. According to Trueb (1973), state 1 reflects reduced ossification, and is often seen in small frogs. Paired sphenethmoids have been noted in the literature for some *Leptopelis*, but this state was not evident in any specimens of this genus examined for this study. Griffiths (1959a) recorded paired sphenethmoids for *Sooglossus*, but Wu (1994) scored them as fused. Ford (1990) observed paired sphenethmoids in *Mantella*, but this was not evident in the single osteological preparation examined here. Similarly, there is controversy regarding the state of this character in *Cardioglossa escalaerae* (R.C. Drewes, pers. comm.). This character thus appears to be more variable within species and genera than previously thought, and may depend on the age of the specimen. Furthermore, L. Trueb (pers. comm.) notes that the exact position of any fusion of sphenethmoids needs to be explicitly stated when coding this character, because sphenethmoids may be unfused both dorsally and ventrally, fused dorsally and free ventrally, fused ventrally and free dorsally, or fused dorsally and ventrally (as is the typical condition in frogs). Lack of explicitness regarding exactly which part(s) of the sphenethmoids may be fused when defining this character may explain the inconsistent observations found in the literature. The ventral sphenethmoid appears to be unossified in adult *Amnirana* and *Hydrophylax*, which appear to exhibit an extensive cartilaginous *solum nasi*, requiring further investigation.

34. Ventral sphenethmoid, extent of forward expansion of mineralized anterior portion (*antrum pro lobo olfactoria sensu* Gaupp, 1896): (0) ventral sphenethmoid narrow, adpressed to braincase in the region of the *planum antorbitale*, no additional mineralization extending anteriorly; (1) mineralization of the ventral sphenethmoid extends forward considerably, covering at least half the palate or more. Drewes (1984) coded the dorsal extent of the sphenethmoid, but it was coded ventrally in this study, as a variation of the usage by Ford (1990). The extreme condition of state 1, whereby mineralization extends forward to two-thirds or more of the palate, is illustrated in Lynch (1971, p. 50) fig. 23.

35. Ethmoid cartilage, *septum nasi*: (0) thin, nasal capsules close together; (1) thick, nasal capsules medially separate (Myers and Ford, 1986, p. 5, fig. 3).

36. Neopalatines: (0) present as separate elements, well developed; (1) present as separate elements, but reduced to thin slivers of bone only; (2) absent or indistinguishably fused to other elements. Neopalatines are occasionally absent in Neobatrachia, e.g., most Dendrobatidae, some Microhylidae and Ptychadeninae. If the neopalatines are absent, their loss is usually compensated for (Parker, 1934; Trueb, 1993). In Ptychadeninae, compensation is by the anterior ramus of the pterygoid being elongated and curved medially over the *planum antorbitale* (Character 49: 2). If the neopalatines cannot be distinguished in adult specimens, then developmental series must be studied to determine whether they are indeed absent, or merely indistinguishably fused to other elements, such as the pterygoids or vomers (L. Trueb, pers. comm.). Such investigations were beyond the scope of this study. The perceived absence in Ptychadeninae was the only occurrence of state 2 observed in Ranidae s.l., but may not be homologous to the condition found in some Microhylidae or Sooglossidae. Clarification of the homologies implied by state 2, as presented here, requires further study of developmental series.

37. Neopalatines: (0) touching the sphenethmoid, but not nearly meeting medially; (1) touching the sphenethmoid, nearly meeting each other medially, medial portion may be slightly expanded. Neopalatines ossify late in the developmental series, and are thus prone to reduced ossification in small or poorly ossified taxa (Trueb, 1993).

38. Vomers, development and position: (0) not reduced, central point of the bulk of the vomer is not situated lateral to an imaginary longitudinal axis originating from the point of articulation of maxilla and premaxilla, but is approximately posterior to this articulation (Lynch, 1971, p. 49, figs 22D, F; Duellman and Trueb, 1986, p. 315, figs 13, 18A–H); (1) reduced, vomers placed distinctly laterally, central point of the bulk of the vomer situated posterolateral to an imaginary longitudinal axis originating from the point of articulation of maxilla and premaxilla (Lynch, 1971, p. 49, figs 22B, C, E). Lynch (1971) noted that the vomers are widely spaced in some leptodactylids, and are reduced in these cases, as observed here. The presence of reduced lateral vomers interferes with scoring of the extent of the anterior process of the vomer and its overlap with the articulation of *pars palatinae* premaxilla and maxilla (Character 39). Often the reduced condition is correlated with absence of the posterior (dentigerous) process of the vomer (Character 42: 1), but this was considered to be an independent character in this study, due to the inclusion of the positional reference.

39. Vomer, anterior process: (0) short or absent, separated by a small or large gap from articulation of premaxilla and maxilla (Clarke, 1981, p. 298, figs 5B, C); (1) long, passing dorsally to the *pars palatinae* of the premaxilla and maxilla in region of the articulation (Clarke, 1981, p. 298, fig. 5A); (2) long, but curving anteriorly and laterally and passing dorsally to anterior portion of *pars palatina* of maxilla (Clarke, 1981, p. 298, fig. 5D). This character differs from the version used by Ford (1990), in that the anterior process was considered present if an anteriorly directed point could be discerned.

40. Vomer, postchoanal process: (0) poorly developed, in same plane (horizontal) as prechoanal process and body of vomer (Fig. 5B; Clarke, 1981, p. 298, fig. 5B); (1) strongly developed, vertical or oblique, not in same plane as prechoanal process (Fig. 5D; Clarke, 1981, p. 298, figs 5A, C). This character refers to whether post- and prechoanal processes are in same plane or not, and is thus not the same as the characterization of the entire vomer as presented in Ford's (1990) character 36. The complexity and degree of development of the postchoanal process of the vomers usually reflects that of the vomers in general. The depth of the head and requirement of support for the choana may be indicated to some extent by this character.

41. Vomer, postchoanal process: (0) not fused to sphenethmoid; (1) fused to sphenethmoid. All taxa exhibiting state 1 display heavily ossified skulls, and the distinction between the postchoanal process and the sphenethmoid cannot be readily determined.

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

43. Vomer, posterior process, if present: (0) connected to main mass of vomer; (1) separate from main mass of vomer. Du Toit (1943) first noted that the vomers of certain species of *Petropedetes* were divided, the posterior process being fused to the *planum antorbitale*. He noted this state elsewhere only in *Crinia georgiana* Tschudi, 1838 and some Malagasy and Indo-Malayan Microhylidae.

44. Vomerine teeth: (0) present; (1) absent. Loss of the vomerine teeth appears to occur readily. The presence of a dentigerous process on the vomer is thought to be independent of the presence of vomerine teeth, but in this study the scoring was found to be identical, with the exception of *Kassina senegalensis*, *Conraua crassipes* and *Tomopterna marmorata*, which appear to possess dentigerous processes but not vomerine teeth.

45. Maxillary and premaxillary teeth: (0) present; (1) absent. The absence of maxillary teeth can be correlated to microphagy (Vences et al., 1998), but often it is not, as in many bufonids.

46. Premaxilla (ventral view), medial palatine process: (0) wider than lateral palatine process; (1) equal in width to lateral palatine process (Fig. 5D); (2) narrower than lateral palatine process; (3) narrower than lateral palatine process, which slants outwards and is therefore longer than the medial palatine process (Fig. 5B).

47. Maxilla, anteromedial flange of *pars palatina*: (0) absent (Fig. 5D); (1) present (Fig. 5F; Clarke, 1981, p. 296, fig. 4B); (2) present and large, expanding medially away from maxilla, creating a strongly concave anterior margin of the maxilla and a large semicircular fenestra between the maxilla and premaxilla (Clarke, 1981, p. 296, fig. 4A; Haas, 1999, p. 27, fig. 4B). Clarke's (1981) character 8 referred to whether the anterior edge of the maxilla was concave, convex or straight. Whether the edge is concave or not depends on the presence of the flange (Ford, 1990). Here, the variation noted in ranids of the anterior edge of the maxilla by Clarke is coded rather in terms of the degree of development of the flange and its expansion away from the maxilla. Some taxa, notably most Arthroleptidae, brevicipitine microhylids and some ranids, particularly the Hylarana section, appear to lack the flange (state 0), but it is highly developed in other taxa (state 1). State 2 is highly developed and therefore obvious, and occurs primarily in large fanged ranids. Fabrezi and Emerson (2003) noted that the fenestra created by the highly concave anterior edge of the *pars palatina* delimits a space into which the mandibular odontoids fit when the jaws are closed. Therefore, some correlation between state 2 and the presence of mandibular odontoids (Character 50: 1) is to be expected.

48. Pterygoid, anterior ramus: (0) in contact with, or adpressed to maxilla; (1) separated slightly but noticeably from maxilla by cartilage. This character ignores expansion of the pterygoid process. Ford's (1990) discussion of her characters 19 and 32 indicated some of the difficulty in quantifying this character. In the present study, it was coded from the inside of the oral cavity, facing dorsolaterally at the junction between the anterior ramus of the pterygoid and maxilla. Only fully ossified adult specimens were coded. L. Trueb (pers. comm.) noted that the maxilla and anterior ramus of the pterygoid should always be separated by cartilage (pterygoid and posterior maxillary process), and that fusion should be absent, although it is possible that the ventrolateral edge of the ramus might fuse to the lingual edge of the *pars palatina*.

49. Pterygoid, anterior ramus in relation to neopalatines and *planum antorbitale*: (0) falling far short of neopalatines, extending only to approximately mid-orbital level; (1) slightly overlapping or almost reaching neopalatines and *planum antorbitale*; (2) long, curving medially away from maxilla towards an enlarged, wider *planum antorbitale*, separated from lateral border of *planum antorbitale* by a wide gap. State 2 is discussed by Clarke (1981). See discussion of Character 36 presented earlier.

50. Mandibular odontoids: (0) absent; (1) present as laminar projections of anterior edge of dentary. Mandibular odontoids are discussed in detail by Fabrezi and Emerson (2003).

51. Mandibular tooth-like tusks, breeding males only: (0) absent; (1) present, fine and pointed posteriorly, not situated at anterior edge of dentary, but further back (Noble, 1922, plate I). Noble (1931) reported that the "teeth" in *Dimorphognathus* (state 1) are the hypertrophied margins of the prearticular bone. These structures were not considered to be homologous with mandibular odontoids (*sensu* Fabrezi and Emerson, 2003) in the present study. Tooth-like tusks are probably used in male combat, as documented in *Phrynodon* by Amiet (1981).

52. Mentomeckelian bone, relative height of medial versus lateral edges (anterior aspect): (0) height of medial edge equal to height of lateral edge; (1) height of medial edge less than height of lateral edge. This character is inapplicable to Sooglossidae, which lack the mentomeckelian bones (Wu, 1994), and to *Phrynoglossus*, where the mentomeckelian bone is long and fused with the angulosplenial. The latter condition suggests an absence of gular fluttering during respiration (L. Trueb, pers. comm.) and thus hints at an aquatic lifestyle for *Phrynoglossus*.

53. Mentomeckelian bone, lateral process: (0) absent (Fig. 9A); (1) shorter than or equal in length to mentomeckelian bone (Fig. 9B); (2) longer than mentomeckelian bone (Fig. 9C). The state of this character is distinct only in preparations in which cartilage has stained well.

54. Parasphenoid, shape of tip of cultriform process: (0) rounded or serrated (Fig. 5F); (1) sharply pointed (Fig. 5B). Clarke's (1981) character 12 was separated into two characters in this study, because many permutations were evident in states of this character and those of Character 55.

55. Parasphenoid, shape of cultriform process: (0) borders straight, process relatively wide (Fig. 5F; Clarke, 1981, p. 300, fig. 6A); (1) borders convex, with a slight expansion medially and a narrower posterior section (Fig. 5B; Clarke, 1981, p. 300, fig. 6B); (2) borders not straight but slightly tapering, often very thin (Clarke, 1981, p. 300, fig. 6C); (3) borders strongly converging, forming a triangular cultriform process (Fig. 5G).

56. Parasphenoid, length of cultriform process: (0) reaching anterior 1/5 of the orbit, but falling just short of the level of neopalatines and *planum antorbitale* (Fig. 5F); (1) shorter, reaching only to a maximum of

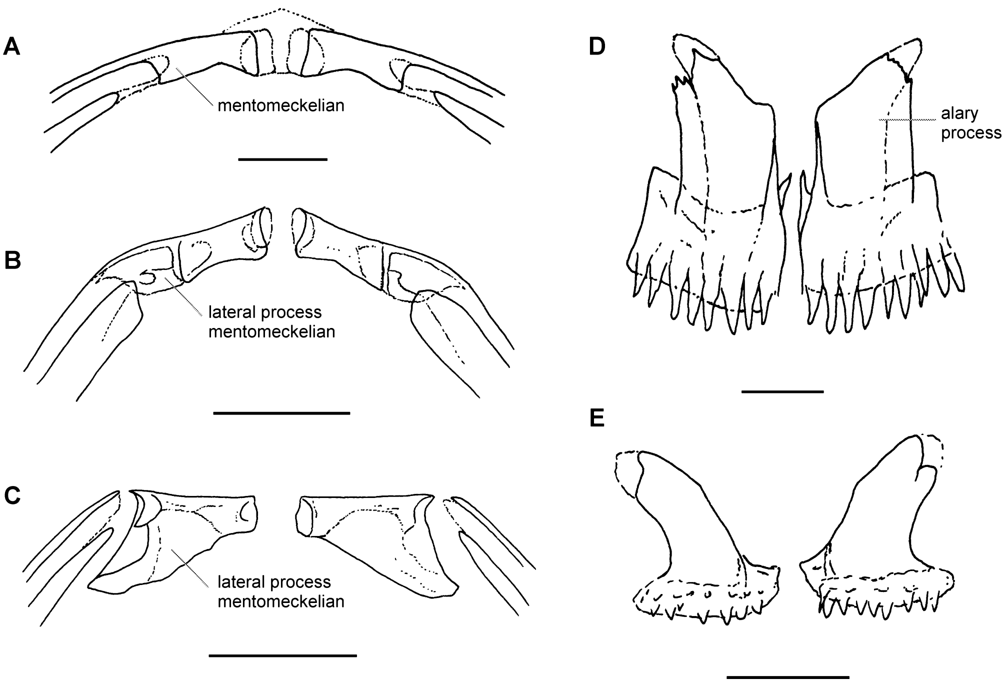

Fig. 9. Lower jaw, anterior edge: (A) *Poyntonia paludicola* (CNC 6636). (B) *Natalobatrachus bonebergi* (PEMA 2505). (C) *Hemisus marmoratus* (ES). Premaxilla: (D) *Scotobleps gabonicus* (TMSA 84313). (E) *Natalobatrachus bonebergi* (PEMA 2505). Scale bar = 1 mm.

around 2/3 length of orbit (Fig. 5H); (2) long, reaching the level of neopalatines and *planum antorbitale* (Fig. 5D).

57. Pterygoid, medial ramus: (0) long and relatively wide (Fig. 5F); (1) reduced in proportional length, even to rudimentary bumps (Fig. 5H, Duellman and Trueb, 1986, p. 314, fig. 13.17D); (2) proportionally long but narrow (Fig. 5D). State 0 is the common state, while state 1 occurs only in some Cacosterninae, *Mantella*, *Breviceps* and *Hemisus*. State 2 occurs only in Astylosterninae and *Leptopelis*.

58. Pterygoid, articulation of medial ramus: (0) on anteroventral surface of rounded prootic, medial ramus of pterygoid and prootic may be separated slightly by fibrous or cartilaginous material (Fig. 5H); (1) on ventrolateral edge of otic capsule, may contact parasphenoid ala; (2) anterior to and strongly adpressed to parasphenoid ala for at least 3/4 its length, in same frontal plane (Sheil, 1999, p. 52, fig. 1B). This character is a modification of Clarke's (1981) character 14, which coded the extent of overlap of the anterior border of the parasphenoid ala and the medial ramus of pterygoid in the anterior to posterior plane, which is not independent of the position of the articulation. Clark's 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). Expressing the position of the articulation appears to be less influenced by these measurements, coded here in Characters 57 and 60. State 1 is the common state in ranids, and state 2 occurs in *Pyxicephalus* and *Aubria*.

59. Parasphenoid alae, in frontal plane: (0) perpendicular to body axis (lateral); (1) pointing slightly anterolaterally (Duellman and Trueb, 1986, pp. 314–315, figs 13.17C and 13.18G); (2) pointing distinctly posterolaterally (Duellman and Trueb, 1986, p. 314, fig. 13.17A). State 0 is the common condition, while state 1 is autapomorphic in this taxon set for *Breviceps*. The direction of the alae in state 1 and 2 does not appear to influence the position of the articulation of the medial ramus of the pterygoid (Character 58). Comparison of the state distribution between these two characters does not suggest that they are correlated.

60. Parasphenoid alae: (0) moderately long (Fig. 5B); (1) reduced or short (Fig. 5G). Lynch (1971) noted the occurrence of this variation in leptodactylids, where the parasphenoid alae may be short or long, oriented at right angles to the anterior rami or deflected posteriorly, and may or may not be overlapped by the median rami of the pterygoids.

Osteology: skull, dorsal view

61. Cranial exostosis on frontoparietals, maxillae, zygomatic rami of squamosals and nasals: (0) absent; (1) present. In the taxon sample examined in this study, cranial exostosis was observed only in *Aubria*, *Pyxicephalus* and *Nannophrys*. Both *Pyxicephalus* and *Nann-*

ophrys also exhibit extensive co-ossification of skin and dermal roofing bones, documented in Sheil (1999) and Clarke (1983), respectively. Co-ossification and exostosis are not considered to be independent in the present study, hence only one of these characters was used in this analysis. The extent and level of development of the exostosis is reduced in *Aubria* compared with *Pyxicephalus* and *Nannophrys*, figured in Sheil (1999, p. 52) figs 1A, C, and Clarke (1983, p. 383) figs 2A, C, respectively. The unspecific description of "cranial exostosis present" as a diagnostic character for tribe Pyxicephalini of Pyxicephalinae (e.g., Dubois, 2003) requires specific redefinition, because the extent and distribution of cranial exostosis differs on various cranial elements in different taxa. Ford (1990) and Sheil (1999) discussed exostosis in detail.

62. Nasals, overlap with sphenethmoid in transverse plane: (0) overlapping the sphenethmoid; (1) not overlapping the sphenethmoid, separated by some distance. This character could be influenced by the stage of development of the specimens examined, and was therefore scored only in adult specimens.

63. Nasals, median contact: (0) widely separate, not in contact; (1) extensive contact along medial margin. Ford (1990) found the extent of contact between the nasals to be correlated with the size of the nasals, but was a less subjective measure than the relative size of the nasals.

64. Nasals, shape: (0) large, triangular (Bolkay, 1915, p. 172, fig. 1); (1) large, rectangular or square to round; (2) small, thin triangular or club-shaped (Figs 5A, C). This character has traditionally been difficult to assess. In the present study, a more conservative coding strategy than that employed by Ford (1990) was used, according to which orientation was not considered.

65. Degree of development of otic plate of squamosal and its relationship with prootic: (0) otic plate present, partly overlapping *crista parotica*, in some cases posteriorly only or the lateral border of prootic only (Clarke, 1981, p. 293, fig. 3A); (1) overlapping all or most of *crista parotica* and 1/4 to 1/2 of prootic (Bolkay, 1915, p. 172, fig. 1; Clarke, 1981, p. 293, fig. 3B); (2) otic plate rudimentary or absent, only a thin rib of bone overlapping outside of *crista parotica* (Fig. 5E, Clarke, 1981, p. 293, fig. 3C); (3) otic plate rudimentary, otic ramus extends posteriorly for approximately 1/2 width of lateral border of prootic in an arc, otic plate overlaps *crista parotica* in this region only (Clarke, 1981, p. 293, fig. 3D).

66. *Crista parotica*, cartilaginous process extending from posterolateral edge towards suprascapula: (0) absent or present and very short, not more than a slight bulge (Fig. 5C); (1) present, long and thin, cartilaginous (Fig. 5A); (2) present, robust and thick, mineralized; (3) cartilaginous, extending around to fuse with and form part of the top of a large tympanic annulus. Da Silva (1997) noted fusion of the tympanic annulus with the *crista parotica*, as in state 3, in *Pseudacris* Fitzinger, 1843. State 2 occurs only in some heavily ossified fanged ranids, and state 3 is restricted to some Petropedetinae.

67. *Crista parotica*, nature: (0) cartilaginous; (1) mostly mineralized. The *crista parotica* is only mostly mineralized in the fanged ranids and the burrowing *Hildebrandtia*.

68. *Crista parotica*, angle: (0) perpendicular to body axis in frontal plane; (1) angled forward in frontal plane, assessed from position of anterior margin of *crista parotica* (Fig. 5C). State 0 is the common state in ranids. In state 1, the *crista parotica* is distinctly displaced forward, and much narrower distally than proximally. The otic capsules are extremely rounded in some taxa displaying state 1, which may partly account for this unique geometry. Laurent (1973) discussed rounded versus transversely elongated otic capsules as a character in Arthroleptidae.

69. Frontoparietal fenestra: (0) large, exposing more than 1/3 of width of frontoparietals and fenestra together, often frontoparietals severely reduced and narrower than fenestra (Fig. 5E); (1) present as a small gap, with each frontoparietal slightly reduced but wider than fenestra; (2) merely a suture, frontoparietals large and touching centrally; (3) small, a round gap at posterior edge of orbits (Clarke, 1983, p. 383, figs 2A, B). State 0 occurs only in some Microhylidae and *Cacosternum*. State 1 occurs only in two other Cacosterninae and *Sooglossus*, whereas state 3 is autapomorphic for *Nannophrys*.

70. Frontoparietals, anterior margins: (0) medial edges do not extend forward as much as lateral edges (Drewes, 1984, p. 7, fig. 1A); (1) medial edges extend forward to the same level as the lateral edges and the central portion (Fig. 5A); (2) medial edges extends forward beyond the lateral edge, including if this is due to the apparent inward curvature of the anterior section of a poorly ossified frontoparietal (Drewes, 1984, p. 7, fig. 1B); (3) medial and lateral edges do not extend forward as far as the medial portion, which is expanded anteriorly, leading to a heart-shaped frontoparietal arrangement. State 2 was assigned when the frontoparietals were weakly ossified and reduced, and thus appeared to curve inwards (as in Figs 5C, E).

71. Frontoparietal, overall shape: (0) rectangular; (1) wider anteriorly than posteriorly; (2) wider posteriorly than anteriorly; (3) roughly an isosceles triangle, apex of triangle facing laterally, base adpressed to other frontoparietal. This character is concerned with lateral expansion of the whole anterior or posterior section of both frontoparietal bones, and the distribution of states is independent to that of the extent of relative forward projection of the anterior lateral versus anterior medial margins referred to in Character 70. The presence of a posterior medial frontoparietal ridge (Bolkay, 1915, p. 172, fig. 1; Clarke, 1981, character 3: 1) was not included in this study, as the failure to clear adequately in many large specimens rendered it difficult to score with accuracy, but this character of fanged ranids should be considered in future studies.

72. Squamosal, width of zygomatic versus otic ramus: (0) otic ramus appears thicker than zygomatic ramus in dorsal view, as a distinct angular bend, or "twist", not evident where the otic ramus joins the zygomatic ramus, otic ramus in approximately the same plane as zygomatic ramus; (1) both rami appear approximately the same width, where the rami join there appears to be a distinct change of angle, or "twist", so that these two rami are not in the same plane; (2) zygomatic ramus noticeably expanded, bend at junction of the zygomatic and otic rami not evident. This character, coded in dorsal view, defines the relative degree of lateral development and alignment of these two rami, which is not expressed in the traditional form of this character, given below (Character 73).

73. Squamosal, length of zygomatic ramus relative to length of otic ramus: (0) zygomatic ramus longer than otic ramus; (1) zygomatic ramus approximately equal in length to otic ramus; (2) zygomatic ramus shorter than otic ramus.

74. Maxilla, shape of *pars facialis* in lateral view: (0) well developed anteriorly and posteriorly, rectangular; (1) reduced anteriorly, therefore triangular; (2) absent or reduced anteriorly and posteriorly, may be rectangular. The *processus palatinus* (= *p. frontalis*) was not included in the assessment of this character, as it appears to be consistently present in all taxa examined for this study. Variation in the flange extending anterior to the *processus palatinus* is assessed here instead.

75. Quadratojugal, contact with maxilla: (0) continuous, articulating with maxilla, slanting over each other or strongly overlapped; (1) anterior process of quadratojugal not touching maxilla. The quadratojugal is one of the most frequently reduced anuran skull bones (Lynch, 1973; Trueb, 1973).

76. *Pars articularis*: (0) mineralized; (1) not mineralized, descending ramus of squamosal appears separated from descending ramus of pterygoid only by cartilaginous or clear connective tissue (i.e., unmineralized structures, not bone adjacent to bone). De Villiers (1931, p. 389) noted that the "quadrate cartilage is totally unossified … [in] *Cacosternum*, and the quadrato-maxillary does not invade the quadrate cartilage, but is merely applied to it". This condition, observed only in some Hyperoliidae and Cacosterninae, is presumably caused by a lack of mineralization in the *pars articularis*.

77. *Pars externa plectri* of breeding males: (0) large, rounded, covering 1/3 to 2/3 of area inside tympanic annulus (Fig. 5B); (1) small and rod-like, or absent (Fig. 5C). Specimens in which the tympanum may have been torn during preparation were not used for scoring.

78. Premaxilla, projection of *pars facialis* (alary process) in relation to *pars dentalis*, longitudinal plane: (0) vertical (dorsal), perpendicular to *pars dentalis*; (1) backwards (posterodorsally); (2) forwards (anterodorsally). This character does not appear to be correlated with the extent to which the tip of the snout projects forward (Character 128), as the *pars facialis* is vertical in *Phrynobatrachus*, where the snout is wedge-shaped and considerably overshot.

79. Premaxilla, angle of *pars facialis* (alary process), transverse plane: (0) dorsally, perpendicular to *pars dentalis* (Fig. 9D); (1) inclined laterally outwards away from midline (Fig. 9E).

80. Tympanic annulus: (0) complete; (1) incomplete, rounded (Fig. 5E); (2) absent; (3) incomplete, pear-shaped, involving squamosal as its dorsal limit, with dorsal section of cartilage fused onto squamosal. Care was taken to code this character from undamaged specimens, or to consider any potential damage to the tympanic annulus during specimen preparation. State 3 occurs predominantly in Arthroleptidae and Hyperoliidae.

81. Stapes (columella): (0) present; (1) absent.

Hyolaryngeal apparatus, ventral view

82. Hyoid, hyale, free flange towards jaw just anterior to jaw angle: (0) absent; (1) present (Fig. 10C).

83. Medial element of anterior process of hyale (anterior horn): (0) long, straight, thin (Fig. 10B); (1) long and usually curled, relatively thick (Fig. 10E); (2) small nipple-shaped knob only (Fig. 10C) (3) slightly elongated, but not more than three times its width (Fig. 10D); (4) absent (Duellman and Trueb, 1986, p. 321, figs 13.21A, C, D, F). The condition observed in Microhylidae was interpreted as the absence of the entire anterior horn (both medial and lateral elements), following Drewes (1984, p. 12).

84. Hyoid, shape of stalk of anterolateral (alary) process: (0) narrow, pinched, blade-like (Fig. 10B); (1) thick, rounded, slightly less than or equally as expanded as the thick distal portion (Figs 10D, F).

85. Hyoid, anterolateral (alary) process, width of base: (0) approximately equal to stalk (Fig. 10B); (1) distinctly broader than stalk (Fig. 10D).

86. Hyoid, shape of distal expansion of anterolateral (alary) process: (0) oval, slanted posteriorly at 45° to body axis; (1) large, rounded to trumpet-shaped or slightly triangular expansions (Fig. 10A); (2) extremely small, rounded, edges may be ragged (Fig. 10B); (3) small, narrow, blade-like, slanting posteriorly at 45° (Fig. 10E).

87. Hyoid, angle of stalk of anterolateral (alary) process: (0) angled anteriorly (Figs 10B, E); (1) angled laterally (Figs 10A, F).

88. Hyoid, hyoglossal sinus: (0) deeper than anterior border of base of alary processes (Figs 10B, C, E); (1) shallow, less than or just reaching anterior border of base of alary processes (Figs 10A, D, F); (2) shallow,

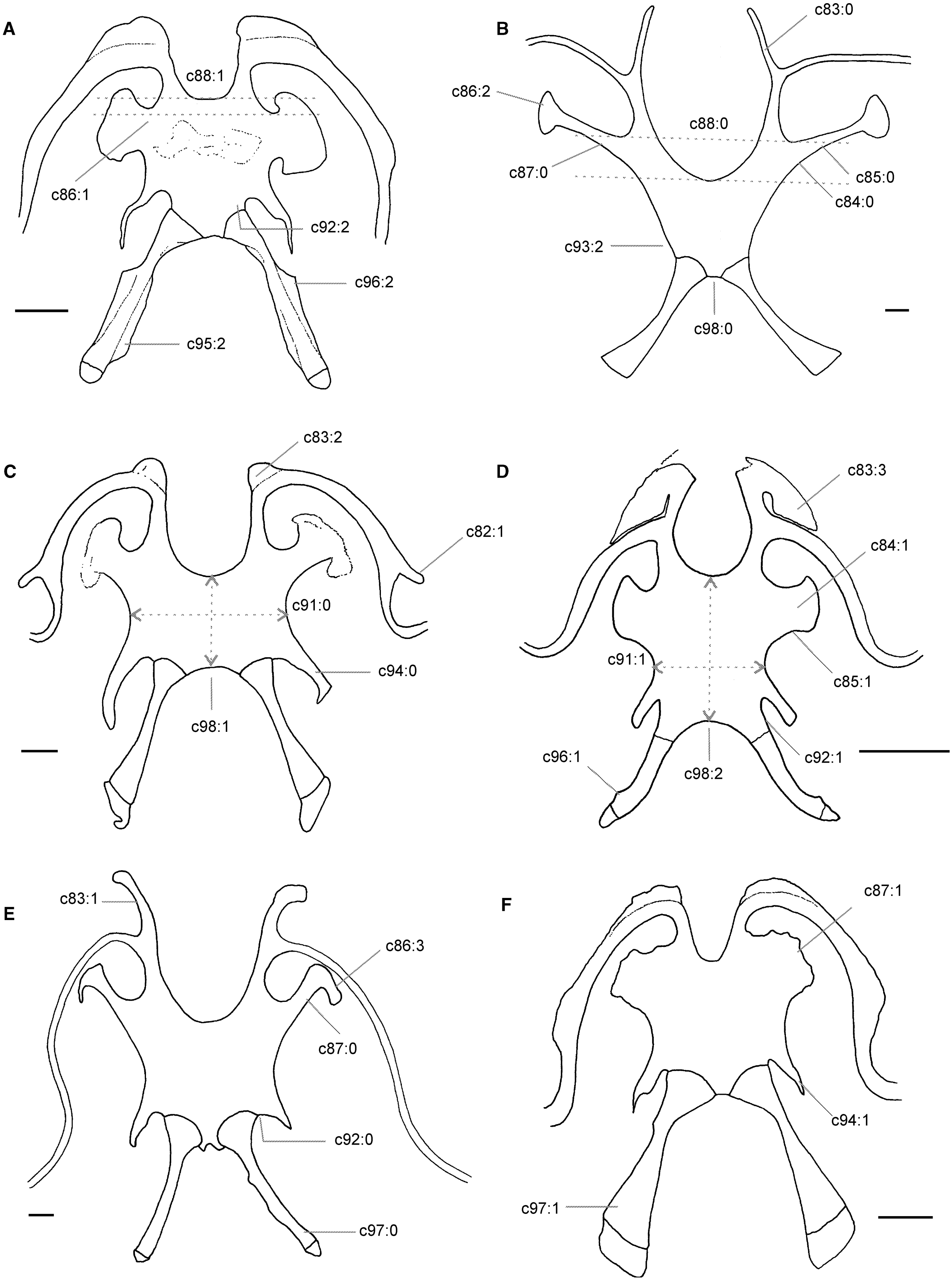

Fig. 10. Hyoid apparatus: (A) *Phrynobatrachus natalensis* (ES 288). (B) *Leptopelis vermiculatus* (ES 717). (C) *Tomopterna tandyi* (AC 1561). (D) *Cacosternum boettgeri* (ES 152). (E) *Arthroleptides martiensseni* (ES 704). (F) *Poyntonia paludicola* (MB 1254). Scale bar = 1 mm.

with fibrous suture of a deep sinus visible. Reference lines used to assess this character are illustrated in Figs 10A and B. State 2 is autapomorphic in the current taxon sample for *Hemisus*.

89. Hyoid plate, calcification: (0) uncalcified or only slight calcification centrally, but never calcified between thyrohyals; (1) well calcified, with large proximal expansions at bases of thyrohyals, which appear almost fused at posterior end of hyoid plate. Parahyoid bones do not occur in the taxa examined in this study, although parahyoid calcification is common. Only calcification between the thyrohyals is described in this character, and this was observed only in *Hemisus*, *Breviceps* and in some Asian Ceratobatrachinae.

90. Hyoid, fibrous uncalcified suture on hyoid plate: (0) absent; (1) present centrally, running transversely across entire width of hyoid plate; (2) present centrally, running longitudinally and not present at extreme anterior and posterior edges of hyoid plate. State 1 is visible in the region where the parahyoid bone is illustrated for *Rhinophrynus dorsalis* Duméril and Bibron, 1841 in Duellman and Trueb (1986, p. 321) fig. 13.21B.

91. Hyoid plate, shape: (0) wide, width greater than or equal to length (Fig. 10C); (1) narrow, longer than wide (Fig. 10D). Measured from the medial point between the thyrohyals to the anteromedial edge of the hyolaryngeal sinus, and across the narrowest point underneath the alary processes. Reference lines used to assess this character are illustrated in Figs 10C and D.

92. Hyoid, posteromedial process (thyrohyal): (0) cartilaginous stalk absent (Fig. 10E); (1) cartilaginous stalk present, long (Fig. 10D); (2) hyoid plate pinched above thyrohyals, posterior lateral processes originating close to base of alary processes (Fig. 10A). Trewavas (1933) noted that the absence of a stalk is the common condition. Laurent (1978) discussed the importance of cartilaginous stalks of the thyrohyals in supporting putative hyperoliid–arthroleptid relationships. Stalks appeared to be present in a single slightly immature specimen of *Amnirana albolabris* that was examined. The hyoid plate is pinched above thyrohyals (state 2) when the thyrohyals are situated close together, and attached to a cartilaginous base formed by the narrowing of the posterior portion of the hyoid plate. This narrow section could conceivably be the fused vestiges of the stalks, or it could represent a prestalked condition. State 2 is equivalent to Faivovich's (2002) character 9: 1. The full stalked condition (state 1) was not observed in *Arthroleptella* or *Cardioglossa* (cf. Blommers-Schlösser, 1993). However, the presence of Faivovich's (2002) state 1 in some species of both of these genera indicates that state 2, as defined in the present study, was considered to be "stalked" by both Blommers-Schlösser (1993) and Faivovich (2002), although its usage by Laurent regarding hyperoliids and arthroleptids is only equivalent to state 1 of the present study.

93. Hyoid, posterolateral process: (0) present; (1) extremely reduced, small bumps only; (2) absent (Fig. 10B). Laurent (1978) considered state 2 to support his proposed relationship between Hyperoliidae and Arthroleptidae (Laurent, 1951), although many Astylosterninae exhibit posterolateral processes.

94. Hyoid, posterolateral processes, length: (0) long, greater than 1/3 length of posteromedial process (thyrohyal) (Fig. 10C); (1) short, less than 1/3 length of posteromedial process (Fig. 10F); (2) rudimentary bumps or stumps. This character was assessed by comparison to the thyrohyals. Although the coding used here is therefore dependent on the length of the thyrohyals (i.e., long thyrohyals make the processes appear short), this method was nevertheless considered to be objective for quantifying the length of the posterolateral processes.

95. 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 presents a concave inside edge (Fig. 10A). Wu (1994) mentioned flanges on the inner surfaces of the thyrohyals in Microhylidae.

96. Hyoid, posteromedial process (thyrohyals), expanded flange on lateral side: (0) absent; (1) present distally, small (Fig. 10D); (2) present medially, with curved edge (Fig. 10A). Wu (1994) mentioned flanges on the outer surfaces of the thyrohyals in Microhylidae.

97. Hyoid, thyrohyals, distal ends: (0) unexpanded (Fig. 10E); (1) expanded (Fig. 10F).

98. Hyoid, distance between posteromedial processes (thyrohyals): (0) close together, less than one times the width of proximal expansion of thyrohyal apart (Fig. 10B); (1) approximately one times the width of proximal expansion of thyrohyal apart (Fig. 10C); (2) more than 1.5 times the width of proximal expansion of thyrohyal apart (Fig. 10D).

99. Cricoid ring, esophageal process: (0) present; (1) absent. Trewavas (1933) suggested that a mediodorsal esophageal process is restricted to, and diagnostic for, Ranidae s.l and Rhacophorinae. However, this process occurs widely in leptodactylids (Lynch, 1971) as well as some Microhylidae, Dendrobatidae and Sooglossidae (Wu, 1994). It is scored present where observed, but absence records for some taxa may be artifacts of preparation and staining. Some equivocal cases were scored as indeterminate. The length of the process was found to vary in ranids and should be further investigated.

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

101. Larynx, arytenoid cartilages of breeding male: (0) rounded; (1) disproportionately elongated and oval-shaped, relative to width of entire larynx. Coded from ventral aspect, not dorsal aspect as in Faivovich's (2002) character 15.

Osteology: limbs

102. Carpal state *sensu* Laurent and Fabrezi (1990): (0) Type A, 7 elements, distal carpalia 3, 2 and Y element (or preaxial *centrale* of Jarošovà, 1973) free; (1) Type B, 6 elements, fusion of distal carpal 2 with Y element, distal carpal 3 free; (2) Type C, 5 elements, distal carpal 3 fused to distal carpal 2 plus Y element; (3) Type D, 6 elements, distal carpal 2 and Y element both free, distal carpal 3 fused with 4–5; (4) Type E, 5 elements, distal carpal 2 fused to Y element, distal carpal 3 fused with 4–5; (5) Type F, 4 elements, Y element and all distal carpalia 2–5 fused to form a larger distal carpal; (6) as D, 6 elements, but incomplete fusion of carpal 3 with 4–5, suture visible. The six states of this character, recognized by and illustrated in Laurent and Fabrezi (1990), were scored from the original paper, and extrapolated to other taxa with similar carpal structure. Additional unpublished observations kindly provided by M. Fabrezi (pers. comm.) were also incorporated. This coding scheme is considered the best representation of the complexities of carpal structure because, as noted by Ford (1990), three factors hinder the traditional approach of simply determining the raw number of carpal elements. Firstly, there is disagreement concerning the homology of the different elements that form during ontogeny. Secondly, different patterns of fusion may lead to the same reduced numbers. Thirdly, taxonomic variation is evident in the individual elements involved in the fusion (Holmgren, 1933; Jarošovà, 1973; De Saint-Aubain, 1981; Ford, 1990). State 4 does not occur in any taxa in the matrix assembled for the present study, but was included here as a reference for future use of this complicated character. The carpus of *Tomopterna* appears complex and requires further evaluation.

103. Tarsal one (not *naviculare*): (0) absent as an independent element, fused; (1) present as an independent element, not fused. The terminology of Ford (1990) was used in this character, which could not be assessed for many of the larger ranids, due to insufficient clearing.

104. Distal intercalary elements: (0) absent; (1) present, thick concave discs; (2) present, wedge-shaped, rounded anteriorly and slightly concave posteriorly; (3) present, wedge-shaped, not rounded anteriorly and concave posteriorly. The presence of intercalary elements is considered an adaptation to an arboreal habit (Laurent, 1964). Drewes (1984) stated that the intercalary elements in Hyperoliidae are probably homologous, but noted different shapes in other groups of Anura. Paukstis and Brown (1990) also noted variation between the intercalary cartilages of Hyperoliidae and those of Rhacophorinae and Mantellinae. These differences were incorporated into the coding used here, but require further investigation. The thick concave discs in *Phrynomantis* were assigned a separate, autapomorphic state, as in Drewes (1984).

105. Digital subarticular sesamoids of hand: (0) absent; (1) present (Drewes, 1984, p. 16, fig. 9 for foot). Drewes (1984) reported the presence of digital subarticular sesamoids in *Ptychadena oxyrhynchus* (Smith, 1849). Among the ptychadenine exemplars examined for the present study, these elements were found only in *Ptychadena mascareniensis*. Digital subarticular sesamoids occur only sporadically in ranids. These are also referred to in the literature by Laurent (1940, 1941a,b, 1942).

106. Sesamoid(s) on ventromedial surface of tarsometatarsal joint: (0) absent; (1) present. Although Ford (1990) did not distinguish between ventromedial sesamoids and ventrolateral sesamoids, both the number and placement of elements were found to be variable in the present study. The character was therefore separated into two. The variation observed occurs primarily in Cacosterninae.

107. Sesamoid(s) on ventrolateral surface of tarsometatarsal joint: (0) absent; (1) one present; (2) two present; (3) three present.

108. Sesamoid in the *aponeurosis palmaris*: (0) none; (1) one. Wu (1994) referred to the dorsal carpal sesamoid, not the ventral sesamoid referred to here.

109. *Os sesamoides tarsale*: (0) absent; (1) present. Nussbaum (1982) discussed this character in detail, and noted that it occurs only in some petropedetine ranids, Sooglossidae and Pipidae Gray, 1825. In ranids, this element generally occurs only in small taxa, probably serving a protective function over the Achilles' tendon.

110. *Cartilago sesamoides*: (0) present; (1) absent. Nussbaum (1982) discussed this character, which is more common in ranids than the *os sesamoides tarsale*.

111. Prepollex: (0) not fused to Metacarpal II to form fighting spike; (1) fused to Metacarpal II to form a fighting spike. State 1 occurs in most Petropedetinae s.s.

112. Prepollex: (0) composed of two or more elements; (1) composed only of a single element. Length variation in the prepollex was used by Wu (1994), but was found difficult to code rigorously. Fabrezi (2001) defined prepollical variation in terms of the number and shape of elements, which should be followed in future studies. In *Amolops*, the prepollex was found to be curved and almost the same length as Metacarpal II. This condition probably also supports the characteristic enlarged spiny nuptial pads of the dicroglossine genus *Paa*, or some of its subgenera.

113. Flange (*crista lateralis sensu* Gaupp, 1896) on dorsolateral surface of humerus of mature male: (0) absent; (1) present proximally, large (Lynch, 1971, p. 64, fig. 41B); (2) present distally, small. Lynch (1971) noted that the greatly enlarged forelimbs of males of some species of *Leptodactylus* Fitzinger, 1826 have been mentioned frequently in the literature (illustrated in Noble, 1931, p. 110, fig. 37B). The skeletal basis for this is the presence of enlarged flanges on the humeri of mature males, which are sexually dimorphic (small in females). The position of the *crista lateralis* and *crista ventralis* (of Character 114 below) are illustrated in Duellman and Trueb (1986, p. 345) fig. 13.35C, E.

114. Flange (*crista ventralis sensu* Gaupp, 1896) on ventral surface of humerus: (0) long, about 1/2 the length of humerus, grading into bone; (1) small, about 1/4 to 1/3 the length of humerus, ending abruptly; (2) long, about 1/2 the length of humerus, but squared off and ending abruptly. Variation in this feature across Ranoidea was initially noted by D.E. van Dijk (pers. comm.).

115. Metacarpal of Digit IV in breeding males, distal tuberosity: (0) absent; (1) present (Liem, 1970, p. 39, fig. 35). Liem (1970) noted that this tuberosity is the point of insertion for the third slip of the *musculus humerodorsalis*.

116. Metacarpal of Digit II of breeding male: (0) no enlargement; (1) enlarged flange-like nuptial tuberosity, distally on the outer edge (Gaupp, 1896, pp. 72–73, figs 43, 44). This tuberosity was named the *tuberositas pro musculus abductor indicis longus* by Gaupp (1896), who noted that it is the point of insertion for the *musculus abductor indicus longus*. Duellman and Trueb (1986, p. 345, fig. 13.35A) referred to this as the nuptial tuberosity.

117. Metacarpal of Digit II 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, leaving distal phalanges set off at an angle to axis of Digit II (Parker, 1936, p. 145, fig. 1); (2) like other metacarpals. The second metacarpal is enlarged into a spike (state 1) only in Petropedetinae s.s. (excluding *P. natator*, which exhibits the common state 2). The spike does not penetrate the skin in *Arthroleptides*, but does so in *Petropedetes*. Parker (1936) observed that in *Petropedetes johnstoni* (Boulenger, 1887), males in their first breeding season often exhibit a nuptial pad at the dislocation of the second metacarpal-phalangeal joint, and that the spine may not yet protrude. In fully mature breeding males, however, Parker (1936) noted that the spine is always present and the nuptial pad absent. This requires verification, but it is possible that in *Arthroleptides*, development of the spine merely arrests earlier than in *Petropedetes*. See Characters 111 and 133.

118. Shape of tips of terminal phalanx of Digit IV of hand: (0) bifurcate, T- or Y-shaped; (1) knob-like, simple; (2) sharply pointed, slightly elongated. This is a simplified version of this widely used character (discussed further below).

119. Shape of terminal phalanx of Digit IV of foot: (0) large T-shaped; (1) small T- or Y-shaped; (2) simple or only slightly dilated; (3) long, sharply pointed; (4) Y-shaped, arms bearing flattened ovate flanges; (5) pointed, truncated (short) to triangular, tip may be a small globule; (6) long, sharply pointed, as in state 3, but tip separated from the body of terminal phalanx and bent sharply downwards (may or may not perforate the integument in life). This character represents a much finer level of coding than in the traditional usage. Blommers-Schlösser (1993) suggested that *Phrynodon* has large T-shaped tips but only Y-shaped tips were observed in the present study. This suggests either variability within this taxon, or demonstrates that T- versus Y-shaped tips sometimes cannot easily be distinguished. Accordingly, they were not coded as separate states in this character, but rather combined into state 1. This state is distinctly different to the tips described by state 4, which display oval flanges. Sanderson (1936) reported that state 6 seems to be retractile in Astylosterninae. State 6 was not observed in the species of *Ptychadena* examined for this study, in which the tip remained attached to the terminal phalanx (thus scoring as state 3).

External morphology: mouth and snout

120. 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 was frequently noted in species descriptions from older literature (e.g., Boulenger, 1882, 1920; Noble, 1924; Ramaswami, 1934, 1935; Narayan Rao, 1937; Inger, 1954; Loveridge, 1954; Poynton, 1964; Poynton and Broadley, 1985), but information concerning this character was only recently synthesized by Grant et al. (1997). In the present study, the medial lingual process was coded following Grant et al. (1997), with some minor modifications. The Type D process, defined by Grant et al. (1997), was not observed, rather *Arthroleptis variabilis* was instead scored for a Type C process (state 3), whereas a different species of *Discodeles* was scored for a Type A, cone-shaped process (state 1). *Arthroleptides martiensseni* was here considered to exhibit a Type B (state 2) process, as in *Petropedetes*. In many cacosternine taxa, the occasional overstaining with alcian blue revealed the presence of a rudimentary medial lingual process, 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 displaying this state, but they may exhibit a slight indent medially on the lingual surface, as noted by Poynton (1963) and Grant et al. (1997).

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

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

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

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

125. Tongue, shape: (0) maximum width approximately equal to medial length; (1) medial length greater than maximum width; (2) wide, but just short of being wider than long; (3) heart-shaped. Perret (unpublished) demonstrated some of the variation in this character that is observed in petropedetine and arthroleptid frogs. State 3 is the nominate condition for *Cardioglossa*. Variation in this character requires further study.

126. Tongue, distal margin: (0) not indented, entire; (1) indented in center, lobed. This feature is mentioned extensively in older literature (Boulenger, 1882; Noble, 1931; Deckert, 1938; Laurent, 1950, 1986).

127. Posterior palatal fold: (0) absent; (1) present. Wu (1994) noted that the presence of one or two transverse dermal folds is usually considered the most reliable diagnostic character of Microhylidae (although it is absent in some Malagasy cophylines). One or two folds, which may be smooth or bear various numbers of papillae, may be present anterior to the larynx on the roof of the mouth cavity. Zweifel (1972) found from 5 to 20 papillae on these folds. Wu (1994) further noted that, when both the anterior and posterior folds are present, the posterior fold is always wider than the anterior fold, and when only one fold is present, it should be regarded as the posterior fold.

128. Snout profile: (0) rounded and overshot (Lynch, 1971, p. 29, fig. 4D); (1) wedge-shaped (Lynch, 1971, p. 29, fig. 4C). Inger (1954) mentioned the shape of the snout extensively in his treatment of the Philippine ranids. This variation was also observed in leptodactylids (Lynch, 1971).

129. Callused dorsal snout of breeding males: (0) absent; (1) present. A callused tip of the snout was observed 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 males than in females.

Muscles

130. *Musculus cutaneus pectoris*: (0) absent; (1) present as thin slip; (2) present as thick slip. Refer to Tyler (1971) for a discussion of the distribution of this muscle.

Secondary sexual characteristics

131. Breeding males, color 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 and Basu (1957) first noted black pigment on the testes of *Cacosternum* and, to a lesser extent, *Ptychadena mascareniensis*. Besides most Cacosterninae and *Ptychadena*, *Phrynobatrachus natalensis* was the only other taxon displaying state 1 in this sample. This species also exhibits a graying of the bone marrow cavities and excess pigmentation in many organs, which are probably not homologous with the character described here. The configuration of the Wolffian ducts was used by Liem (1970) for Hyperoliidae, and variation in this feature was observed in taxa examined for the present study. Bhaduri and Basu (1957) also noted variation in the configuration of the "uterus" (ovisac) in ranid frogs. This variation warrants further investigation concerning its utility in future phylogenetic studies.

132. Breeding males, nuptial excrescences on hand: (0) absent; (1) velvety, on Digit II only; (2) velvety, on Digits II and III; (3) velvety, on Digits II, III and IV; (4) short spines on Digits II, III and IV; (5) pad of small white spines on Digit II; (6) pad of large black spines at base of Digit II. Stewart (1967) meticulously described variation in this feature for Malawian frogs. Inger (1954) recorded variation in nuptial excrescences for Philippine ranids. Lynch (1971) and Heyer (1975) noted various states of pads or spines in leptodactylids. A cluster of sharp black cones at the base of Digit II (state 6) occurs only in *Leptodactylodon* and *Trichobatrachus* within the present taxon sample and, combined with their enlarged humeral flanges (Character 113: 1), represents a breeding condition that occurs also in Leptodactylidae Werner, 1896 (Duellman and Trueb, 1986). A condition similarly described as state 6 appears to define the dicroglossine tribe Paini (Dubois, 1992). Parker (1940) suggested that spines and pads are an adaptation to aquatic amplexus, since he observed that frogs that amplex on land often lack nuptial pads, but those that amplex in water possess them. However, no spines or pads are evident in some aquatic African ranids, such as *Aubria* (Perret, 1994).

133. Breeding males, subterminal spike formed from Metacarpal II: (0) absent or non-protruding; (1) present, protruding through skin (Noble, 1931, p. 116, fig. 40C). A protruding spike-like metacarpal (state 1) occurs in *Petropedetes parkeri* and *P. newtoni* of the taxa examined here, as well as in additional species of this genus. In *Arthroleptides*, where Metacarpal II is thickened, the phalanges of Digit II do not displace laterally out of alignment with the phalanges, and Metacarpal II does not protrude through the skin. See discussion of Character 117. Noble (1931) mentioned this spike in *Petropedetes* and suggested that it might function to assist in grasping the female during amplexus. The humeral flange is enlarged (Character 113: 1), for additional attachment of hypertrophied muscles, in species of *Arthroleptides* and *Petropedetes* in which the spike occurs. Males are larger than females in these taxa, and larger males are often substantially scarred, suggesting that the spike of Metacarpal II is used as a weapon during male combat.

134. Breeding male, length of Digit IV of hand: (0) normal; (1) considerably longer than other digits, dorsal or lateral surface of Digits III and IV may be covered in dermal denticles (Noble, 1931, p. 116, fig. 40A). An elongated Digit IV, with or without associated denticles (state 1) occurs in many species of *Arthroleptis* and *Cardioglossa* (Laurent, 1957).

135. Breeding males, hedonic glands on forearm: (0) diffuse glandular region on inside of forearm; (1) hemispherical disc-like glandular flaps (suprabrachial glands) near axilla (Duellman and Trueb, 1986, p. 59, fig. 3.14); (2) none. Glandular regions on the inside of the forearms (state 0) are well known in Hyperoliidae, but appear to occur also in the outgroup *Heleophryne*. Inger (1954, p. 314) noted that male *Pulchrana signata* (Günther, 1872) display "humeral glands". Noble (1931) suggested that pectoral glands function in holding the female during amplexus. Drewes (1984) suggested that, in Hyperoliidae, the glands are hedonic in nature, and probably related to the unusual mode of amplexus in Hyperoliidae. Large glandular regions inside the forearm probably function like pectoral glands. Hemispherical disc-like glandular flaps near the axilla (state 1) occur in many species of *Amnirana* (Perret, 1977), and are well developed in *Hydrophylax*. According to Perret (1994, p. 256), in *Aubria occidentalis* Perret, 1994 "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, p. 259) figs 1A, B, the gland appears to be well developed and, compared to *Amnirana* (see Duellman and Trueb, 1986, p. 59, fig. 3.14 and Perret, 1977, p. 856, fig. 6), appears to be homologous. These glands are more strongly developed in the female, as is the case with femoral glands in *Aubria* (Perret, 1994; Ohler, 1996). This information is not contained in this matrix, since the exemplar species included, *A. subsigillata*, scores differently. *Dimorphognathus* displays raised cylindrical disc-like swellings on the dorsal surfaces of the wrists, the function of which is unknown, but probably hedonic. These structures are unlikely to be homologous with the character described here, due to their different position. Duellman and Trueb (1986, p. 58) report a similar structure to that observed in *Dimorphognathus* as present on the wrist of *Hemisus*, but this was not evident in the specimens of *H. marmoratus* examined here.

136. Gular gland in breeding males: (0) absent; (1) present (Duellman and Trueb, 1986, p. 58, fig. 3.12A). The gular gland is a complex character of Hyperoliidae (Liem, 1970; Drewes, 1984), but for the purpose of this analysis, it was simply coded as present or absent, due to the small sample of Hyperoliidae included in this study. The gland was scored absent in *Hemisus* (cf. Haas, 2003), because Drewes (1984, p. 20) stated that it is merely a "hollow cutaneous pouch, no more glandular than dorsal skin" in this genus and Liu (1935, legend to plate 4) describes *Hemisus* as simply having a "small accessory lobe". A true gular gland, as evident in Hyperoliidae, was not observed in *Hemisus* examined for this study.

137. Vocal sac breeding male, nature: (0) single median; (1) paired, internal or external; (2) absent. 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), which was used to score this character, e.g., Boulenger (1920), Liu (1935), Dubois (1992), Dubois and Ohler (2000, 2001), Dubois et al. (2001). Information was often equivocal and errors may exist in the scoring of this character (and the related Character 138). Unknown states were assigned to taxa where doubt exists.

138. Vocal sac breeding male, if paired: (0) internal; (1) external.

139. Sexual dimorphism: (0) adult females similar in size or larger than adult males; (1) adult males much larger than adult females. An increase in the size of males compared with females appears to be correlated with male combat or male parental care, and is a well-documented character of some of the fanged ranids of Asia (Emerson and Berrigan, 1993; Emerson and Ward, 1998). However, none of the exemplars of Asian fanged ranids included in the present study were scored as Character 139: 1. Thus, the condition of males larger than females was not responsible for grouping the African and Asian fanged ranids together in the present analyses, although larger size in males and enlarged heads remain potentially synapomorphic for some of these taxa.

140. Femoral glands in males: (0) absent; (1) present. This character would be more informative within ranids if the types of glands were coded, following dissection, as in Glaw et al. (2000). Although these authors also coded the position of the gland, distinguishing between glands situated closer to the knee, the vent or intermediate between them, this positional reference is difficult to quantify objectively. The presence of femoral glands is listed as a characteristic of Pyxicephalinae (Dubois, 2003), but these were not observed in *Pyxicephalus* species in the present study (cf. Ohler, 1996), and they have not been documented in other works dealing with the genus (e.g., Poynton, 1964; Lambiris, 1989a; Passmore and Carruthers, 1995; Channing, 2001). However, Parry (1982) mentioned the occurrence of femoral glands in the subspecies *P. adspersus angusticeps* Parry, 1982, from Mozambique, and they appear to be visible in two of the four juvenile paratypes (Parry, 1982, p. 289, fig. 5). However, specimens of *Pyxicephalus* from Senegal, Chad and Mali, deposited at MHNHP, do exhibit femoral glands.

141. Femoral granules: (0) obvious, well-defined, confined to a small region proximally, extending less than 2/5 length of thigh; (1) absent or extremely faint, slight ridges may be evident; (2) as in state 0, but extending 1/2 to 3/4 length of thigh from vent. The skin of the ventral surface of the thighs is coarsely granular in many species, and the extent of these femoral granules varies. Femoral granules are here considered to be independent of the presence of femoral glands, contrary to Glaw et al. (2000), who considered these structures as homologous. Both may be observed in the same individual. Daly et al. (1996, p. 5) also reported that "the purported [femoral] glands are coexistent with the patch of granular skin on the underside of the thigh" in *Mantella*. Femoral granules and femoral glands thus fail the criterion of conjunction required for two structures to be considered homologous (Patterson, 1982; De Pinna, 1991). The development of the femoral granules may be affected by breeding condition (although they do not appear to be sexually dimorphic), or the state of preservation of the specimen (Daly et al., 1996). The presence of a patch of large raised spines around the vent, described for some *Chaparana* (Dubois, 2003), is not considered as constituting state 0 here, and also occurs in some *Pyxicephalus*. Mature breeding males of *Conraua goliath* also display keratinized spines on the chest, belly and chin, listed by Dubois (2003) as characteristic of tribe Paini. These keratinizations, which appear to be related to breeding condition, require further investigation, particularly in fanged ranids.

142. Secretory papilla in the center of tympanum, breeding males: (0) absent; (1) present (Noble, 1931, p. 116, fig. 40C). Parker (1936) discussed this feature extensively. Du Toit (1943) described it as an outgrowth of the tympanic membrane. Duellman and Trueb (1986) followed Noble (1931) in considering it an outgrowth of the columella, whereas Klemens (1998) restated Du Toit's (1934) original views. Recently, Narins et al. (2001) investigated the histology of these papillae, and concluded that they are secretory in function. Parker (1936, plate I) suggested that this feature may regress out of the breeding season in *Petropedetes johnstoni*.

External morphology: general

143. Supratympanic fold: (0) strong, may be glandular; (1) weak or absent; (2) strong, encircling entire dorsal section of a large tympanum. This character was mentioned in species descriptions for Philippine ranids by Inger (1954), and discussed in detail by Lynch and Duellman (1997).

144. Tympanic membrane, visibility from exterior: (0) indistinct, covered by skin of similar thickness to that on remainder of head; (1) distinct, as skin over tympanum is thinner; (2) partly distinct, partly covered, only a crescent visible. Some covering of part of the tympanum is evident in particular *Afrixalus* species, but the manner in which this is obscured was not investigated in the present study. Dissection revealed that the posterior half of the tympanum is covered by muscle in *Ericabatrachus baleensis*, but this is not visible externally. A similar condition is well-documented in Dendrobatidae (Ford, 1990), where muscle covers part of the tympanum. State 0 occurs in all taxa in which the tympanic annulus is absent (Character 80: 2), but also in many taxa in which this structure is present. Refer to Lynch and Duellman (1997) for a discussion of the confusing descriptions and terminology previously applied to the tympanum.

145. Width of eye versus tympanum, adult male: (0) tympanum less than radius of eye; (1) tympanum greater than radius but less than diameter of eye; (2) tympanum greater than diameter of eye. Various authors (Boulenger, 1920; Noble, 1931; and others) have noted sexual dimorphism in tympanum size in many ranids (illustrated in Noble, 1931, p. 121, fig. 43). Although the size of the tympanum is sexually dimorphic in some American ranid taxa, e.g., *Aquarana catesbeiana* (Shaw, 1802) and *A. clamitans* (Latreille, 1801), this is rarely observed among African ranids (Noble, 1931).

146. Shape of pupil: (0) rhomboid; (1) horizontal; (2) round; (3) vertical. Laurent (1957, 1986) used this character extensively in discussing a possible relationship between Hyperoliidae and Arthroleptidae. For the present study, this character was scored mainly from the literature or photographs because the shape distorts in preservation. The shape of the pupil in *Heleophryne* was not scored as vertical, as in Lynch (1973), or horizontal as in Heyer (1975), as it is better described as rhomboidal. The pupil shape of *Conraua*, *Nannophrys*, *Euphlyctis*, *Limnonectes* and *Hoplobatrachus*, observed in photographs of live animals, is also best described as rhomboidal, i.e., predominantly horizontal with distinct dorsal and ventral points of inflection. This state probably occurs more widely in fanged ranids, e.g., *Fejervarya*, *Lankanectes* and *Sphaerotheca*. Examination of preserved *Nannophrys* indicated distortion of the pupil to such an extent that it could be considered vertical, which would be an erroneous character score, as *Nyctibatrachus* is the only ranid reported to exhibit a vertical pupil. Future studies should examine pupil shape, the presence of umbraculae and lines of pigmentation in the eyes. Such characters should be scored from live animals, or photographs thereof.

147. Webbing between toes: (0) extensive; (1) rudimentary, 1/4 to 1/2 of longest toe; (2) trace at the base of toes, or no web. This character is highly variable intragenerically, and may be more indicative of adaptations to contemporary environments (Laurent, 1964) than historical relationships.

148. Dorsal digital scutes on terminal phalanx of feet: (0) absent; (1) present (Noble, 1931, p. 116, fig. 40C). Digital scutes were mentioned by Du Toit (1943) and Lynch (1971). Digital scutes are rare in ranids, but a condition which could be described as incipient scutes or weak scutes is sometimes observed (e.g., in both of the rhacophorine exemplars examined in this study).

149. Relative length of Digit III of hand: (0) Digit II not reaching tip of Digit III; (1) Digit II equal in length or extending beyond Digit III. This character is similar to Ford's (1990) character 114, which portrayed the relative lengths of the metacarpals. Dubois (1992, in lit.) has variously used this feature when describing particular taxa.

150. Relative length of Digit IV of hand, adult males: (0) Digit IV marginally longer than Digit II; (1) Digit IV and II equal in length; (2) Digit IV substantially longer than Digit II, usually covered in dermal denticles. This character was mentioned extensively in species diagnoses by Inger (1954). It is considered independent from Character 149, based on the distribution of states. State 2 occurs in many Arthroleptinae.

151. Color pattern on posteroventral surface of thighs: (0) uniformly solid, usually dark, extending onto plantar surfaces (Stewart, 1967, p. 109, fig. 44); (1) reticulate blotches or broken stripes, not extending onto plantar surfaces (Stewart, 1967, p. 69, fig. 26); (2) mottled. The use of color pattern as a higher-level phylogenetic character in Anura is generally avoided on the grounds that it is too variable to be informative. However, the specific patterns described here contain consistent variation at higher taxonomic levels. These patterns have successfully been used to diagnose the various species of *Ptychadena* (Poynton, 1964; Stewart, 1967) in which they are highly consistent. The uniform, wide, single dark brown bands observed on the thighs of many African and Asian ranoids, which usually extend from around the cloaca to the soles of the feet, are assumed to be plesiomorphic, based on their widespread distribution across major ranoid clades. The character warrants further study.

152. Tip of terminal phalanx of Digit IV of foot: (0) deltoid, triangular or semicircular expansion of digit tip into a digital disc, with circum-marginal groove; (1) even width tip of digit, not enlarged and without terminal bead or circum-marginal groove; (2) digit narrows near tip, crowned by a hard, narrow bead-like covering. Digital discs, used by Inger (1954) in his species diagnoses, are thought to be associated with an arboreal habit (Laurent, 1964; Lynch, 1971). Deltoid discs may be an adaptation to fast-flowing riparian habitats, in which frogs require additional grip on slippery wet rock surfaces. Discs on the fingers are usually similar to those on the toes, with few notable exceptions, such as *Natalobatrachus*. The presence of a hardened bead (state 2) was not noted in the literature, but its hard texture can readily be determined by feel (tactically). Where beads are present, the tips of the digits also appear to be narrower than those of frogs exhibiting non-expanded digit tips and lacking beads (state 1), and are usually slightly lighter in coloration. Phalangeal beads usually occur on the tips of both fingers and toes, but tend to be more strongly developed on the toes.

153. Outer two metatarsals: (0) deeply incised, separated by web almost to base (Inger, 1954, p. 206, fig. 35); (1) forming part of a fleshy sole, only separated distally (Inger, 1954, p. 206, fig. 34). This character was referenced to in Inger's (1954) species diagnoses as the outer metatarsal region united for at least 2/3 of length, or separated for at least 2/3 of length. Poynton (1963, 1964) and Poynton and Broadley (1985) referred to the outer metatarsals as bound into a fleshy sole to describe state 1 of this character. Deeply incised and separated metatarsals (state 0) tend to occur in heavily webbed aquatic forms, and may represent an adaptation to increase the surface area of the webbing. Metatarsals bound into a fleshy sole have been suggested to be an adaptation to a terrestrial habit (Poynton, 1964). However, there are many obvious exceptions to these generalizations, e.g., in *Mantidactylus*.

154. Inner metatarsal tubercle of female, length compared to length of Digit V (as measured from the base of the subarticular tubercle to tip of Digit V): (0) shorter than or equal to Digit V; (1) longer than Digit V, flattened and indistinct; (2) longer than Digit V, expanded into a protruding digging flange. The position of features on hands and feet, as well as terminology applied to them in this study, are detailed in Fig. 11. The inner metatarsal tubercle is always present, but varies in size. It was found to be sexually dimorphic in some Arthroleptinae, and was therefore consistently scored from female specimens.

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

156. Tarsal fold: (0) absent; (1) present, entire length of tarsus; (2) present, connecting to mid-tarsal tubercle, not extending entire length of tarsus. Tarsal folds are common in some taxa, e.g., bufonids, but less so within ranids. Inger (1954) mentioned tarsal folds in his descriptions of Philippine ranids.

157. Lateral margin of Digit V and Metatarsal V, loose well-developed flap of skin: (0) absent; (1) present (Perret, 1994, p. 259, fig. 3). A loose flap of skin on the outside of Digit V and Metatarsal V (state 1), extensively illustrated and referred to in Inger's (1954) diagnoses of Philippine ranids, occurs in many aquatic forms, probably assisting in swimming.

158. Mid-tarsal tubercle: (0) absent; (1) present. The presence of a mid-tarsal tubercle, together with the presence of a medial lingual process, was previously thought to be diagnostic for *Phrynobatrachus* (Poynton, 1964). However, this combination also occurs in some Dendrobatidae of the genus *Colostethus* Cope, 1866, e.g., *C. atopoglossus* Grant, Humphrey and Myers, 1997 (Grant et al., 1997). The structure appears to be morphologically identical in these taxa.

159. Heel tubercle: (0) absent; (1) single, small and round to spike-like; (2) row of three. State 1 occurs in most Phrynobatrachinae, whereas state 2 is autapomorphic for *Platymantis* among the taxa examined in this study.

160. Basal (proximal) row of subarticular tubercles of feet: (0) abnormally large, tending to square; (1) large, round to oval; (2) 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 *Sooglossus* and *Ericabatrachus baleensis*, both of which lack subarticular tubercles.

161. Subarticular tubercles of feet: (0) spherical or conical; (1) oval, long, flattened; (2) raised perpendicularly, moderately to markedly elongated but roughly semihemispherical in shape, distal subarticular tubercles of fourth toe coalescing. State 2, described in detail by Clarke (1983), is autapomorphic for *Nannophrys* among the exemplars examined in this study.

162. Outer metacarpal tubercle: (0) divided, middle section smaller than or equal in size to outer section; (1) divided, middle section larger than outer section; (2) entire. The surface of the manus usually bears an outer metacarpal (sometimes called the palmar) tubercle and an inner metacarpal (sometimes called the thenar) tubercle proximally. The outer metacarpal tubercle is divided in many Neobatrachia, and may even be separated into two sections, resulting in what Lambiris (1989b) referred to as the middle metacarpal tubercle, as illustrated in Fig. 11A. This character appears to be suitable for distinguishing species in generic-level revisions.

163. Palm of hand: (0) smooth; (1) granular. Granular palms were only observed in Rhacophorinae and arboreal Hyperoliidae.

164. Number of distal subarticular tubercles present on Digit IV of hand, excluding basal (proximal) row of subarticular tubercles: (0) one; (1) none; (2) two. Some frogs, notably some Cacosterninae, lack distal subarticular tubercles on Digit IV, and exhibit only the basal subarticular tubercle. This configuration is potentially diagnostic for separating the southern African *Afrana fuscigula* (state 0) from *Afrana angolensis* (state 1), two species that are otherwise almost impossible to distinguish on the basis of external morphology.

165. Palmar supernumerary tubercles, proximal to the basal row of subarticular tubercles: (0) indistinct or absent; (1) distinct in one or two rows; (2) indistinguishable from granular palms. The palmar tubercles (*sensu* Lambiris, 1989b), here referred to as palmar supernumerary tubercles (Fig. 11), may be faint or distinct within a species, but are always present or absent in a particular species.

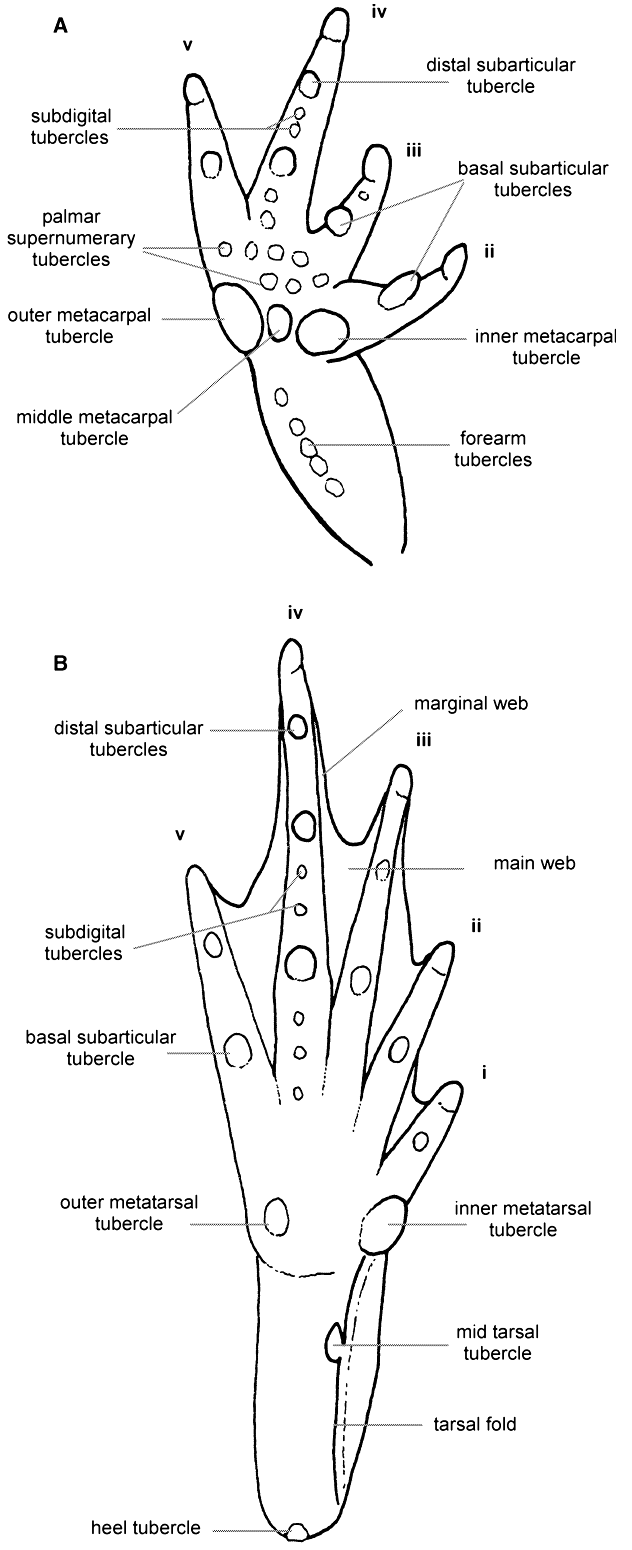

Fig. 11. Generalized composite schematic illustrations of hand (A) and foot (B) of anurans, redrawn from Lambiris (1989b), indicating the terminology used in character descriptions. Numerals represent digit ontogeny followed.

166. Tubercle on ventrolateral surface of wrist: (0) absent; (1) present. This weak tubercle, laterally displaced off the palm, occurs in most Phrynobatrachinae and three Asian taxa.

167. Dorsal raphe running along spine: (0) absent; (1) present. The raphe is a narrow, indented fold in the dorsal skin, visible as a fine line. Laurent (1957) mentioned this character in his work on Arthroleptidae. This character is polymorphic in *Hemisus*. The dorsal raphe is also present in many species of Microhylidae, as shown in figures from Zweifel (1985) and Dunn (1949), and *Mantella*, as shown in figures from Glaw and Vences (1994).

168. Transverse fold across head behind eyes: (0) absent; (1) present (Noble, 1931, p. 530, fig. 173B). A transverse fold across the back of the head occurs in many large fanged ranids, and many Microhylidae (Dunn, 1949), although this was not used as a character by Wu (1994).

169. Abdominal coloration: (0) uniform or slightly mottled; (1) small, regular round spots; (2) irregular spots; (3) small reticulations; (4) large reticulations, semicircular, may fade to uniform in adult. (5) single large circular bulls-eye or target pattern. Refer to discussion of reservations when using color characters in Character 151.

170. Abdominal skin: (0) coarsely granular throughout; (1) smooth throughout; (2) some granulation evident on posterior half of abdomen, chest region smooth. This character was scored from well-preserved specimens or photographs of live animals, as granulations may become distorted and even disappear as a result of poor preservation or extreme specimen age.

171. Gular skin of female, texture: (0) granular or rippled; (1) smooth. Granulation of the gular skin in females does not appear to be correlated with granulation of the abdominal skin, and is thus assumed to be independent.

172. Sacral gland: (0) none; (1) present, single; (2) present, separated into two dorsolateral strips of glands, continuous and complete, or incomplete and broken into paired oval glands in the lumbar and sacral regions. Body glands were described in detail by Lynch (1971) and used in inferring leptodactylid relationships by Heyer (1975).

173. Skin ridges on dorsum: (0) none; (1) few, broken or distinctly discontinuous (Stewart, 1967, p. 55, fig. 20); (2) more than six, approximately continuous (Stewart, 1967, p. 67, fig. 25); (3) two well-developed, continuous, raised, thick glandular dorsolateral ridges; (4) chevron-shaped glands in scapular region, or running down length of body (Stewart, 1967, p. 94, fig. 37). The number and form of the dorsal skin ridges was used in keys to African ranids (e.g., Poynton, 1964; Poynton and Broadley, 1985). Inger (1954) mentioned the form of this character in his diagnoses of the Philippine ranids. The variable nature of skin features across the Anura suggests that these structures should be coded conservatively for higher-level analyses. State 3 is highly conservative, and was referred to by Dubois (2003, in lit) as "dorsolateral folds", a major characteristic in his classification of Ranidae. This state is present in many ranids not included in the present analysis. Chevron-shaped glands (state 4) are ridges of skin that originate in the scapular region, and may be short, or extend the entire length of the body to the level of the groin. They are usually rounded in profile and exhibit a distinct point of inflection. The figures in the original description of *Ericabatrachus baleensis* illustrate chevrons (Largen, 1991), but these were not present on the specimens examined for this study, and were therefore scored absent for this species.

Breeding behavior

174. Amplexus position: (0) inguinal; (1) axillary; (2) male "glued" to female in modified inguinal pose; (3) weak or straddling; (4) male forearms along female flanks, male vent half a body length back from female vent. State 2 is autapomorphic in this taxon sample for *Breviceps*. Glaw et al. (1998) hypothesized that weak or straddling amplexus (state 3), as displayed by Mantellinae, may occur in some of the petropedetine taxa that exhibit femoral glands. However, due to a lack of information regarding their amplexus, many Petropedetinae were scored unknown, or as having axillary amplexus, as observed in the majority of ranids. State 4 occurs only in Hyperoliidae.

Larvae

175. Tadpole feeding: (0) exotrophic; (1) endotrophic, feeds from yolk. This coding substitutes for the condition of "direct development". Ontogenetic pathways to "direct development" may vary considerably but, in all instances, larval endotrophy (at least during part of their development) is assumed to be common. *Phrynodon* was scored for the presence of exotrophic larvae, although the tadpoles of this taxon develop differently from those of most other Phrynobatrachinae (see Amiet, 1981). Direct development requires further detailed investigation in Ranoidea.

176. Tadpoles, behavior: (0) not schooling in tight swarms; (1) schooling in tight swarms, usually with adult protection. State 1 of this character was scored only for *Pyxicephalus* and *Aubria*, but is known to occur in other fanged ranids (Emerson, 2001; Dubois, 2003). The presence of schooling in *Phrynomantis* was noted by Spieler (2003), although these aggregations appear to dissipate at night.

Karyology

177. Haploid chromosome complement (n): (0) 13; (1) 13, with 5 chromosomes substantially larger than the others; (2) 12; (3) 11; (4) 9; (5) 14; (6) 8 or fewer. This character was scored from the literature (Morescalchi, 1973, 1981; Bogart and Tandy, 1981; Channing and Bogart, 1996; Supaprom and Baimai, 2003), and is therefore incomplete.

Appendix 3

Chronological references to previous phylogenetic use of morphological characters included in the present analysis, and followed by the original character number. Most characters were modified from previous use; identical or equivalent states are not implied.

2. Lynch (1973) 9, Heyer (1975) 33, Heyer and Liem (1976) 11. Drewes (1984) mentioned this in his character 7, and in personal communication. Analogous to Ford (1990) 71. **3.** Drewes (1984) 8, and mentioned by Lynch (1973). **4.** Lynch (1973) 10, Lynch (1978) 12, Drewes (1984) 6, Ford (1990) 72, Wu (1994) 136. **7.** Lynch (1973) 3, Heyer and Liem (1976) 9, Clarke (1981) 20, Wu (1994) 139. **8.** Ford (1990) 99 alluded to variation in the degree of calcification of the suprascapula. **10.** Ford (1990) 79. **11.** Lynch (1973) 7, Lynch (1978) 13, Ford (1990) 77, Blommers-Schlösser (1993) 4, Wu (1994) 145. **12.** Clarke (1981) 21, Cannatella (1985) 109, Ford (1990) 101, Wu (1994) 166, Glaw et al. (1998) 13. **13.** Heyer (1975) 36, Heyer and Liem (1976) 14, Clarke (1981) 21, Cannatella (1985) 104, Ford (1990) 102, Wu (1994) 165. **14.** Lynch (1973) 6, Heyer (1975) 34, Lynch (1978) 22, Heyer and Liem (1976) 12, Ford (1990) 75, Wu (1994) 143, Faivovich (2002) 21. **16.** Heyer and Liem (1976) 12, Wu (1994) 142. **17.** Liem (1970) 17, Lynch (1978) 21. **18.** Inger (1967), Liem (1970) 16, Lynch (1973) 4, Heyer and Liem (1976) 8, Drewes (1984) 5, Ford (1990) 65, Wu (1994) 140, Vences (1999) 11. **19.** Lynch (1973) 5, Heyer (1975) 29, Heyer and Liem (1976) 10, Lynch (1978) 11, Clarke (1981) 15, Drewes (1984) 29, Ford (1990) 10, Blommers-Schlösser (1993) 23, Wu (1994) 125, Glaw et al. (1998) 1, Vences (1999) 5. **20.** Lynch (1973) 14, Ford (1990) 83, Trueb and Cloutier (1991) 46, Blommers-Schlösser (1993) 24, Wu (1994) 151. **21.** Clarke (1981) 17, Cannatella (1985) 93, Ford (1990) 84, Wu (1994) 152. **22.** Similar to Ford (1990) 32, **23.** Inger (1967), Lynch (1973) 11, Clarke (1981) 18, Duellman and Trueb (1986) C, Ford (1990) 88, Wu (1994) 158, Emerson et al. (2000a) 1, Haas (2003) 144. **25.** Tyson (1988) 48, Ford (1990) 80, Wu (1994) 149. **26.** Drewes (1984) 15, Wu (1994) 146. **28.** Lynch (1973) 12, Lynch (1978) 14, Cannatella (1985) 85, Tyson (1988) 61, Ford (1990) 89, Blommers-Schlösser (1993) 24, Wu (1994) 159–161. **29.** 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. **31.** Lynch (1978) 15, Clarke (1981) 19, Ford (1990) 93. **32.** Heyer (1975) 32. **33.** Liem (1970) 21, Heyer and Liem (1976) 5, Drewes (1984) 2, Cannatella (1985) 17, Ford (1990) 7, Wu (1994) 63. **34.** Liem (1970) 20, Drewes (1984) 1, Ford (1990) 6, Glaw et al. (1998) 3. **35.** Cannatella (1985) 14, Ford (1990) 48. **36.** Lynch (1973) 22, Clarke (1981) 11, Cannatella (1985) 12, Duellman and Trueb (1986) E, Ford (1990) 35, Trueb and Cloutier (1991) 7, Wu (1994) 95, Haas (2003) 146. **37.** Duellman and Trueb (1986) E, Ford (1990) 35, Wu (1994) 95. **39.** Clarke (1981) 10, Ford (1990) 37, Wu (1994) 89. **40.** Alternate version of Ford (1990) 36. **42.** Ford (1990) 32, Wu (1994) 92. **44.** Liem (1970) 22, Heyer (1975) 26, Heyer and Liem (1976) 7, Drewes (1984) 4, Ford (1990) 43, Wu (1994) 94, Vences (1999) 7. **45.** Lynch (1973) 21, Heyer and Liem (1976) 1, Cannatella (1985) 64, Ford (1990) 20, Wu (1994) 21, Glaw et al. (1998) 5, Vences (1999) 8. **46.** Cannatella (1985) 52 and 53, Ford (1990) 14, Wu (1994) 73. **47.** Clarke (1981) 8, Cannatella (1985) 55, Ford (1990) 17, Vences (1999) 5. **48.** Clarke (1981) 9, Ford (1990) 32, Wu (1994) 86. **49.** Lynch (1978) 8, Clarke (1981) 13, Cannatella (1985) 35, Ford (1990) 32. **50.** Emerson and Berrigan (1993) 7. **52.** Ford (1990) 52, Wu (1994) 103. **53.** Wu (1994) 105. **54.** Clarke (1981) 12, **55.** Clarke (1981) 12, Ford (1990) 45. **56.** Lynch (1978) 10, Cannatella (1985) 30, Ford (1990) 46, Wu (1994) 99, Vences (1999) 9. **57.** Cannatella (1985) 37, Ford (1990) 33. **58.** Lynch (1978) 9, Ford (1990) 34, Wu (1994) 87. **61.** Clarke (1981) 2, Cannatella (1985) 3, Ford (1990) 4, Wu (1994) 62. **62.** Heyer (1975) 23, Heyer and Liem (1976) 2, Wu (1994) 54, Faivovich (2002) 0. **63.** Lynch (1978) 2, Clarke (1981) 1, Ford (1990) 1, Wu (1994) 51, Vences (1999) 1. **64.** Liem (1970) 20, Clarke (1981) 1, Cannatella (1985) 4, Ford (1990) 2, Wu (1994) 52. **65.** Lynch (1978) 5, Clarke (1981) 5, Ford (1990) 29, Faivovich (2002) 4. **67.** Ford (1990) 49, in a simplified form. **69.** Heyer (1975) 24, Heyer and Liem (1976) 4, Lynch (1978) 3, Cannatella (1985) 22, Ford (1990) 5, Trueb and Cloutier (1991) 16, Wu (1994) 56, Faivovich (2002) 3. **70.** Liem (1970) 19, Wu (1994) 61, Glaw et al. (1998) 4. **71.** Liem (1970) 19, Ford (1990) 3. **73.** Heyer (1975) 25, Heyer and Liem (1976) 6, Clarke (1981) 6, Cannatella (1985) 42, Ford (1990) 30, Glaw et al. (1998) 7, Vences (1999) 2. **74.** Clarke (1981) 7, Ford (1990) 16, Wu (1994) 76, Glaw et al. (1998) 6, Vences (1999) 3 and 4. **75.** Heyer (1975) 21, Drewes (1984) 3, Ford (1990) 21 and 22, Wu (1994) 75. **76.** Similar to Lynch (1978) 1, Ford (1990) 21, Wu (1994) 78. **78.** Ford (1990) 12, Wu (1994) 68. **79.** Wu (1994) 72. **80.** Wu (1994) 66. **81.** Lynch (1973) 22, Lynch (1978) 20, Cannatella (1985) 45, Ford (1990) 11, Wu (1994) 67. **83.** Heyer (1975) 30 part, Heyer and Liem (1976) 19, Drewes (1984) 11 part, Ford (1990) 55, Wu (1994) 110, Faivovich (2002) 8. **84.** The shape of the alary processes was used by Liem (1970) 12, Heyer (1975) 31, Heyer and Liem (1976) 18, Ford (1990) 59, Wu (1994) 112. **88.** Ford (1990) 57, Wu (1994) 111. **89.** Emerson and Berrigan (1993) 36. **90.** Wu (1994) 118. **91.** Emerson and Berrigan (1993) 37, Wu (1994) 108. **92.** Liem (1970) 10, Heyer and Liem (1976), Drewes (1984) 10, Ford (1990) 62, Blommers-Schlösser (1993) 9, Wu (1994) 114, Emerson et al. (2000a) 5, Faivovich (2002) 9. **93.** Liem (1970) 15, Drewes (1984) 9, Ford (1990) 60, Wu (1994) 113, Vences (1999) 21. **94.** Liem (1970) 15 part, Ford (1990) 61. **95.** Wu (1994) 116. **96.** Wu (1994) 117. **97.** Wu (1994) 115. **98.** Liem (1970) 10, Ford (1990) 63. **99.** Wu (1994) 120, Faivovich (2002) 11. **100.** Blommers-Schlösser (1993) 8, Wu (1994) 115. **101.** Faivovich (2002) 15. **102.** Laurent and Fabrezi (1990). **103.** Lynch (1973) 18, Drewes (1984) 27, Ford (1990) 120, Blommers-Schlösser (1993) 25, Wu (1994) 180, Vences (1999) 16. **104.** Lynch (1973) 16, Drewes (1984) 24, Duellman and Trueb (1986) J, Tyson (1988) 26, Ford (1990) 116, Blommers-Schlösser (1993) 6, Wu (1994) 178–9, Glaw et al. (1998) 8, Vences (1999) 15, Emerson et al. (2000a) 2, Haas (2003) 151. **105.** Drewes (1984) 13, Ford (1990) 113, Blommers-Schlösser (1993) 16. **106.** Ford (1990) 123 in part, Wu (1994) 183. **107.** Ford (1990) 123 part, Wu (1994) 174. **108.** Tyson (1988) 32, Ford (1990) 108 and Wu (1994) 168. **109.** Wu (1994) 179. **111.** Wu (1994) 182. **113.** Lynch (1978) 23. **115.** Liem (1970) 26. **118.** 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, Faivovich (2002) 23, Haas (2003) 156. **119.** Liem (1970) 27, Heyer (1975) 35, Drewes (1984) 14, Blommers-Schlösser (1993) 20, 26. Glaw et al. (1998) 9, Vences (1999) 19, Faivovich (2002) 23, Haas (2003) 156. **120.** Grant et al. (1997). **127.** Blommers-Schlösser (1993) 11, Wu (1994) 8 and 9 combined, Emerson et al. (2000a) 10. **130.** Drewes (1984) 28, Tyson (1988) 65, Blommers-Schlösser (1993) 10, Wu (1994) 38, Emerson et al. (2000a) 3. **132.** Liem (1970) 35, Heyer (1975) 3, Emerson and Berrigan (1993) 8, Glaw et al. (1998) 15b, Vences (1999) 24. **134.** Blommers-Schlösser (1993) 19. **136.** Liem (1970) 36, Drewes (1984) 18, Blommers-Schlösser (1993) 22. **137.** Emerson and Berrigan (1993) 4. **140.** Blommers-Schlösser (1993) 28, Glaw et al. (1998) 17, Vences (1999) 22 and 23. **143.** Wu (1994) 6 as "tympanic fold". **144.** Heyer (1975) 2, Drewes (1984) 23, Wu (1994) 4, Emerson and Berrigan (1993) 1. **145.** Vences (1999) 38. **146.** Lynch (1973) 24, Heyer (1975) 1, Heyer and Liem (1976) 34, Lynch (1978) 17, Drewes (1984) 22, Blommers-Schlösser (1993) 30, Wu (1994) 3, Haas (2003) 143. **147.** Heyer (1975) 9, Heyer and Liem (1976) 37, Wu (1994) 19, Vences (1999) 32. **148.** Heyer (1975) 5 state E. **149.** Ford (1990) 114, Wu (1994) 10, Glaw et al. (1998) 18, Vences (1999) 30. **150.** Blommers-Schlösser (1993) 19. **152.** Heyer (1975) 5, Wu (1994) 15. **153.** Vences (1999) 32. **154.** Heyer (1975) 8, Heyer and Liem (1976) 38, Wu (1994) 16. **155.** Lynch (1973) 29, Heyer and Liem (1976) 39, Lynch (1978) 18, Wu (1994) 17, Vences (1999) 35. **156.** Heyer (1975) 6 state B. **157.** Heyer (1975) 6 state F, but no description presented. **158.** Heyer (1975) 6 state *C*. **170.** Heyer and Liem (1976) 35. **172.** Heyer (1975) 4. **174.** Lynch (1973) 23, Duellman and Trueb (1986) P, Blommers-Schlösser (1993) 15 and 29, Glaw et al. (1998) 15a, Haas (2003) 139.

Appendix 4

Distribution of 178 morphological characters among exemplar species. Character states are scored 0–8, ? (indeterminate), – (inapplicable), A (polymorphic 0/1). Refer to Appendix 2 for character descriptions. Page 1 of 4, characters 0–89

	0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85
Heleophryne purcelli	000000000000000000000000000000-00000000000000000000000000000000000000000000000000000000000
Afrana angolensis	131010101211022003120102010020104000010010000011110001002010001020000200100001100002011010
Afrana fuscigula	131000101211022003120102010020104000010010000001111000?002010000100000200100001100002011010
Afrixalus fornasinii	0311000012111110000001320000210-8100000000001001010001112012101010000212022010003000011010
Amnirana albolabris	131001101211012100120112010021114000000000000001011000100201200102010021010000101?000013010
Amolops ricketti	0?100100121111200012010201002011?0110101000000001000001112010000020000210100001010000001?000
Anhydrophryne rattrayi	130111001111111012103-320100101160111010001-1031010001012010001012000210011001110002111110
Arthroleptella hewitti	1301110011111110121021320110201160110010001-1031010001010010001012000210011001110002111110
Arthroleptella landdrosia	1301110011110120121021320100201160100000001-1031000011120010001022000210011101100002111110
Arthroleptides martiensseni	11100110011102200011011201002110?0000100000001011110011010010001010300200111001000001011000
Arthroleptis stenodactylus	13100100121111220120001320100210-1000001-001-101100001101000000001000022002100?113000?????0
Arthroleptis variabilis	11100010121111220020001320110210-1000011-001-1011000011012010000001000022002100113000101000
Astylosternus diadematus	1310001012110220010101020101210-80000100100000010110001102210000110000230110001103000010010
Aubria subsigillata	13100?101211022103120101010021114010010111000012011010112020010101210210200001100002111000
Batrachylodes vertebralis	0310111002110221021001320100211160-00000--00101201001100001000010000022002000110000-?1?000
Breviceps mossambicus	00021000000010000201201320110000-4--02-00001-1100-100020001111010200010120021000?A0?4000101
Cacosternum boettgeri	03020100000A100021103-3211000-1160001000000001031110001030002101022001022012111001003111110
Cacosternum capense	030201000001100011103-3201100-11600000000000010111110001130000001022001002011011000001011010
Cacosternum nanum	030201000001100021103-3211000-11600010000000010111110001031102001022001022012111000003111110
Cardioglossa escalaerae	1310100012110220021001320100210-8110001-001-1110000000000010000010000220020001010000111110
Cardioglossa gracilis	1010100012110220010001320100210-1010001-001-1110100000000001000?010000220020001010000111110
Chiromantis xerampelina	111000001111011003100112010021126010000000000031010001012012000020000201120001000001000010
Conraua crassipes	1310001012110221031201020100211060100101110010110110100120100000001010210101001000002111000
Conraua goliath	?3100?10121102210312010101002110601001001100001201101?112010000001?10210?01001000002111000
Dimorphognathus africanus	131101001211022102101112010021103000001-001-1011010111010012000110000210010001010002111110
Discodeles bufoniformis	131001101211022100110101010021116000010100000001101001100201000010000022010000110000?111001
Ericabatrachus baleensis	0?10110A111A111012003-320000100-?0110010001-1011110001011010000010000200021010003000011010
Euphlyctis cyanophlyctis	??100?1012110210031101120100211040000100100000221110000020?000010??10210101001000002111??0
Hemisus marmoratus	00110000?101011110100132-000212-0102--00??1-11-0--00120001-010?1?0001220022101??2104000121
Hildebrandtia ornata	031111111211022103-2--220100211140102-0210000011120000002010000023110200100001100002003100
Hoplobatrachus occipitalis	??100?1012110221031201010100211040100101110000120110000120?000010??10210101001000002111000
Hydrophylax galamensis	131001101211012103120112010021114000000000000001011000000201200102010021010000101?000013010
Hyperolius marmoratus	13110010121111110001001320000210-81000100000001011010001A10012101010000210020010003000012010
Kassina senegalensis	?3110?1010011110001101320000210-800000001000100111000?12201010111000022202001000000001??10
Leptodactylodon ventrimarmoratus	1310000012110220011001020001210-00000101100000100100010102120010200000200000000103000111000
Leptopelis mossambicus	11100010121111121000101320100200-7010010010001001010000110210001010000201110001100000002000
Leptopelis vermiculatus	11100010121111121000101320100200-7010010010000001010000110210001010000201110011100000002000

Appendix 4
Continued

Distribution of 178 morphological characters among exemplar species. Character states are scored 0–8, ? (indeterminate), – (inapplicable), A (polymorphic 0/1). Refer to Appendix 2 for character descriptions. Page 2 of 4, characters 0–89

	0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85
Limnonectes blythii	`13100110121102200312013201002110?0?001011000002?111000002010000101210210101000000000?111010`
Mantella aurantiaca	`03100110?111111011?001120100211110110010??1-11?000000100010?10000000021002200?21?00???????`
Mantidactylus femoralis	`??10??100211??2?0311011201002111600100111000?01101001100201000100000021011000101?001011010`
Microbatrachella capensis	`030211001001110012102132211010116100001000001031110001020110101022000102?11011100002011110`
Nannophrys ceylonensis	`131100001201110000101132010010116000010100000012000011012010010100000210-000010000???1?010`
Nanorana parkeri	`1?100110011101200212013101002110?000000000000011?10000000000001102011332111??11021????????`
Natalobatrachus bonebergi	`011101001111022102100112010021116001001-001-1010010001000010000010000210020001010002011010`
Nothophryne broadleyi	`031111000011101012103-3201002010200000000001-1011110001010000001020000102111011100002011?10`
Nyctibates corrugatus	`1310001012110220010101020001210-8000010010000010110001102210000010000230020001103000010010`
Pantherana pipiens	`131000101211022103120112010020104000000000000001111000002010000100000200100001100001011010`
Petropedetes cameronensis	`111011000111122002110112010021102000010010010011110011010010001020000200111001000000013000`
Petropedetes natator	`13100110?111122102111112010021102??00100000000111101??00201000101000020010100101000?013000`
Petropedetes newtoni	`111001100111122000110112010021102000010000010011110011010010001020300200111001000001013000`
Petropedetes parkeri	`111001100111122000110112010021102000010000010011110011010010000020000200111001000000011000`
Philautus surdus	`1110110011110120021011120100201210100000100000310100 1?010010001020000200120000000000000010`
Phrynobatrachus acridoides	`131101001211022102101112010021103000101-001-10210100010000010000110000210020001010002111110`
Phrynobatrachus cricogaster	`0311??00121102210210111201002110301?101-00??10?101000100001?001010000210?100?10?0002????10`
Phrynobatrachus krefftii	`03110?101211022102101112010021103000001-001-1021010011011012000010000210010001010002111110`
Phrynobatrachus natalensis	`131101001211122102101112010021103000001-001-10210100010000012000010000210020001000002111110`
Phrynobatrachus plicatus	`03110?001211022102101112010021103000001-001-1021010011000012000110000210110001010002111110`
Phrynodon sandersoni	`131001001211022002101112010020111001001-001-10110101110100120010100002101110?1110002111110`
Phrynoglossus laevis	`1311011012110221021101010100211060000100000010300100--132000000100001222100001000002111001`
Phrynomantis bifasciatus	`130200000001100013103-3200100-0-41002-00??1-1101110012030002101020001002022000001004101100`
Platymantis corrugatus	`1110?110021102210010013101002111600001011000001101001100201000010000021112000111000211110 1`
Poyntonia paludicola	`031111001111011012112132011020106000000000001030110000110110000010000202011000000002111110`
Ptychadena anchietae	`131111111211022100-2--220100211140102-0010000011120001002010000022100200100001000002003100`
Ptychadena mascareniensis	`031111111211022100-1--220100211140102-0010000011120000002010000022100200100001000002003100`
Pyxicephalus adspersus	`?31000101211022103120101010021114010010111000012011010112020010101210213200001100002011000`
Pyxicephalus edulis	`?3100?10121102210312010?010021114010010111000012011010112020010101210213200001?00002111000`
Schoutedenella taeniata	`0010110012111220120001320100210-1000001-001-1010110011002010000010000220021001113000101110`
Scotobleps gabonicus	`1310001012110220011101020001210-0000010010000010110001102210000100000200000001103000010010`
Sooglossus sechellensis	`???1??00???001002?0000000000000-500?2-????1-1?1?0?00--0?00???0011????11???10?1012101101100`
Staurois natator	`1110010A021111210310011201002011?0110010001-1011010001002012000020000200122001010000010010`
Strongylopus grayii	`131110101211022003120112010021114000010010000010110001002010001020000200100001100002011010`
Tomopterna marmorata	`021100101211212100110112010021116010010110001001010001012010000020000232020001000012111100`
Tomopterna tandyi	`121100101211212100110112011021116010010110000001010001012010000020000232020001000012111100`
Trichobatrachus robustus	`1310001012110220011?0102000?210-?01001011000001001000101221?000100000220??0000103000?????0`

Appendix 4
Continued

Distribution of 178 morphological characters among exemplar species. Character states are scored 0–8, ? (indeterminate), – (inapplicable), A (polymorphic 0/1). Refer to Appendix 2 for character descriptions. Page 3 of 4, characters 90–177

	90 95 100 105 110 115 120 125 130 135 140 145 150 155 160 165 170 175
Heleophryne purcelli	00000000000000000000000000000000----0000000000?00-00000000000000000000000000000000000000
Afrana angolensis	00000001100030000000100000002230----21000201002010002001110010120001000100010000411011001
Afrana fuscigula	00000001000030000000100000002230----21000201002010002001110010120001000100000000411011001
Afrixalus fornasinii	0112-00021010021000000001102150----110100000010-002012030000000010100302102000001?04002
Amnirana albolabris	21?000001?0031000000000001002010----210002?1001011002001110010000010000110001000021031001
Amolops ricketti	00000001000?310000000000012010000----210102050020??0020000100000000100000110001000000000?00?
Anhydrophryne rattrayi	00200100100030000000100010021 24----1101111000200-00001101200001100000010001000031100 11-0
Arthroleptella hewitti	002001?0100030000000A000100211?----1101011100200-000011012000011000000100010000311 0011-?
Arthroleptella landdrosia	01001100100130000201100010021 2?----1100011000200-002010012000011010000101011000011 0011-?
Arthroleptides martiensseni	000000001000300000001101100100210002100020400201011212121211000110000010000100002100100?
Arthroleptis stenodactylus	0112-0002000110100000010100201 0----0100000001200-0000100120120112000001000010100000 0?1-5
Arthroleptis variabilis	0112-0002000110100000000100212301000 10000?000200-00001001201200120000010000101000000?1-?
Astylosternus diadematus	0012-000200?310100000000010021 60----0100000100200-0020010320102010000000010??00001110?003
Aubria subsigillata	00000001000011000000100000021 20----11000200000 20???1101111001102000100020000000042100101?
Batrachylodes vertebralis	010000000110131000000000001002000----100112000020??0120100120000011100001110011100100 0?10?
Breviceps mossambicus	1100000101101000100010100002120----1010000000200-001010-1201001121000010100101000 10021-2
Cacosternum boettgeri	01101010200130011311000010021 24----1100011100200-001010-1200001101000020100100021110100?
Cacosternum capense	00100000200130000111000210121 20----1100011200200-000010-1200001120000020000100021120100?
Cacosternum nanum	011000102?013000A00100001002124----11000?1100200-001010-120000110A0000100001000211 10100?
Cardioglossa escalaerae	0122-011000001010000000101002120----3101000001200-00201101201210120000010100000031100?00?
Cardioglossa gracilis	0122-000000001010000000101002120----310100?001200-00201101201220120000010000000031100?005
Chiromantis xerampelina	00001000000030300000100001020 40----0100000200201000200001000000000000000?021020000000 01000
Conraua crassipes	20000001000030000000000000002120----210002?100202-?010001000110200011002000000001 0110010?1
Conraua goliath	0000?001??003?000000?000?002120----210002?100202-10100?00001102000110020000000101 10010??
Dimorphognathus africanus	002012000000150000000000000100201301011100020000200-011000?110000010120111010001000 11041002
Discodeles bufoniformis	1000000000011101000000000200215110-0210102?00020??002000010010001110000110001000000 00?1-?
Ericabatrachus baleensis	00000001100150000000100000002123011111000??000200-01101?-121000010000000--201?0001?1001???
Euphlyctis cyanophlyctis	00000001?0003?0000000000?002230----11000201002011001000100011120001100201000000411 0010?1
Hemisus marmoratus	100000000110500110001000000 2120----1011?00000200-001010-3201001120000020200 00A101?000002
Hildebrandtia ornata	0000000110003000000010000000 2120----110002?3002011002011111000120200000100000000 02100100?
Hoplobatrachus occipitalis	0000000111003000000000000 2002230----210002?1002011001001100011020001100201000001411 0010?1
Hydrophylax galamensis	210000001101310000000000001002010----21000201001011002001110010120010000110001000021031001
Hyperolius marmoratus	0112-0002101002000000000001102150----01000?0000010-00?010-1000000000010030210200000100 4002
Kassina senegalensis	0112-0002101002100000000001102010----110000000010-00201003200001101000030200100000 1004002
Leptodactylodon ventrimarmoratus	2010000020010101000000011010120----010000?600200-101010032011011000000000?02000031?00?00?
Leptopelis mossambicus	0102-000000100200000000000102150----0100000000000-00201103100000120000010000201000000?00?
Leptopelis vermiculatus	0102-000000100200000000000102150----0100000000000-00201113100000120000010000201000000?002

Appendix 4
Continued

Distribution of 178 morphological characters among exemplar species. Character states are scored 0–8, ? (indeterminate), – (inapplicable), A (polymorphic 0/1). Refer to Appendix 2 for character descriptions. Page 4 of 4, characters 90–177

	90 95 100 105 110 115 120 125 130 135 140 145 150 155 160 165 170 175
Limnonectes blythii	0000000010003?00000010001002230----2100020000202-0010000000111201011001100000010110010?1
Mantella aurantiaca	0??0?0010???313?020000001002040----110002?000200-01201001200000101000010?000000011003000
Mantidactylus femoralis	0000100100003?300000100010020410000110102000020??012000010000000000001100001000001003000
Microbatrachella capensis	0110100021013000000000020002124----1100011100200-001010-1000001000000010101000031100100?
Nannophrys ceylonensis	0000000010003?0?000000021002110----1100020000201001200100200001110000012000001100000?0??
Nanorana parkeri	??000001????1?0???0000000010230----2100020000202-001010??001102000000020?00000031100?0??
Natalobatrachus bonebergi	000010000001300012A000001012000----1101010100200-00201111000000000000110000100001104100?
Nothophryne broadleyi	002000112001300000100002100212301111100010100200-000010-1200001100000010101100021100100?
Nyctibates corrugatus	0111200020016101000000001002120----0100000100200-0020100310102010101000010?000000000?003
Pantherana pipiens	0000000100003000000000000002230----210002010020100020011100101200111001000010000210310?1
Petropedetes cameronensis	00000000100030000000110110010021000010002?000201011200101110000100000010000000002100?000
Petropedetes natator	000000001000?000000010001002000----0101020100201001200001010000010000011100000000000?000
Petropedetes newtoni	000000000001300000001101100100210002100020010201001212121210000100000010000000002100?00?
Petropedetes parkeri	000000001000300000001101100100210002100020010201011212121211000110000010000100002100?00?
Philautus surdus	00001100000030300000000011020410000010000?1002010002000010000000000000?021021000000011-0
Phrynobatrachus acridoides	00201220000051000000000010020130101110000??100200-001011011000001010011101000100010041004
Phrynobatrachus cricogaster	00001220?00?5?000000000010020130111110002?100200-0?100001100000101201110100010051104100?
Phrynobatrachus krefftii	0000222010003100000000001002013011111010201002 00-0110001100000000120111010000?0001104100?
Phrynobatrachus natalensis	0020122010015100000000001002013010111000011002 00-0110000110000110120111010001000110 01004
Phrynobatrachus plicatus	000012200001510100000000100201301111101 02??00200-011001111000000012?1010100010001104100?
Phrynodon sandersoni	000022201101300000000000100200301011101020100200-01100001100000101201A101000000011001???
Phrynoglossus laevis	1000000000003101000000001002000----200002?00020??001010?100100200010002000000010000000?1
Phrynomantis bifasciatus	0000000011103010000010001002000----0111000000200-001010-2200000120000010200000000?1010?0
Platymantis corrugatus	100001100000100100000000100215110-0210102?000201000200101201100111000210100110000000?1-?
Poyntonia paludicola	0000100110013000000000000002124----1000011000200-001010-12000011200000202010000111101002
Ptychadena anchietae	0000110111013000000010001002230----11000213002011002011110000120001000101001000021021002
Ptychadena mascareniensis	0000110111013001000010001002230----11000213002011002011110000120001000101000000021021002
Pyxicephalus adspersus	0000?00100001100000010000002120----110002020020??101011111010021200000200000000041101101?
Pyxicephalus edulis	0000?001??0?11000000100??002120----110002020020??1010111110100212000002000000000411011011
Schoutedenella taeniata	0112-000200020010000001010021230???1100000000000-0020110120020?100000010102101022000?1-?
Scotobleps gabonicus	01101000200?0101000000001002160----0100000000200-0?201103101021101000000002100001100?00?
Sooglossus sechellensis	0000000100010?0?01?10000??02220----100000?000200-001010?12000001110000--201000001?0001-0
Staurois natator	010121012000110000000001201200110-0110101?10020??001001010000000110000100000000000000?00?
Strongylopus grayii	0000000000003000000010000002230----2100020200201000201101201011100100010000100001100100?
Tomopterna marmorata	000000011?01?000000010000??120----110002?200200-002010011010011200001201001000011001001
Tomopterna tandyi	000000011001?00000001000001 2120----1100020200200-002010010010111210000201001000011001001
Trichobatrachus robustus	0?10?0002???01010000000110?0160----1100000600200-10100003101100100010000002100002100?00?

Appendix 5

Distribution of unambiguous apomorphies on the tree topology obtained from the simultaneous analysis with equal weights (Fig. 4). Terminal taxa are listed alphabetically, and clades according to node numbers presented in Fig. 4. Morphological character numbers are indicated first and refer to Appendix 2. Character transformations are denoted thereafter by listing the ancestral and derived states separated by a " > ". The number of molecular apomorphies follows thereafter in brackets.

Afrana angolensis: 164: 0 > 1, [42]. ***Afrana fuscigula***: 63: 0 > 1, 64: 2 > 0, [21]. ***Afrixalus***: 0: 1 > 0, 6: 1 > 0, 74: 0 > 2, 128: 0 > 1, 144: 0 > 2, [45]. ***Amnirana albolabris***: 17: 3 > 0, 152: 2 > 0, [52]. ***Amolops ricketti***: 0: 1 > 0, 15: 1 > 0, 17: 3 > 0, 22: 1 > 0, 37: 0 > 1, 39: 0 > 1, 46: 1 > 0, 49: 1 > 0, 54: 0 > 1, 55: 0 > 1, 70: 0 > 1, 88: 1 > 0, 117: 2 > 0, 132: 1 > 5, 144: 1 > 0, 155: 1 > 0, 161: 0 > 1, [62]. ***Anhydrophryne rattrayi***: 20: 2 > 3, 28: 2 > 1, 36: 0 > 1, 56: 0 > 2, 129: 0 > 1. ***Arthroleptella hewitti***: 26: 0 > 1, 119: 2 > 1, 132: 0 > 1. ***Arthroleptella landdrosia***: 49: 1 > 0, 52: 0 > 1, 54: 0 > 1, 55: 1 > 2, 64: 1 > 2, 75: 0 > 1, 91: 0 > 1, 107: 0 > 2, 109: 0 > 1, 155: 0 > 1, 165: 0 > 1, [32]. ***Arthroleptides martiensseni***: 44: 0 > 1, 66: 0 > 3, 132: 0 > 4, 149: 0 > 1, 165: 0 > 1, [47]. ***Arthroleptis***: 58: 1 > 0, 118: 1 > 0, 119: 2 > 1, 152: 0 > 1, [30]. ***Arthroleptis variabilis***: 6: 0 > 1, 26: 0 > 1, 37: 0 > 1, 88: 1 > 0, 112: 1 > 0, [24]. ***Astylosternus diadematus***: 25: 0 > 1, 48: 0 > 1, 55: 1 > 0, 93: 0 > 2, 102: 0 > 3, 132: 6 > 1, 144: 0 > 1, 151: 0 > 2, 162: 0 > 1, 172: 0 > 1, [29]. ***Aubria subsigillata***: 140: 0 > 1, 170: 1 > 2, [52]. ***Batrachylodes vertebralis***: 4: 0 > 1, 47: 1 > 2, 98: 0 > 1, 99: 0 > 1, 128: 0 > 1, 129: 0 > 1, 140: 0 > 1, 155: 0 > 1, 161: 0 > 1, 162: 0 > 1, 165: 0 > 1, 166: 0 > 1, 167: 0 > 1, 170: 0 > 1, 175: 0 > 1. **Brevicipitinae**: 4: 0 > 1, 16: 1 > 2, 19: 0 > 2, 25: 0 > 1, 59: 0 > 1, 73: 2 > 0, 91: 0 > 1, 97: 0 > 1, 112: 0 > 1, 155: 0 > 1, 162: 2 > 1, 165: 0 > 1, 174: 0 > 2, 175: 0 > 1, [55]. ***Cacosternum boettgeri***: 46: 1 > 3, 60: 0 > 1, 80: 0 > 1, 94: 0 > 1, 105: 0 > 1, 107: 0 > 3, [14]. ***Cacosternum capense***: 54: 0 > 1, 87: 1 > 0, 107: 0 > 1, 116: 0 > 1, 120: 4 > 0, 132: 1 > 2, 141: 1 > 0, 154: 0 > 2, [12]. ***Cacosternum nanum***: 56: 0 > 1, 57: 0 > 1, [12]. ***Cardioglossa***: 33: 0 > 1, 96: 0 > 1, 97: 0 > 1, 162: 0 > 1, [36]. ***Cardioglossa gracilis***: 1: 3 > 0, 48: 0 > 1, [17]. ***Chiromantis***: 5: 1 > 0, 14: 2 > 1, 40: 1 > 0, 52: 1 > 0, 59: 0 > 2, 71: 0 > 1, 114: 1 > 0, [61]. ***Conraua crassipes***: 44: 0 > 1, 90: 0 > 2, 145: 0 > 1, [33]. ***Conraua goliath***: 23: 2 > 1, 39: 1 > 0, 54: 0 > 1, [21]. ***Dimorphognathus africanus***: 51: 0 > 1, 55: 0 > 1, 96: 2 > 0, 132: 1 > 0, [34]. ***Discodeles bufoniformis***: 101: 0 > 1, 114: 1 > 2, 161: 0 > 1. ***Ericabatrachus baleensis***: 3: 1 > 0, 18: 1 > 0, 25: 1 > 0, 30: 1 > 0, 35: 0 > 1, 38: 0 > 1, 56: 0 > 1, 73: 1 > 2, 80: 0 > 3, 83: 2 > 0, 87: 1 > 0, 102: 3 > 5, 109: 0 > 1, 140: 0 > 1, 148: 0 > 1, 152: 1 > 0. ***Euphlyctis cyanophlyctis***: 14: 2 > 1, 19: 2 > 1, 39: 1 > 0, 46: 1 > 2, 48: 0 > 1, 151: 0 > 1, 168: 1 > 0, [46]. ***Hemisus marmoratus***: 2: 0 > 1, 3: 2 > 1, 9: 0 > 1, 14: 0 > 1, 15: 0 > 1, 28: 0 > 2, 30: 0 > 2, 63: 0 > 1, 69: 0 > 2, 80: 01 > 2, 81: 0 > 1, 88: 0 > 2, 105: 0 > 1, 146: 1 > 3, 160: 1 > 2, 168: 0 > 1, 170: 0 > 1, [103]. ***Hildebrandtia ornata***: 39: 0 > 2, 67: 0 > 1, 78: 0 > 1, 147: 0 > 1, 154: 0 > 2, [44]. ***Hoplobatrachus occipitalis***: 15: 0 > 1, 23: 2 > 1, 34: 0 > 1, 41: 0 > 1, 99: 0 > 1, [47]. ***Hydrophylax galamensis***: 101: 0 > 1, [52]. ***Hyperolius marmoratus***: 37: 0 > 1, 46: 0 > 1, 105: 1 > 0, 146: 3 > 1, [64]. ***Kassina senegalensis***: 9: 2 > 0, 10: 1 > 0, 19: 0 > 1, 40: 0 > 1, 48: 0 > 1, 55: 1 > 2, 63: 0 > 1, 70: 1 > 2, 80: 3 > 0, 118: 1 > 0, 119: 5 > 1, 152: 0 > 1, 165: 2 > 1, [32]. ***Leptodactylodon***: 6: 1 > 0, 59: 0 > 2, 62: 0 > 1, 64: 1 > 2, 84: 0 > 1, 88: 1 > 0, 90: 0 > 2, 116: 0 > 1, 152: 0 > 1, 169: 0 > 3, [47]. ***Leptopelis***: [21]. ***Leptopelis vermiculatus***: 44: 1 > 0, 76: 0 > 1, 145: 0 > 1, [15]. ***Limnonectes blythii***: 46: 1 > 2, 48: 0 > 1, 66: 0 > 2, 77: 1 > 0, 97: 1 > 0, 151: 0 > 1, 154: 0 > 1, 160: 2 > 1, 161: 0 > 1, [45]. ***Mantella aurantiaca***: 14: 2 > 1, 16: 0 > 1, 17: 3 > 1, 32: 6 > 1, 42: 0 > 1, 45: 0 > 1, 47: 1 > 0, 49: 1 > 0, 52: 1 > 0, 56: 2 > 0, 57: 0 > 1, 58: 1 > 0, 60: 0 > 1, 72: 1 > 0, 74: 0 > 2, 78: 0 > 2, 107: 0 > 2, 110: 1 > 0, 147: 0 > 2, 153: 0 > 1, 155: 0 > 1, 170: 0 > 1, [34]. ***Mantidactylus femoralis***: 39: 0 > 1, 62: 0 > 1, 73: 2 > 1, 120: 0 > 1, 128: 0 > 1, 159: 0 > 1, 165: 0 > 1, [48]. ***Microbatrachella capensis***: 20: 3 > 2, 24: 0 > 2, 33: 0 > 1, 38: 0 > 1, 46: 1 > 3, 57: 0 > 1, 60: 0 > 1, 94: 0 > 1, 99: 0 > 1, 147: 2 > 0, 153: 1 > 0, 169: 2 > 3, [42]. ***Nannophrys ceylonensis***: 3: 0 > 1, 6: 1 > 0, 10: 1 > 0, 12: 0 > 1, 14: 2 > 0, 17: 3 > 0, 19: 2 > 0, 20: 0 > 1, 28: 2 > 1, 29: 1 > 0, 31: 0 > 1, 49: 1 > 0, 52: 0 > 1, 53: 0 > 1, 61: 0 > 1, 67: 1 > 0, 74: 1 > 0, 97: 1 > 0, 113: 0 > 2, 118: 2 > 1, 119: 3 > 1, 140: 0 > 1, 141: 1 > 2, 147: 0 > 2, 149: 1 > 0, 150: 1 > 0, 152: 2 > 1, 153: 0 > 1, 154: 0 > 1, 160: 2 > 1, 161: 0 > 2, 167: 0 > 1, 170: 1 > 0, 171: 1 > 0, [24]. ***Nanorana parkeri***: 8: 1 > 0, 9: 2 > 1, 17: 3 > 2, 23: 2 > 1, 37: 1 > 0, 39: 1 > 0, 56: 2 > 0, 58: 1 > 0, 62: 0 > 1, 68: 0 > 1, 69: 2 > 3, 70: 1 > 3, 71: 0 > 2, 73: 0 > 1, 78: 0 > 1, 80: 0 > 2, 81: 0 > 1, 102: 3 > 1, 116: 0 > 1, 117: 2 > 0, 143: 0 > 1, 168: 1 > 0, 169: 0 > 3, [30]. ***Natalobatrachus bonebergi***: 1: 3 > 1, 9: 2 > 1, 35: 0 > 1, 47: 1 > 0, 55: 1 > 0, 73: 1 > 2, 84: 1 > 0, 87: 1 > 0, 98: 1 > 0, 106: 0 > 1, 107: 0 > 2, 116: 0 > 1, 130: 2 > 1, 144: 0 > 1, 162: 1 > 0, 165: 0 > 1. ***Nothophryne broadleyi***: 32: 6 > 2, 72: 0 > 1, 96: 0 > 1, 131: 1 > 0, 141: 1 > 0. ***Nyctibates corrugatus***: 70: 0 > 3, 93: 0 > 1, 102: 0 > 6, 132: 0 > 1, 157: 0 > 1, 162: 0 > 1, 171: 1 > 0, [52]. ***Pantherana pipiens***: 5: 1 > 0, 31: 1 > 0, 63: 0 > 1, 64: 2 > 0, 78: 0 > 1, 83: 0 > 1, 118: 0 > 2, 156: 0 > 1, 157: 0 > 1, [48]. ***Petropedetes cameronensis***: 4: 0 > 1, 6: 1 > 0, 40: 0 > 1, 147: 2 > 1, [28]. ***Petropedetes natator***: 20: 0 > 1, 51: 0 > 1, 79: 0 > 1, 128: 0 > 1, 132: 0 > 1, 161: 0 > 1, 162: 0 > 1. ***Petropedetes newtoni***: 66: 0 > 3, 98: 1 > 0, 101: 0 > 1, 139: 1 > 0. ***Petropedetes parkeri***: 62: 1 > 0, 149: 0 > 1, 165: 0 > 1. ***Philautus***: 4: 0 > 1, 17: 3 > 2, 20: 0 > 1, 29: 1 > 0, 32: 6 > 1, 56: 2 > 0, 62: 0 > 1, 77: 1 > 0, 95: 0 > 1, 110: 1 > 0, 120: 0 > 1, 166: 0 > 1, 175: 0 > 1, [49]. ***Phrynobatrachus acridoides***: 36: 0 > 1, 59: 2 > 0, 101: 1 > 0, 140: 1 > 0, 143: 0 > 1, 144: 0 > 1, 156: 2 > 0, 171: 1 > 0, [5]. ***Phrynobatrachus cricogaster***: 34: 0 > 1, 36: 0 > 1, 169: 0 > 5,

[8]. ***Phrynobatrachus krefftii***: 6: 0 > 1, 31: 1 > 0, 46: 1 > 2, 56: 0 > 1, 101: 1 > 0, 103: 0 > 1. ***Phrynobatrachus natalensis***: 12: 0 > 1, 79: 1 > 0, 98: 0 > 1, 152: 0 > 1, 173: 4 > 0, [10]. ***Phrynobatrachus plicatus***: 105: 0 > 1, 144: 0 > 1, 145: 0 > 1, 153: 1 > 0, [47]. ***Phrynodon***: 3: 1 > 0, 15: 1 > 0, 29: 1 > 0, 35: 0 > 1, 51: 0 > 1, 74: 0 > 1, 78: 0 > 1, 99: 0 > 1, 123: 1 > 0, [40]. ***Phrynoglossus laevis***: 3: 0 > 1, 31: 1 > 0, 46: 1 > 3, 47: 1 > 0, 54: 0 > 1, 55: 0 > 3, 58: 1 > 0, 68: 0 > 1, 71: 0 > 2, 141: 2 > 1, 152: 0 > 2, 156: 0 > 1, 160: 1 > 2, 168: 0 > 1, [33]. ***Phrynomantis***: 12: 0 > 1, 17: 0 > 3, 20: 0 > 3, 33: 0 > 1, 55: 0 > 3, 59: 0 > 2, 84: 0 > 1, 98: 0 > 1, 104: 0 > 1, 146: 1 > 2, 172: 0 > 1, 174: 0 > 1, [35]. ***Platymantis***: 1: 3 > 1, 40: 0 > 1, 70: 2 > 1, 71: 0 > 1, 73: 0 > 2, 79: 0 > 1, 87: 0 > 1, 95: 0 > 1, 96: 0 > 1, 144: 0 > 1, 147: 0 > 2, 150: 0 > 1, 159: 0 > 2, 162: 0 > 1, 166: 0 > 1. ***Poyntonia paludicola***: 19: 0 > 1, 26: 0 > 1, 42: 1 > 0, 47: 1 > 0, 53: 1 > 0, 54: 0 > 1, 57: 0 > 1, 126: 1 > 0, 154: 0 > 2, 160: 1 > 2, 172: 0 > 1, [39]. ***Ptychadena anchietae***: 165: 0 > 1, [57]. ***Ptychadena mascareniensis***: 19: 2 > 1, 105: 0 > 1, [46]. ***Pyxicephalus adspersus***: [23]. ***Pyxicephalus edulis***: 84: 1 > 0, [21]. ***Schoutedenella***: 0: 1 > 0, 4: 0 > 1, 48: 0 > 1, 49: 0 > 1, 55: 1 > 0, 102: 1 > 2, 103: 1 > 0, 125: 0 > 1, 135: 2 > 0, 144: 0 > 1, 149: 1 > 0, 154: 2 > 0, 162: 0 > 1, 164: 0 > 2, 169: 0 > 2, 170: 0 > 2, [95]. ***Scotobleps gabonicus***: 63: 0 > 1, 64: 1 > 0, 119: 2 > 6, 144: 0 > 1, 152: 0 > 1, [79]. **Sooglossidae:** 3: 0 > 1, 16: 0 > 2, 46: 0 > 1, 63: 0 > 1, 69: 0 > 1, 70: 0 > 1, 74: 0 > 1, 79: 0 > 1, 80: 0 > 2, 81: 0 > 1, 84: 0 > 1, 97: 0 > 1, 107: 0 > 1, 109: 0 > 1, 118: 0 > 2, 119: 0 > 2, 155: 0 > 1, 164: 0 > 1, 170: 0 > 1, 175: 0 > 1, [101]. ***Staurois***: 8: 1 > 0, 19: 2 > 0, 38: 0 > 1, 42: 0 > 1, 44: 0 > 1, 59: 0 > 2, 73: 0 > 2, 74: 0 > 2, 91: 0 > 1, 93: 0 > 1, 94: 0 > 2, 95: 0 > 1, 98: 0 > 2, 102: 3 > 1, 120: 0 > 1, 125: 2 > 1, 130: 2 > 1, 141: 2 > 1, 165: 1 > 0, [73]. ***Strongylopus grayii***: 47: 1 > 0, 97: 1 > 0, 132: 1 > 2, 147: 0 > 2, 165: 0 > 1, [26]. ***Tomopterna marmorata***: 147: 0 > 1, 159: 0 > 1, [23]. ***Tomopterna tandyi***: 26: 0 > 1, 155: 0 > 1, [11]. ***Trichobatrachus robustus***: 34: 0 > 1, 64: 1 > 0, 125: 0 > 1, 147: 2 > 1, 157: 0 > 1, 170: 1 > 2, [33]. **Node 1:** 44: 0 > 1, 86: 0 > 1, 117: 0 > 2, 141: 0 > 1, 143: 0 > 1, 146: 0 > 1, 147: 0 > 2, 153: 0 > 1, [85]. **Node 2:** (Ranoidea + Microhyloidea) 11: 0 > 1, 21: 0 > 1, 22: 0 > 3, 23: 0 > 2, [30]. **Node 3:** ((*Hemisus* + Brevicipitinae) *Phrynomantis*) 3: 0 > 2, 16: 0 > 1, 45: 0 > 1, 60: 0 > 1, 64: 01 > 2, 68: 0 > 1, 74: 0 > 2, 83: 01 > 4, 99: 0 > 1, 100: 0 > 1, 110: 0 > 1, 127: 0 > 1, [10]. **Node 4:** (*Hemisus* + Brevicipitinae) 57: 0 > 1, 75: 0 > 1, 86: 1 > 0, 89: 0 > 1, 90: 0 > 1, 106: 0 > 1, 118: 0 > 1, 119: 0 > 2, 149: 0 > 1, 152: 0 > 1, 177: 0 > 2, [37]. **Node 5:** Ranoidea s.s. 2: 0 > 1, 6: 0 > 1, 9: 0 > 2, 10: 0 > 1, 14: 0 > 2, 28: 0 > 2, 69: 0 > 2, 141: 1 > 2, [11]. **Node 6:** (((*Afrixalus* (*Hyperolius* + *Kassina*)) Arthroleptidae) *Leptopelis*) 55: 0 > 1, 93: 0 > 2, 118: 0 > 1, 119: 0 > 5, 146: 1 > 3, 177: 0 > 2, [15]. **Node 7:** Genus *Leptopelis* 1: 3 > 1, 19: 0 > 1, 34: 0 > 1, 37: 0 > 1, 40: 0 > 1, 57: 0 > 2, 71: 0 > 1, 72: 0 > 1, 73: 2 > 1, 86: 1 > 2, 144: 0 > 1, 147: 2 > 1, 167: 0 > 1, [36]. **Node 8:** ((*Afrixalus* (*Hyperolius* + *Kassina*)) Arthroleptidae) 80: 0 > 3, 88: 0 > 1, 92: 0 > 1, 98: 0 > 2, 105: 0 > 1, 171: 0 > 1, [10]. **Node 9:** (*Afrixalus* (*Hyperolius* + *Kassina*)) 3: 0 > 1, 14: 2 > 1, 60: 0 > 1, 70: 0 > 1, 76: 0 > 1, 77: 1 > 0, 99: 0 > 1, 136: 0 > 1, 160: 1 > 3, 162: 0 > 2, [39]. **Node 10:** (*Hyperolius* + *Kassina*) [34]. **Node 11:** Arthroleptidae s.l. 46: 0 > 1, 103: 0 > 1, 119: 5 > 2, 149: 0 > 1, [12]. **Node 12:** Astylosterninae 22: 3 > 0, 27: 0 > 1, 37: 0 > 1, 40: 0 > 1, 44: 1 > 0, 57: 0 > 2, 93: 2 > 0, 160: 1 > 0, 164: 0 > 2, [14]. **Node 13:** (*Nyctibates* + *Scotobleps*) 48: 0 > 1, 55: 1 > 0, 147: 2 > 1, 151: 0 > 2, 155: 0 > 1, [12]. **Node 14:** ((*Astylosternus* + *Trichobatrachus*) *Leptodactylodon*) 91: 1 > 0, 132: 0 > 6, [14]. **Node 15:** (*Astylosternus* + *Trichobatrachus*) 63: 0 > 1, 119: 2 > 6, 143: 1 > 0, [16]. **Node 16:** Arthroleptinae 6: 1 > 0, 38: 0 > 1, 42: 0 > 1, 49: 1 > 0, 70: 0 > 2, 79: 0 > 1, 84: 0 > 1, 101: 1 > 0, 112: 0 > 1, 146: 3 > 1, 150: 0 > 2, [24]. **Node 17:** Genus *Cardioglossa* 4: 0 > 1, 34: 0 > 1, 45: 0 > 1, 53: 1 > 0, 55: 1 > 0, 80: 3 > 0, 92: 1 > 2, 98: 2 > 0, 125: 0 > 3, 128: 0 > 1, 144: 0 > 1, 169: 0 > 3, [8]. **Node 18:** ((*A. variabilis* + *Schoutedenella*) *Arthroleptis*) 52: 0 > 1, 74: 0 > 1, 102: 0 > 1, 167: 0 > 1, 171: 1 > 0, 175: 0 > 1, [21]. **Node 19:** (*A. variabilis* + *Schoutedenella*) 120: 0 > 3, [17]. **Node 20:** Ranidae s.l. 5: 0 > 1, 30: 0 > 1, 46: 0 > 1, 130: 0 > 2, [0]. **Node 21:** 37: 0 > 1, 56: 0 > 2, 72: 0 > 1, 73: 2 > 0, 147: 2 > 0, [0]. **Node 22:** ((*Discodeles* + *Platymantis*) *Phrynoglossus*) 23: 2 > 1, 84: 0 > 1, 89: 0 > 1, 90: 0 > 1, 105: 0 > 1, 149: 0 > 1, [27]. **Node 23:** (*Discodeles* + *Platymantis*): 39: 0 > 1, 102: 3 > 1, 118: 0 > 1, 119: 0 > 5, 120: 0 > 1, 128: 0 > 1, 155: 0 > 1, 165: 0 > 1, 175: 0 > 1, [0]. **Node 24:** 110: 0 > 1, 174: 0 > 1, [12]. **Node 25:** Petropedetinae 31: 1 > 0, 32: 6 > 2, 48: 0 > 1, 62: 0 > 1, 64: 0 > 1, 74: 0 > 1, 98: 0 > 1, 140: 0 > 1, 148: 0 > 1, [0]. **Node 26:** (((*P. newtoni* + *P. parkeri*) *P. cameronensis*) *Arthroleptides*) 1: 3 > 1, 15: 1 > 0, 55: 0 > 1, 56: 2 > 0, 73: 0 > 1, 111: 0 > 1, 113: 0 > 1, 117: 2 > 1, 120: 0 > 2, 139: 0 > 1, 144: 0 > 1, 147: 0 > 2, 170: 0 > 2, [0]. **Node 27:** ((*P. newtoni* + *P. parkeri*) *P. cameronensis*) 43: 0 > 1, 64: 1 > 2, [34]. **Node 28:** (*P. newtoni* + *P. parkeri*) 133: 0 > 1, [29]. **Node 29:** 17: 02 > 3, 40: 0 > 1, [8]. **Node 30:** (Mantellinae + Rhacophorinae) 13: 2 > 1, 15: 1 > 0, 37: 1 > 0, 73: 0 > 2, 94: 0 > 1, 104: 0 > 3, [13]. **Node 31:** Mantellinae 35: 0 > 1, 38: 0 > 1, 70: 0 > 1, 79: 0 > 1, 140: 0 > 1, 174: 1 > 3, [21]. **Node 32:** Rhacophorinae 1: 3 > 1, 6: 1 > 0, 31: 1 > 2, 46: 1 > 3, 55: 0 > 1, 64: 0 > 2, 85: 1 > 0, 86: 1 > 0, 115: 0 > 1, 130: 2 > 0, 162: 0 > 2, 163: 0 > 1, 165: 0 > 2, [30]. **Node 33:** 114: 1 > 0, 118: 0 > 1, 149: 0 > 1, 152: 0 > 2, 170: 0 > 1, 177: 0 > 1, [6]. **Node 34:** Newly construed Pyxicephalinae, or fanged ranids of Africa plus Asia 22: 1 > 0, 39: 0 > 1, 50: 0 > 1, 65: 0 > 1, 67: 0 > 1, 70: 0 > 1, 84: 0 > 1, 141: 2 > 1, 160: 1 > 2, [12]. **Node 35:** (*Pyxicephalus* + *Aubria*) 23: 2 > 1, 54: 0 > 1, 58: 1 > 2, 61: 0 > 1, 66: 0 > 2, 72: 1 > 2, 78: 0 > 1, 102: 3 > 1, 103: 0 > 1, 145: 0 > 1, 169: 0 > 4, [16]. **Node 36:** Genus *Pyxicephalus* 71: 0 > 3, 132: 0 > 2, 147: 0 > 1, 153: 0 > 1, 154: 0 > 2, 173: 0 > 1, [16]. **Node 37:** (((*Limnonectes* (*Nanorana* ((*Euphlyctis* + *Hoplobatrachus*) *Nannophrys*))) *Conraua*) 31: 1 > 0, 74: 0 > 1, 146: 1 > 0, 168: 0 > 1, [11]. **Node 38:** Genus

Conraua 132: 0 > 1, [23]. **Node 39:** (*Limnonectes* (*Nanorana* ((*Euphlyctis* + *Hoplobatrachus*) *Nannophrys*))): 15: 1 > 0, 22: 0 > 3, 52: 1 > 0, 98: 0 > 1, 118: 1 > 2, [14]. **Node 40:** (((*Euphlyctis* + *Hoplobatrachus*) *Nannophrys*) *Nanorana*) [23]. **Node 41:** ((*Euphlyctis* + *Hoplobatrachus*) *Nannophrys*) 137: 2 > 1, [26]. **Node 42:** (*Euphlyctis* + *Hoplobatrachus*) 132: 0 > 1, 138: 0 > 1, 145: 0 > 1, 162: 0 > 1, 169: 0 > 4, [18]. **Node 43:** 52: 1 > 0, 64: 0 > 2, 132: 0 > 1, [8]. **Node 44:** (Raninae + Ptychadeninae) 145: 0 > 1, 170: 1 > 2, [18]. **Node 45:** Ptychadeninae 4: 0 > 1, 7: 0 > 1, 22: 1 > 2, 36: 0 > 2, 49: 1 > 2, 85: 1 > 0, 87: 0 > 1, 132: 1 > 3, 149: 1 > 0, [23]. **Node 46:** Genus *Ptychadena* 17: 3 > 0, 94: 0 > 1, 95: 0 > 1, 99: 0 > 1, 101: 0 > 1, 114: 0 > 1, 118: 1 > 2, 156: 0 > 1, 162: 0 > 1, 173: 0 > 2, [30]. **Node 47:** (((*Amolops* + *Staurois*) *Pantherana*)(*Amnirana* + *Hydrophylax*)) 40: 1 > 0, 83: 2 > 0, 110: 1 > 0, 118: 1 > 0, 155: 0 > 1, 165: 0 > 1, [24]. **Node 48:** (*Amnirana* + *Hydrophylax*) 47: 1 > 0, 59: 0 > 2, 62: 0 > 1, 70: 0 > 1, 90: 0 > 2, 91: 0 > 1, 97: 1 > 0, 114: 0 > 1, 135: 2 > 1, 161: 0 > 1, [23]. **Node 49:** ((*Amolops* + *Staurois*) *Pantherana*) 29: 1 > 0, [12]. **Node 50:** (*Amolops* + *Staurois*) 6: 1 > 0, 12: 0 > 1, 35: 0 > 1, 48: 1 > 0, 113: 0 > 1, 114: 0 > 2, 116: 0 > 1, 128: 0 > 1, 145: 1 > 0, 149: 1 > 0, 152: 2 > 0, 154: 0 > 1, 170: 2 > 0, 171: 1 > 0, [15]. **Node 51:** "African clade" [13]. **Node 52:** Strongylopinae, i.e., (*Strongylopus* + *Afrana*) 15: 1 > 0, 78: 0 > 1, 118: 1 > 2, 156: 0 > 1, [4]. **Node 53:** Genus *Afrana* 22: 1 > 0, 29: 1 > 0, 31: 1 > 0, 145: 0 > 1, 169: 0 > 4, 173: 0 > 1, [5]. **Node 54:** (Tomopterninae (Cacosterninae + Phrynobatrachinae)) 55: 0 > 1, 72: 1 > 0, 84: 0 > 1, 87: 0 > 1, 101: 0 > 1, 137: 1 > 0, 162: 0 > 1, [4]. **Node 55:** Tomopterninae 1: 3 > 2, 12: 0 > 2, 39: 0 > 1, 46: 1 > 0, 71: 0 > 2, 82: 0 > 1, 132: 1 > 2, 154: 0 > 2, 160: 1 > 2, 165: 0 > 1, [13]. **Node 56:** (Phrynobatrachinae + Cacosterninae) 6: 1 > 0, 37: 1 > 0, 40: 1 > 0, 42: 0 > 1, 56: 2 > 0, 64: 2 > 1, 149: 1 > 0, 177: 1 > 2, [7]. **Node 57:** Phrynobatrachinae 38: 0 > 1, 79: 0 > 1, 118: 1 > 0, 119: 2 > 01, 152: 1 > 0, [9]. **Node 58:** (*Natalobatrachus* + *P. krefftii*) 145: 0 > 1, 153: 1 > 0, [16]. **Node 59:** ((*P. cricogaster* + *P. plicatus* + ((*P. acridoides* + *P. natalensis*) *Dimorphognathus*)) *Phrynodon*) 147: 0 > 1, [25]. **Node 60:** (*P. cricogaster* + *P. plicatus* + ((*P. acridoides* + *P. natalensis*) *Dimorphognathus*)) 31: 1 > 0, 55: 1 > 0, 102: 3 > 5, 166: 0 > 1, [32]. **Node 61:** ((*P. acridoides* + *P. natalensis*) *Dimorphognathus*) 92: 0 > 2, 123: 1 > 0, [8]. **Node 62:** (*P. acridoides* + *P. natalensis*) 73: 1 > 2, 177: 2 > 4, [43]. **Node 63:** Cacosterninae 4: 0 > 1, 9: 2 > 1, 15: 1 > 0, 16: 0 > 1, 22: 1 > 3, 29: 1 > 0, 74: 0 > 1, 130: 2 > 1, 131: 0 > 1, 132: 1 > 0, 147: 0 > 2, 164: 0 > 1, [4]. **Node 64:** (*Arthroleptella* + *Anhydrophryne*) 2: 1 > 0, 62: 0 > 1, 65: 0 > 2, 78: 0 > 1, 95: 0 > 1, 175: 0 > 1, [9]. **Node 65:** (*A. hewitti* + *A. rattrayi*) 12: 0 > 1, 35: 0 > 1, 38: 0 > 1, 79: 0 > 1, 92: 0 > 2, 101: 1 > 0, 128: 0 > 1, 144: 0 > 1, 162: 1 > 0, 169: 0 > 3 [0]. **Node 66:** ((((*Cacosternum* + *Microbatrachella*) *Nothophryne*) *Ericabatrachus*) *Poyntonia*): 48: 0 > 1, 169: 0 > 1, [5]. **Node 67:** (((*Cacosternum* + *Microbatrachella*) *Nothophryne*) *Ericabatrachus*) 12: 0 > 1, 20: 2 > 3, 76: 0 > 1, 84: 1 > 0, [0]. **Node 68:** ((*Cacosternum* + *Microbatrachella*) *Nothophryne*) 9: 1 > 0, 62: 0 > 1, 64: 1 > 2, 69: 2 > 1, 98: 1 > 2, 113: 0 > 2, 132: 0 > 1, 169: 1 > 2, [0]. **Node 69:** (*Cacosternum* + *Microbatrachella*) 2: 1 > 0, 3: 1 > 2, 10: 1 > 0, 14: 1 > 0, 42: 1 > 0, 65: 0 > 2, 97: 1 > 0, [0]. **Node 70:** Genus *Cacosternum* 4: 1 > 0, 17: 2 > 1, 68: 0 > 1, 69: 1 > 0, 109: 0 > 1, 164: 1 > 0, [7]. **Node 71:** (*C. nanum* + *C. boettgeri*) 16: 1 > 2, 24: 0 > 1, 36: 0 > 1, 59: 0 > 2, 70: 0 > 2, 74: 1 > 2, 75: 0 > 1, 84: 0 > 1, 96: 0 > 1, 113: 2 > 0, [5].

Appendix 6

Taxonomic emendations implemented in the present study. See Appendix 7 for the updated classification.

Leptopelidae Laurent, 1972 **New Rank**
Ceratobatrachinae Boulenger, 1884 **New Rank**
Phrynobatrachinae Laurent, 1941 **New Rank**
Tomopterninae Dubois, 1987 **New Rank**
Strongylopinae **New Subfamily**
Dicroglossinae Anderson, 1871 = Pyxicephalinae Bonaparte, 1850 **New Synonym**
Pyxicephalini Bonaparte, 1850 = **New Tribe** of Pyxicephalinae Bonaparte, 1850
Limnonectini Dubois, 1992 transferred to Pyxicephalinae Bonaparte, 1850
Paini Dubois, 1992 transferred to Pyxicephalinae Bonaparte, 1850
Dicroglossini Anderson, 1871 transferred to Pyxicephalinae Bonaparte, 1850
Conrauini Dubois, 1992 transferred to Pyxicephalinae Bonaparte, 1850
Afrana Dubois, 1991 **New Rank** transferred to Strongylopinae **New Subfamily**
Batrachylodes Boulenger, 1887 transferred to Ceratobatrachinae Boulenger, 1881
Nanorana Günther, 1896 transferred to Paini Dubois, 1992 of Pyxicephalinae Bonaparte, 1850
Ericabatrachus Largen, 1991 transferred to Cacosterninae Noble, 1931
Staurois Cope, 1865 transferred to Amolopini Yang, 1989 of Raninae Rafinesque-Schmaltz, 1814
Anhydrophryne hewitti (FitzSimons, 1947) **New Combination**
Phrynodon Parker, 1935 = *Phrynobatrachus* Günther, 1862 **New Synonym**
Dimorphognathus Boulenger, 1906 = *Phrynobatrachus* Günther, 1862 **New Synonym**
Arthroleptides Nieden, 1910 = *Petropedetes* Reichenow, 1874 **New Synonym**

Appendix 7

Revised classification of family Ranidae Rafinesque-Schmaltz, 1814 following Dubois (2003), as amended in the present study. Subgenera are listed in brackets, where applicable

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Subfamily Cacosterninae Noble, 1931
Anhydrophryne Hewitt, 1919; *Arthroleptella* Hewitt, 1926; *Cacosternum* Boulenger, 1887; *Ericabatrachus* Largen, 1991; *Microbatrachella* Hewitt, 1926; *Nothophryne* Poynton, 1963; *Poyntonia* Channing & Boycott, 1989.
Subfamily Ceratobatrachinae Boulenger, 1884
Batrachylodes Boulenger, 1887; *Ceratobatrachus* Boulenger, 1884; *Discodeles* Boulenger, 1881; *Ingerana* Dubois, 1987; *Palmatorappia* Ahl, 1927; *Platymantis* Günther, 1859.
Subfamily Lankanectinae Dubois & Ohler, 2001
Lankanectes Dubois & Ohler, 2001.
Subfamily Mantellinae Laurent, 1946
Tribe Boophini Vences & Glaw, 2001: *Boophis* Tschudi, 1838.
Tribe Laliostomini Vences & Glaw, 2001: *Aglyptodactylus* Boulenger, 1919; *Laliostoma* Glaw, Vences & Böhme, 1998.
Tribe Mantellini Laurent, 1946: *Mantella* Boulenger, 1882; *Mantidactylus* Boulenger, 1895.
Subfamily Micrixalinae Dubois, Ohler & Biju, 2001
Micrixalus Boulenger, 1888.
Subfamily Nyctibatrachinae Blommers-Schlösser, 1993
Nyctibatrachus Boulenger, 1882.
Subfamily Occidozyginae Fei, Ye & Huang, 1991
Occidozyga Kuhl & Van Hasselt, 1822; *Phrynoglossus* Peters, 1867.
Subfamily Phrynobatrachinae Laurent, 1941
Natalobatrachus Hewitt & Methuen, 1913; *Phrynobatrachus* Günther, 1862.
Subfamily Petropedetinae Noble, 1931
Petropedetes Reichenow, 1874.
Subfamily Ptychadeninae Dubois, 1987
Hildebrandtia Nieden, 1907; *Lanzarana* Clarke, 1983; *Ptychadena* Boulenger, 1917 [2 subgenera: *Ptychadena* Boulenger, 1917; *Parkerana* Dubois, 1984].
Subfamily Pyxicephalinae Bonaparte, 1850
Tribe Conrauini Dubois, 1992: *Conraua* Nieden, 1908.
Tribe Dicroglossini Anderson, 1871: *Euphlyctis* Fitzinger, 1843; *Fejervarya* Bolkay, 1915; *Hoplobatrachus* Peters, 1863; *Minervarya* Dubois, Ohler & Biju, 2001; *Nannophrys* Günther, 1869; *Sphaerotheca* Günther, 1859.
Tribe Limnonectini Dubois, 1992: *Annandia* Dubois, 1992; *Elachyglossa* Andersson, 1916; *Limnonectes* Fitzinger, 1843; *Taylorana* Dubois, 1987.
Tribe Paini Dubois, 1992: *Chaparana* Bourret, 1939; *Nanorana* Günther, 1896 [2 subgenera: *Altirana* Stejneger, 1927; *Nanorana* Günther, 1896]; *Paa* Dubois, 1975 [3 subgenera: *Eripaa* Dubois, 1992; *Gynandropaa* Dubois, 1992; *Paa* Dubois, 1975]; *Quasipaa* Dubois, 1992.
Tribe Pyxicephalini Bonaparte, 1850: *Aubria* Boulenger, 1917; *Pyxicephalus* Tschudi, 1838.
Subfamily Raninae Rafinesque-Schmaltz, 1814
Tribe Amolopini Yang, 1989: *Amolops* Cope, 1865 [4 subgenera: *Amolops* Cope, 1865; *Huia* Yang, 1991; *Meristogenys* Yang, 1991; *Amo* Dubois, 1992]; *Odorrana* Fei, Ye & Huang, 1990; *Staurois* Cope, 1865.
Tribe Ranini Rafinesque-Schmaltz, 1814: *Rana* Linnaeus, 1758 [30 subgenera: *Amerana* Dubois, 1992; *Amietia* Dubois, 1987; *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; *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; *Sylvirana* Dubois, 1992; *Trypheropsis* Cope, 1866; *Tylerana* Dubois, 1992; *Zweifelia* Dubois, 1992].
Subfamily Ranixalinae Dubois, 1987
Indirana Laurent, 1986.
Subfamily Rhacophorinae Hoffman, 1932
Tribe Buergeriini Channing, 1989: *Buergeria* Tschudi, 1838.
Tribe Rhacophorini Hoffman, 1932: *Chirixalus* Boulenger 1893; *Chiromantis* Peters, 1854; *Kurixalus* Fei, Ye & Dubois in Fei, 1999; *Nyctixalus* Boulenger, 1882; *Philautus* Gistel, 1848; *Polypedates* Tschudi, 1838; *Rhacophorus* Kuhl & Van Hasselt, 1822; *Theloderma* Tschudi, 1838.
Subfamily Strongylopinae New Subfamily
Afrana Dubois, 1992; *Strongylopus* Tschudi, 1838.
Subfamily Tomopterninae Dubois, 1987
Tomopterna Duméril & Bibron, 1841.