A re-evaluation of the phylogeny of Old World treefrogs

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No consensus has yet been reached concerning Old World treefrog systematics. Competing hypotheses are based on differing and sometimes conflicting methodologies. I use cladistic methodology to reanalyse the data from the two most important recent studies. Two monophyletic groups result; Rhacophoridae and Hyperoliidae. Seven subfamilies are recognized; six are monophyletic (Hyperoliidae: Hyperoliinae, Kassininae, Leptopelinae, Tachycneminae; Rhacophoridae: Buergeriinae, Mantellinae), while the Rhacophorinae are polyphyletic. The taxonomic changes from the standard Amphibian Species of the World (Frost 1985) proposed are: *Acanthixalus* is removed from the Leptopelinae and placed in the Hyperoliinae. *Tachycnemis* is removed from the Hyperoliinae and placed in its own subfamily, Tachycneminae. *Opisthothylax* is removed from the Hyperoliinae and placed in the Kassininae. *Afrixalus* and *Kassinula* are removed from the Kassininae and placed in the Hyperoliinae. *Aglyptodactylus* is removed from the Rhacophorinae and placed in the Mantellinae. *Buergeria* is placed in the subfamily Buergeriinae. The Mantellinae, previously in the Ranidae, is demonstrated to be a subfamily within the Rhacophoridae. The biogeography of the group is interpreted in terms of a simplified area cladogram. The most parsimonius vicariance hypothesis proposes that the stock leading to the Hyperoliidae and Rhacophoridae existed before Pangaea broke up. The sequence of fragmentation events leading to the present-day distribution started with the Seychelles, then Asia split from Africa+Madagascar, and finally Africa and Madagascar separated.

Tot dusver is geen konsensus met betrekking tot Ouwêreldboompadda-sistematiek bereik nie. Kompeterende hipoteses word op verskillende en dikwels teenstrydige metodologieë gebaseer. Ek gebruik kladistiese metodologieë om die data van die twee belangrikste onlangse studies te heranaliseer. Dit lei tot twee monofiletiese groepe: Rhacophoridae en Hyperoliidae. Sewe subfamilies word erken: ses is monofileties (Hyperoliidae: Hyperoliinae, Kassininae, Leptopelinae, Tachycneminae; Rhacophoridae: Buergeriinae, Mantellinae), terwyl die sewende (Rhacophorinae), polifileties is. Die taksonomiese veranderinge met betrekking tot die standaard Amphibian Species of the World (Frost 1985) wat voorgestel word, is: *Acanthixalus* word uit die Leptopelinae verwyder en in die Hyperoliinae geplaas. *Tachycnemis* word uit die Hyperoliinae verwyder en in sy eie subfamilie, Tachycneminae, geplaas. *Opisthothylax* word uit die Hyperoliinae verwyder en in die Kassininae geplaas. *Afrixalus* en *Kassinula* word uit die Kassininae verwyder en in die Hyperoliinae geplaas. *Aglyptodactylus* word uit die Rhacophorinae verwyder en word in die Mantellinae geplaas. *Buergeria* word in die subfamilie Buergeriinae geplaas. Die Mantellinae, voorheen deel van die Ranidae, word bewys as 'n subfamilie van die Rhacophoridae. Die biogeografie van die groep word in terme van 'n vereenvoudigde area-kladogram geïnterpreteer. Die direkste vikarians-hipotese stel voor dat die stam wat tot die Hyperoliidae en Rhacophoridae gelei het, bestaan het voor Pangaea opgebreek het. Die volgorde van fragmentasie-gebeure wat tot die huidige verspreiding gelei het, het met die Seychelle-eilande begin; toe het Asië van Afrika+Madagaskar geskei, en uiteindelik het Afrika en Madagaskar geskei.

The treefrogs of the Old World include species in Asia, Africa, Madagascar and the Seychelles. While they share certain similarities and were previously placed in one family (Ahl 1931), subsequent opinions have resulted in groupings with other genera in various families (Noble 1931; Laurent 1951; Liem 1970; Dubois 1981; Drewes 1984). There is as yet no consensus concerning treefrog classification at the family level. The arrangement in Frost (1985) highlights conflicting views. Two consequences stem from the fact that little agreement has been reached in treefrog classification: (i) The classification of these groups is very unstable at family level, where broad agreement would be expected, and (ii) analyses of relationships within any of the treefrog genera, many of them large and in need of revision, are hampered by the difficulty of selecting outgroups. A major reason for the lack of agreement is that various methodologies have been applied by earlier workers.

In view of these problems and the need for a well-supported phylogeny of Old World treefrogs as a base for further analyses, I consider it appropriate to reanalyse the data from two major works, Liem (1970) and Drewes (1984).

The genera referred to in this paper are those which are currently recognized, while the OTUs are species. Future changes to the generic assignments of these species will not affect the validity of this analysis, although a careful interpretation of these results will be required.

Systematic review

Old World treefrogs were initially assigned to 12 genera by Ahl (1931), who placed them in the Polypedatidae, distinguished by the presence of a firmisternous pectoral girdle, not or only slightly dilated sacral diapophyses and a distal intercalary cartilage.

A major series of changes to the taxonomy was suggested by Laurent (1951), who recognized two firmisternous families, Ranidae and Hyperoliidae. Some treefrog genera were placed in the Rhacophorinae of the Ranidae, while most African treefrogs, excluding the genus *Chiromantis,* were placed in the Hyperoliidae. The treefrogs from Madagascar, excluding *Boophis,* were placed in the Mantellinae of the Ranidae.

Liem (1970) divided the Old World treefrogs into two families. He believed that the Rhacophoridae was basically an Asian group, with four primitive genera in Madagascar and only the genus *Chiromantis* occurring in Africa. The Hyperoliidae included the rest of the African treefrogs with endemics in Madagascar and the Seychelles. Liem suggested that both these families were independently derived from primitive ranids.

A later detailed morphological study by Drewes (1984) was based on representatives of all the currently recognized genera within the Hyperoliidae. Drewes presented analyses both of the phylogenetic relationships within the kassinoid genera, and of the relationships of the genera within the Hyperoliidae.

The presently accepted relationships of genera within the Hyperoliidae (Frost 1985) is based on the work of Dubois (1981) who followed Laurent. Laurent (1976, 1986) disagrees with Liem's (1970) placement of *Afrixalus* as the sister group of *Hyperolius*, and his splitting of the *Phlyctimantis, Kassina* and *Hylambates (K. maculata)* lines, noting that Schiøtz (1967) had previously considered *Phlyctimantis* and *Kassina* to be very closely related, possibly congeneric. Laurent subsequently reiterated his hyperoliid phylogeny (1986) without, however, explaining how he had constructed the supporting cladogram. Cannatella (1985) pointed out that Wagner analysis of Liem's data set showed that Liem's hypothesized relationships were equivocal.

The phylogeny presented by Drewes (1984) is different in many respects from both Liem's (1970) and Laurent's (1976, 1986) proposals. Drewes (1984) places *Afrixalus* as the sister group to *Hyperolius*, and keeps *Phlyctimantis* with the *Kassina* group. Although all three authors agree on the basal position of *Leptopelis* in the Hyperoliidae, Dubois (1981) indicates that *Acanthixalus* is close to *Leptopelis*.

Analyses of relationships within treefrog genera are perplexing. The outgroups for a cladistic analysis of *Hyperolius*, for example, could be *Afrixalus* as sister group, with *Phlyctimantis* and *Cryptothylax* together as the second outgroup, according to Liem (1970); or *Chrysobatrachus* as sister group, with *Heterixalus* as the second outgroup according to Laurent (1986); or *Afrixalus* as the sister group, with *Heterixalus* as the sister group to both of these according to Drewes (1984).

The disagreement about relationships illustrated above suggests a number of questions arising from the present classification of these frogs (Frost 1985).
1. Is the subfamily Hyperoliinae, including *Callixalus, Chrysobatrachus, Cryptothylax, Heterixalus, Hyperolius, Opisthothylax* and *Tachycnemis*, monophyletic?
2. Is the subfamily Kassininae, including *Afrixalus, Kassina, Kassinula, Phlyctimantis, Semnodactylus* and *Paracassina*, monophyletic?
3. Is the subfamily Leptopelinae, including *Acanthixalus* and *Leptopelis*, monophyletic?
4. Is the subfamily Mantellinae correctly placed outside the Rhacophoridae, and which genera should it include?
5. Is the subfamily Rhacophorinae monophyletic (*Aglyptodactylus, Boophis, Buergeria, Chirixalus, Chiromantis, Nyctixalus, Polypedates, Rhacophorus, Theloderma*)?

Methods

Cladistic methodology (shortest trees constructed using synapomorphies, plesiomorphic states determined by outgroup comparison) was applied (Wiley 1981). I follow Liem and earlier workers in initially assuming the monophyly of the Old World treefrogs, believing that the cladogram should indicate monophyletic subgroups where these exist. In the discussion of character states which follows, the Ranidae serves as the outgroup for determination of polarities. Both Liem (1970) and Drewes (1984) provide arguments for the selection of the Ranidae as outgroup. Duellman & Trueb (1986) place the Ranidae and Dendrobatidae with the branch leading to the Rhacophoridae and Hyperoliidae as an unresolved trichotomy.

Data matrices were constructed by recoding and simplifying (where necessary) characters taken from Liem (1970) and Drewes (1984). See below for details. The matrices were analysed on a PC, using PAUP (Phylogenetic Analysis Using Parsimony), version 2.4.1, written by David Swofford. The use of parsimony as a means of deciding between competing hypotheses is well supported (Farris 1983; Kluge 1984). The preferred hypothesis is one which results in the shortest tree. Minimizing the tree length is equivalent to minimizing the number of hypothesized evolutionary 'steps' (transformations from one character state to another) (Swofford 1985). The shortest tree minimizes the number of reversals and convergences needed to explain the evolution of the characters in the hypothesized phylogeny. Tree length is the minimum number of character changes on the tree. The congruence between the data and the cladogram can be measured as a consistency index, which is the minimum number of character changes required by the data, divided by the actual number of changes required by the tree. Consistency indices may be calculated for each character, and for the cladogram. The consistency index varies from zero (poor fit) to one (perfect congruence).

Liem's data: Relationships of Old World treefrogs

Transformation Series

The data set presented in Liem's (1970) examination of the morphology, systematics and evolution of the Old World treefrogs serves as the basis for this analysis. These data are restricted to 21 (presently recognized) genera included in the original work. However, this initial analysis serves to test the monophyly of the Rhacophoridae and Hyperoliidae, and suggests outgroups for further analyses. Liem's data do not include the genera *Callixalus, Chrysobatrachus, Opisthothylax, Tachycnemis*, or *Acanthixalus* (Hyperoliidae of Frost 1985), nor *Nesionixalus, Alexteroon, Arlequinus* and *Chlorolius* (Perret 1988). His character states have been simplified where necessary, to reduce the number of unique, non-informative apomorphies. Some characters do not display a linear sequence of state transformations; these were input using additive binary coding (Brooks, Caira, Platt & Pritchard 1984). Additive binary coding introduces excess code, which is ignored by the program.

As an example, State 0 might be coded 100 in a non-linear transformation. The initial '1' will occur throughout the data matrix, and will thus not be taken into account by the program, which only looks for changes in character states. The extra code is maintained for clarity, as it does not inflate the consistency indices or change the tree topologies in any way. Illustrations of the characters and more detailed discussions are available in Liem (1970). Character descriptions which did not require modification were taken directly from Liem (1970).

1. M. Humerodorsalis. (Liem's Character 1, with his State 2 omitted as it is not present in any of the species represented here. His State 3 is recoded as (2). State 0: The M. humerodorsalis splits into three main, short slips at the level of the carpometacarpal joint, the second, third, and fourth phalangeal slips. State 1: The M. humerodorsalis splits into two main halves at the distal half of the radio-ulna. The medial half consists of two distal slips, the second and third phalangeal slips while the lateral half consists of the fourth phalangeal and the short fourth metacarpal slips. State 2: The M. humerodorsalis is completely divided, inserting on the third and on the fourth metacarpals. State 0 was found in all ranids examined by Liem (1970). Polarity $0 \rightarrow 1 \rightarrow 2$.

2. Palmaris complex (Liem's Character 2). This character was coded using the additive binary method, in order to accommodate the polarity suggested by Liem. State 0 (coded as 100): The distal third of the palmaris longus muscle splits into two, both inserting on the proximal rim of the Aponeurosis palmaris. State 1 (coded as 110): The medianmost portion of the M. palmaris longus inserts on the proximo-medial portion of the Aponeurosis palmaris (Liem's States 1, 5 and 6). State 2 (coded as 101): The outermost slip of the M. palmaris longus inserts on the proximolateral rim of the Aponeurosis palmaris (Liem's States 2, 3, and 4). State 0 is found in some ranids, and is intermediate between typical ranids and treefrogs. Polarity $2 \leftarrow 0 \rightarrow 1$.

3. Extensor Radialis Accessorius Lateralis (Liem's Charater 3). State 0 (coded as 1000): The M. extensor radialis accessorius lateralis is moderately large, originating along the lateral side of the humerus between the crista ventralis and the epicondylus humeri, inserting on the distal tendon of the M. extensor radialis superficialis. State 1 (coded as 1100): As in State 0, except that the insertion is on the dorsal end of the radio-ulna. State 2 (coded as 1110): The M. extensor radialis is very narrow, originating from the lateral side of the crista ventralis. State 3 (coded as 1101): As in State 2, except that the insertion is on the disto-dorsal end of the radio-ulna. State 0 is widely distributed in the ranids examined by Liem (1970).

$$2$$
$$\uparrow$$
Polarity $0 \rightarrow 1$
$$\downarrow$$
$$3$$

4. M. Adductor Longus (Liem's Character 4 un-changed). State 0: The M. adductor longus is present, inserting along the distal half or third of the M. adductor magnus. State 1: The adductor longus is absent. The adductor longus is present in all ranids examined by Liem (1970). Polarity $0 \rightarrow 1$.

5. M. Extensor Digitorum Communis Longus of the tarsus (Liem's Character 5). State 0 (coded as 10000): Three distal slips of the M. extensor Digitorum communis longus are present, inserting on the distal portion of the metatarsals of the third, fourth, and fifth toes. State 1 (coded as 11000): Two distal slips of the M. extensor Digitorum cummunis longus are present, inserting on the distal portion of the metatarsals of the third and fourth toes. State 2 (coded as 11100): One slip of the M. extensor Digitorum cummunis longus is present, inserting on the distal portion of the metatarsal of the fourth toe. State 3 (coded as 11010): Two distal slips of the M. extensor Digitorum communis present, the lateral one inserting on the distal portion of the metatarsal of the fourth toe, and the medial one inserting on the proximal portion of the metatarsal of the third toe. State 4 (coded as 11011): One distal slip of the M. extensor Digitorum cummunis longus is present, inserting on the proximal portion of the metatarsal of the third toe. The largest number of slips with insertions on the distal portion of the metatarsals is found in some ranids (Liem 1970). Liem discusses the hypothesized evolution of this character.

$$2$$
$$\uparrow$$
Polarity $0 \rightarrow 1 \rightarrow 3 \rightarrow 4$

6. Throat musculature (Liem's Character 6). Liem regards his State 1 as primitive. It is here recoded as 0. State 0 (coded as 010): The M. submaxillaris and the M. submaxillaris ventralis are not distinct, forming a continuous layer. State 1 (coded as 110): The M. dentomentalis is fan-shaped, the M. submaxillaris ventralis and the M. submaxillaris are distinct. State 2 (coded as 011): The M. dentomentalis is narrow and runs parallel to the lower jaw. The M. submaxillaris is absent. State 0 is widely distributed in generalized ranids (Liem 1970). Polarity $1 \leftarrow 0 \rightarrow 2$.

7. Most anterior slip of the M. Petrohyoideus Posterior (Liem's Character 7 unchanged). State 0: The most anterior slip of the M. petrohyoideus posterior inserts on the thyrohyal or on the cartilaginous stalk of this process. State 1: The most anterior slip of the M. petrohyoideus posterior inserts on the membrana thyroideus. State 0 is found in the majority of ranids (Liem 1970). Polarity $0 \rightarrow 1$.

8. M. Petrohyoideus (Liem's Character 8). State 0 (coded as 1000): The M. petrohyoideus anterior is separate from the M. petrohyoideus posterior, the latter consists of three equal-sized slips. State 1 (coded as 1100): As in State 0, except that the two posterior slips of the M. petrohyoideus posterior overlap. State 2 (coded as 1110): The M. petrohyoideus anterior is separated from the M. petrohyoideus posterior. The latter consists of two distinct slips, the anterior being 1 to 1,5 times the

width of the posterior one. State 3 (coded as 1101): As in State 2, except that the anterior slip of the M. petrohyoideus posterior is two or three times the width of the posterior one. State 0 is widely distributed in the ranids examined by Liem (1970).

$$3$$
$$\uparrow$$
Polarity $0 \rightarrow 1 \rightarrow 2$

9. M. Geniohyoideus (Liem's Character 9). This character is recoded using the additive binary method, in order to accomodate Liem's suggested polarities. State 0 (coded as 100000): The M. geniohyoideus lateralis straddles the M. sternohyoideus and is separated from the M. geniohyoideus medialis. The external slip of the M. geniohyoideus lateralis inserts on the posterior lateral process. State 1 (coded as 110000): As in State 0, except the external slip of the M. geniohyoideus inserts on the membrana thyroideus. State 2 (coded as 101000): The M. geniohyoideus lateralis and medialis are fused. State 3 (coded as 100100): The internal slip of the M. geniohyoideus lateralis is absent; the M. geniohyoideus lateralis inserts on the posterior rim of the alary process. State 4 (coded as 110011): The internal slip of the M. geniohyoideus is absent; the external slip inserts on the proximal portion of the thyrohyal. State 5 (coded as 110001): The M. geniohyoideus medialis and lateralis are separated; the latter straddles the M. sternohyoideus, whereas the external slip of the M. geniohyoideus inserts on the thyrohyal. State 0 is widely distributed in the ranids examined (Liem 1970).

$$2$$
$$\uparrow$$
Polarity $3 \leftarrow 0 \rightarrow 1 \rightarrow 5 \rightarrow 4$.

10. Thyrohyal (Liem's Character 10). Liem's States 1 and 2 are recoded 2 and 1 respectively, to accomodate his suggested polarities. State 0: The bony thyrohyal abuts on the postero-medial side of the hyoid plate. The space between the proximal ends of the thyrohyal is narrow and is more or less equal to the width of the proximal end of the thyrohyal. State 1: The bony thyrohyal abuts on the postero-medial rim of the hyoid plate. The distance between the proximal ends of the bony thyrohyal is larger than the width of that end. State 2: The bony thyrohyal abuts on a cartilaginous stalk. The distance between the proximal ends of the bony thyrohyal is larger than the width of that end.
Polarity $0 \rightarrow 1 \rightarrow 2$.

11. Presence or absence of the Alary Process (Liem's Character 11, unchanged). State 0: The alary process is present. State 1: The alary process is absent. The presence of the alary process is widely distributed in the ranids examined by Liem (1970). Polarity $0 \rightarrow 1$.

12. Shape of the Alary Process (Liem's Character 12). State 0 (coded as 1000): The alary process is dilated distally. The length of the stalk is less than the width of the distal dilation. State 1 (coded as 1100): The alary process is club-shaped. State 2 (coded as 1110): The alary process is blade-shaped without or with slight

dilation at the distal end. State 3 (coded as 1001): The base of the alary process is broad, two to three times the width of the distal dilation. State 0 is widely distributed in the ranids examined by Liem (1970).
Polarity $3 \leftarrow 0 \rightarrow 1 \rightarrow 2$.

13. Presence or absence of the Anterior Horn of the Hyoid (Liem's Character 13, unchanged). State 0: Anterior horn present. State 1: Anterior horn absent. The anterior horn is present in the majority of ranids examined by Liem (1970). Polarity $0 \rightarrow 1$.

14. Form of the Anterior Horn (Liem's Character 14, unchanged). State 0: The anterior horn consists of a complete arch along the anterior portion of the hyalia. State 1: The anterior horn consists of two processes: a median and a lateral branch. State 2: Only the median branch of the anterior horn is present. State 0 is found in some ranids and in other frogs (Liem 1970).
Polarity $0 \rightarrow 1 \rightarrow 2$.

15. Posterior Lateral Process (Liem's Character 15, unchanged). State 0: The posterior lateral process is long, at least one-third the length of the thyrohyal. State 1: The posterior lateral process is very short, a mere stump on the postero-lateral corner of the hyoid plate. State 2: The posterior lateral process is completely absent. All ranids examined by Liem (1970) have the long posterior lateral process. Polarity $0 \rightarrow 1 \rightarrow 2$.

16. Vertebral column (Liem's Character 16, unchanged). State 0: The vertebrae are diplasiocoelous. State 1: The vertebrae are procoelous. Diplasiocoelous vertebrae are widely distributed in ranids (Liem 1970). Polarity $0 \rightarrow 1$.

17. Shape of the eighth vertebra (Liem's Character 17, unchanged). State 0: The segment of the neuropophysis connecting the centrum and the transverse process attaches on the dorsolateral portion of the centrum. The contour of the centrum viewed ventrally is distinctly cylindrical. State 1: The segment of the neuropophysis connecting the centrum and the transverse process attaches on the lateral portion of the centrum; the neuropophysis is moderately broad and usually it is slightly convex. The contour of the centrum viewed ventrally is only slightly cylindrical. State 2: The segment of the neuropophysis connecting the centrum and the transverse process attaches on the ventro-lateral portion of the centrum. The contour of the centrum is not cylindrical when viewed from the ventral side. State 0 is widely distributed in the ranids (Liem 1970).
Polarity $0 \rightarrow 1 \rightarrow 2$.

18. Dimensions of the vertebral column (Liem's Character 18). Relative length of the vertebral column was expressed as the ratio of vertebral column length / greatest width of transverse processes of the eighth vertebra. State 0 (coded as 100): Relative length of the vertebral column from 1,6 to 2,4. State 1 (coded as 110): Relative length of the vertebral column from 1,0 to 1,5. State 2 (coded as 101): Relative length of the vertebral column more that 2,8. State 0 is widely distributed in ranids. Polarity $2 \leftarrow 0 \rightarrow 1$.

19. Frontoparietal (Liem's Character 19). State 0 (coded as 100000): The frontoparietal is rectangular; the parieto-squamosal arch is absent. State 1 (coded as

110000): The anterior portion of the fronto-parietal is wider than the posterior portion; the parieto-squamosal arch is absent. State 2 (coded as 111000): The anterior end of the frontoparietal is wider than posterior; the parieto-squamosal arch is short, reaching only to the occipito-prootic ridge. State 3 (coded as 111100): As in State 2 except that the parieto-squamosal arch is long, behind the skull, almost reaching to the dorsal prootic plate of the squamosal. State 4 (coded as 111110): The entire fronto-parietal bone is covered by a bony plate; it continues posteriorly by forming a wide parieto-squamosal plate reaching to the outermost edge of the squamosal. State 5 (coded as 100001): The frontoparietal is trapezoidal; the parieto-squamosal arch and plate are absent. The majority of ranids have a frontoparietal similar to State 0, with the parieto-squamosal arch absent (Liem 1970). Polarity $5 \leftarrow 0 \rightarrow 1 \rightarrow 2 \rightarrow 3 \rightarrow 4$.

20. Shape of the nasal and exposure of the sphenethmoid (Liem's Character 20). State 0 (coded as 01000): The nasals are triangular, and the sphenethmoid is barely visible in dorsal view, its exposure being 0,1 to 0,2 of the length of the frontoparietal. State 1 (coded as 11000): The nasals are spindle shaped, and the sphenethmoid is barely visible in dorsal view. State 2 (coded as 01100): Nasals triangular, and the sphenethmoid moderately large, its exposure being 0,3 to 0,5 of the length of the fronto-parietal. State 3 (coded as 01110): Nasals squash-shaped. The sphenethmoid is large, its exposure being 0,6 to 1,0 of the length of the frontoparietal. State 4 (coded as 01111): As in State 3, except that the nasals are club-shaped. State 0 is widely distributed in ranids (Liem 1970). Polarity $1 \leftarrow 0 \rightarrow 2 \rightarrow 3 \rightarrow 4$.

21. Ventro-posterior portion of the sphenethmoid (Liem's Character 21, unchanged). State 0: The ventro-posterior portion of the sphenethmoid forms a fused bony plate in the region of the palatine bone. State 1: The ventro-posterior portion of the sphenethmoid consists of two separate bones and usually does not extend anteriorly beyond the palatine bone. State 0 was found in all ranids examined by Liem (1970). Polarity $0 \rightarrow 1$.

22. Presence or absence of vomerine teeth (Liem's Character 22). Liem's character States 1 and 2 are reversed, to accommodate his polarity. State 0: Vomerine teeth always present. State 1: Vomerine teeth present in 25 to 75% of the sample examined. State 2: Vomerine teeth always absent. State 0 is widely distributed in ranids (Liem 1970). Polarity $0 \rightarrow 1 \rightarrow 2$.

23. Vomerine odontophore (Liem's Character 23, unchanged). State 0: Vomerine odontophore present. State 1: Vomerine odontophore absent. State 0 is widely distributed in ranids (Liem 1970). Polarity $0 \rightarrow 1$.

24. Omosternum (Liem's Character 24, unchanged). State 0: The base of the omosternum is not forked. State 1: The base of the omosternum is slightly forked, the greatest space between arms is less than half the width of one arm. State 2: The base of the omosternum is moderately forked. The greatest space between the arms is one to two times the width of one arm. State 3: The base of the omosternum is broadly forked. The greatest

space between the arms is two to four times the width of one arm. Although States 1, 2 and 3 are almost equally distributed in ranids, State 0 is found in the majority of *Rana* (Liem 1970). Polarity $0 \rightarrow 1 \rightarrow 2 \rightarrow 3$.

25. Metasternum (Liem's Character 25). State 0: Metasternum is a narrow bony stylus. State 1: Metasternum is broad and cartilaginous, sometimes partially ossified. Liem proposed that the cartilaginous metasternum should be considered primitive, even though the outgroup (ranids) possess a bony stylus. I rely on the outgroup evidence when determining character polarity, and consider the cartilaginous metasternum a synapomorphy. Polarity $0 \rightarrow 1$.

26. Metacarpal of the third finger (Liem's Character 26, unchanged). State 0: The distal end of the third metacarpal is not or only slightly dilated and no bony knob is present. State 1: The distal end of the third metacarpal is distinctly dilated and a prominant distomedial bony knob is present. State 0 is found in all ranids (Liem 1970). Polarity $0 \rightarrow 1$.

27. Terminal phalanx (Liem's Character 27). This character is coded according to the additive binary method, to accomodate Liem's proposed character transformations. Liem's State 1 is renumbered as 3, while his States 2 and 3 become 1 and 2 respectively. State 0 (coded as 1000): Obtuse terminal phalanx; the distal end is simple or a rounded knob. State 1 (coded as 1100): Bifurcate terminal phalanx; the distal end is slightly bifurcate but not pointed, and the length of each branch is less than the width of the phalanx. State 2 (coded as 1110): Y-shaped terminal phalanx, the distal ends are pointed and the length of each branch is longer than the width of the phalanx. State 3: (coded as 1001): Claw-shaped terminal phalanges. Polarity $3 \leftarrow 0 \rightarrow 1 \rightarrow 2$.

28. Carpal bones (Liem's Character 28, unchanged). State 0: The first, second and third carpals and the first centrale are free; the fourth and fifth carpals, and the second centrale are fused. State 1: The first and second carpals and the first centrale are free; the third, fourth and fifth carpals, and the second centrale are fused. A free third carpal is found in the ranid genera *Trichobatrachus, Cardioglossa, Astylosternus,* and many species of *Arthroleptis.* However, it is also free in the Pelobatidae, Discoglossidae, Pipidae and Ascaphidae. Liem thus regards a free third carpal as primitive.

Drewes argued that the free third carpal in hyperoliids should be considered as paedomorphic, and hence derived (1984:35). His analysis was based on character correlation, and was motivated in part by the difficulty of constructing a tree using the free third carpal as a primitive character. However, I agree with the view expressed earlier by Liem (1970:9) that it is more parsimonius to assume character state changes of free to fused, rather than the more complex sequence of free to fused to free. Polarity $0 \rightarrow 1$.

29. Tarsal bones (Liem's Character 29, unchanged). State 0: The first and second tarsal bones are free; the third and fourth are fused. State 1: Only the first tarsal is free; the second, third and fourth tarsals are fused. State

0 is widely distributed in the ranids examined (Liem 1970). Drewes (1984:34) draws attention to errors in Liem's identification of individual tarsalia. He also advocates a sequence of unfused to fused to unfused tarsalia. However, I do not consider it necessary to assume an extra evolutionary step (see Character 28, above). Polarity 0 → 1.

30. Vesicula seminalis (Liem's Character 31, unchanged). State 0: Bottle-shaped vesicula seminalis is absent. State 1: Bottle-shaped vesicula seminalis is present. Liem (1970) regarded State 1 as specialized and derived. It occurs in a few ranids. Polarity 0 → 1.

31. Presence or absence of web between the two outer metatarsals (Liem's Character 32, unchanged). State 0: The two outer metatarsals are distinctly separated with webbing in between. State 1: The two outer metatarsals are united or are separated only by a groove. State 0 is found in the majority of the ranids examined by Liem (1970). Polarity 0 → 1.

32. Digital disc (Liem's Character 33). I have reduced the number of transformations in order to increase the number of OTUs sharing synapomorphies. Liem's States 2, 3, and 4 are coded as 2. State 0: Terminal segment of the digit is not dilated. No digital pad or transverse or ventro-marginal groove is present. State 1: Terminal segment of the digit is slightly dilated. Digital pad is elongated and is surrounded distally by a horseshoe-shaped ventro-marginal groove. The transverse groove is absent. State 2: Terminal segment of the digit is extensively dilated. A ventro-marginal groove is present. A transverse groove may be present. Liem (1970) argued that the presence of dilated toe tips is an adaptation to an arboreal existence in this group of treefrogs. Polarity 0 → 1 → 2.

33. Orientation of the pupil (Liem's Character 34, unchanged). State 0: Pupil is horizontal. State 1: Pupil is vertical. State 0 is widely distributed in the ranids (Liem 1970), although Lynch (1973) concluded that a vertical pupil was primitive for amphibians as a whole. Polarity 0 → 1.

34. Nuptial pad (Liem's Character 35, unchanged). State 0: Nuptial pad is present. State 1: Nuptial pad is absent. Nuptial pads are widely distributed in ranids (Liem 1970). Polarity 0 → 1.

The following species were selected from Appendix 3 of Liem (1970) to represent each genus (Liem's species numbers in parentheses): *Afrixalus fornasinii* (8), *Aglyptodactylus madagascariensis* (51), *Boophis tephrae-mystax* (46), *Buergeria robusta* (31), *Chirixalus doriae* (55), *Chiromantis xerampelina* (43), *Cryptothylax gress-hoffi* (13), *Heterixalus madagascariensis* (12), *Hyperolius marmoratus* (1), *Kassina senegalensis* (21), *Kassinula wittei* (23), *Leptopelis bocagei* (17), *Mantidactylus ulcerosus* (48), *Nyctixalus pictus* (52), *Philautus hosei* (42), *Phlyctimantis verrucosus* (14), *Polypedates dugritei* (28), *Rhacophorus microtympanum* (27), *Semnodactylus wealii* (24), *Paracassina obscura* (26), *Theloderma stellatum* (53). Dubois (1981) showed that *Paracassina* is a senior synonym of *Tornierella*. Where more than one species was available within a genus, I selected the species displaying the most pleisiomorphies. The data matrix is presented in Table 1.

Data analyses

The following options were set: MULPARS (searches for multiple equally parsimonius trees), SWAP= GLOBAL (performs branch swapping at all locations on the tree in order to find a shorter tree), HOLD=5 (keeps up to five trees in memory on which to operate to

Table 1 Data matrix modified from Liem (1970). See text for descriptions of character states and details of species selected to represent each genus

Afrixalus	211010000110110110110111001120100101201101100001010001213111001001211
Aglyptodactylus	010110000111001100100010000000100000019999100001011110000001001010101200
Boophis	110110001110001100100010000000011001101110010000101110000200110010000200
Buergeria	110110000111000100100010000000010000200110010000101110000000110011000200
Chirixalus	210111101111000100100010000000199990001010110000001110000101100011000200
Chiromantis	210111001111001101100010000000011000100010011000001110000101110011101200
Cryptothylax	211010000110110110110110010020100101201101100001100010031110010001210
Hyperolius	211010000110110110110100100201001002011011000000100012131110010001201
Heterixalus	211010000110110110110100100201001012011011000000100012131110010001201
Kassina	211010000110110110100011001110100101201101100001010001003111100000011011
Kassinula	211010000110110110110011001120100101201101100001010000292111100000011111
Leptopelis	211010001110100110110011000120110002200100100000011100000111100100011211
Mantidactylus	010010000111001100100010000000010000001210010000101111100100110001011200
Nyctixalus	210111101111001100111010000000010011901210010000001110000101110011101200
Philautus	210111001111000100100010100000011001000100110000011100000011100101011201
Phlyctimantis	211010000110110110110110010020100101201101100001100010031110010001210
Polypedates	210111001111001100100010000000110190111001000000011001010111011001100200
Rhacophorus	210110001111001100100010000000211002010010010000001110000101111011101110200
Semnodactylus	211010000110110110999999999920100101101101100001999999003111000000011011
Theloderma	210111101111001100111099999909999999011100999999999999920101110011190200
Paracassina	211010000110110110999999999990100109901101999999999999920911110000001101

Table 2 Consistency indices for the characters used in the analysis of Liem's data. The initial values refer to the data-matrix columns, with character numbers in parentheses. Three characters 'flip-flop' by being placed at two different positions on the various trees; these result in nine different equal-length trees. Constant character states are redundant, but listed here for completeness as they are part of the non-linear additive binary coding

1. M. Humerodorsalis (1)	0,500
2. Palmaris complex (2)	constant
3. Palmaris complex (2)	1,000
4. Palmaris complex (2)	0,500
5. Extensor Radialis Accessorius Lateralis (3)	constant
6. Extensor Radialis Accessorius Lateralis (3)	0,500
7. Extensor Radialis Accessorius Lateralis (3)	0,500
8. Extensor Radialis Accessorius Lateralis (3)	constant
9. M. Adductor Longus (4)	0,500
10. M. Extensor Digitorum Communis Longus (5)	constant
11. M. Extensor Digitorum Communis Longus (5)	1,000
12. M. Extensor Digitorum Communis Longus (5)	0,500
13. M. Extensor Digitorum Communis Longus (5)	1,000
14. M. Extensor Digitorum Communis Longus (5)	1,000
15. Throat musculature (6)	0,333
16. Throat musculature (6)	constant
17. Throat musculature (6)	1,000
18. M. Petrohyoideus Posterior (anterior)(7)	1,000
19. M. Petrohyoideus (8)	constant
20. M. Petrohyoideus (8)	0,333
21. M. Petrohyoideus (8)	1,000
22. M. Petrohyoideus (8)	0,500
23. M. Geniohyoideus (9)	constant
24. M. Geniohyoideus (9)	0,500
25. M. Geniohyoideus (9)	1,000
26. M. Geniohyoideus (9)	0,500
27. M. Geniohyoideus (9)	1,000
28. M. Geniohyoideus (9)	0,500
29. Thyrohyal (10)	0,667
30. Alary Process (11)	1,000/0,667
31. Shape of Alary Process (12)	constant
32. Shape of Alary Process (12)	0,333
33. Shape of Alary Process (12)	0,333/0,500
34. Shape of Alary Process (12)	0,500
35. Anterior horn of hyoid (13)	0,500
36. Shape of anterior horn (14)	0,286
37. Posterior lateral process (15)	0,667
38. Vertebral column (16)	0,500
39. Eighth vertebra (17)	0,400
40. Vertebral column dimensions (18)	constant
41. Vertebral column dimensions (18)	constant
42. Vertebral column dimensions (18)	0,500
43. Frontoparietal (19)	constant
44. Frontoparietal (19)	1,000
45. Frontoparietal (19)	constant
46. Frontoparietal (19)	constant
47. Frontoparietal (19)	constant
48. Frontoparietal (19)	0,333
49. Sphenethmoid exposure (20)	1,000
50. Sphenethmoid exposure (20)	constant
51. Sphenethmoid exposure (20)	0,500

Table 2 Continued

52. Sphenethmoid exposure (20)	0,500
53. Sphenethmoid exposure (20)	1,000
54. Ventro-posterior Sphenethmoid (21)	0,333
55. Vomerine teeth (22)	0,286
56. Vomerine odontophore (23)	0,500
57. Omosternum (24)	0,375
58. Metasternum (25)	1,000
59. Metacarpal of third finger (26)	0,500
60. Terminal phalanx (27)	constant
61. Terminal phalanx (27)	0,200
62. Terminal phalanx (27)	0,500
63. Terminal phalanx (27)	0,333
64. Carpal bones (28)	0,500
65. Tarsal bones (29)	0,333
66. Vesicula seminalis (30)	0,500
67. Web between outer metatarsals (31)	0,333
68. Digital disc (32)	0,500
69. Pupil (33)	0,333
70. Nuptial pad (34)	0,333

find shorter trees). All other options assumed default values. The analysis yielded nine equally parsimonius trees, each of 134 steps and with consistency indices of 0,478. The trees were rooted using the outgroup 'ranids'. The consistency indices for each character are listed in Table 2.

The trees differed only in the placement of the *Nyctixalus, Polypedates* and *Theloderma* branches, and in the relative positions of *Chirixalus, Rhacophorus* and the branch leading to *Chiromantis* and *Philautus*. The *Paracassina, Kassinula* and branch leading to *Kassina* and *Semnodactylus* could also not be resolved. (However, this relationship is resolved using Drewes' data below). A consensus tree, in which those three areas of uncertainty have been collapsed to show the most generalized topology, is presented in Figure 1, discussed below.

Liem (1970) analysed the relationships of 10 hyperoliid genera. Drewes (1984), however, presented data on fifteen presently recognized hyperoliid genera. Perret (1988) recognizes four other small genera from western Africa, not included in this analysis. Two of Drewes' (1984) aims were to test the hypothesis that the Hyperoliidae was a monophyletic group after the inclusion of additional genera not examined by Liem (1970), and to test Laurent's (1979) placing of the arthroleptine and astylosternine ranids within the Hyperoliidae. He concluded that the Hyperoliidae was monophyletic, and that Laurent's views on arthroleptine and astylosternine relationships with the Hyperoliidae were based on symplesiomorphies and hence unsupported.

As Drewes' phylogenetic analysis was computed by hand (Drewes 1984:6), and as his data are based on all the hyperoliid genera, I considered it worthwhile to reanalyse the data using PAUP, in order to obtain the shortest tree from which to infer the phylogeny of this group. I used a corrected version of Drewes' (1984) data
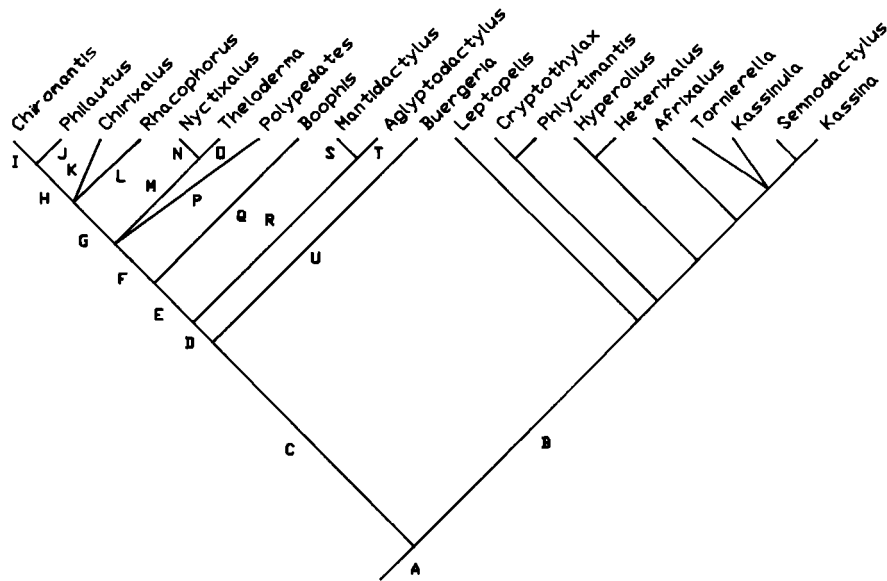
Figure 1 Cladogram of genera of Old World treefrogs, based on Liem (1970). This is a consensus tree derived from nine 134-step trees, each with a consistency index of 0,478. The annotation represents the following character state changes at the indicated nodes of the tree [numerals identify characters (data matrix columns), superscripts indicate hypothesized character state changes].
A — 1^{0-1}, 11^{0-1}, 36^{0-1}, 39^{0-1}, 51^{0-1}, 52^{0-1}, 68^{0-2}; B — 1^{1-2}, 3^{0-1}, 13^{0-1}, 17^{0-1}, 20^{0-1}, 29^{0-2}, 37^{0-2}, 58^{0-1}, 59^{0-1}, 63^{0-1}, 67^{0-1}, 69^{0-1}, 70^{0-1}; C — 4^{0-1}, 12^{0-1}, 48^{0-1}, 61^{0-1}, 64^{0-1}, 65^{0-1}; D — 15^{0-1}, 38^{01}, 57^{0-1}; E — 9^{0-1}, 32^{0-1}, 35^{0-1}; F — 1^{1-2}, 6^{0-1}, 33^{0-1}, 48^{1-0}, 59^{0-1}; G — 35^{1-0}, 39^{1-0}, 66^{0-1}; H — 38^{1-0}, 44^{0-1}; I — 18^{0-1}, 33^{1-0}; J — 15^{1-0}, 25^{0-1}, 57^{1-0}, 65^{1-0}, 67^{0-1}, 70^{0-1}; K — 7^{0-1}, 15^{1-0}, 30^{0-1}, 36^{1-0}, 42^{0-1}, 61^{1-0}, 66^{1-0}; L — 6^{1-0}, 30^{0-2}, 36^{1-2}, 62^{0-1}; M — 7^{0-1}, 20^{0-1}, 21^{0-1}, 32^{1-0}, 33^{1-0}, 34^{0-1}, 66^{0-1}; N — 39^{12}; O — 55^{0-2}; P — 55^{0-1}, 62^{0-1}; Q — 12^{1-0}, 57^{1-2}, 65^{1-0}; R — 1^{1-0}, 36^{1-0}, 39^{1-2}, 53^{0-1}, 64^{10}, 67^{0-1}; S — 4^{1-0}, 54^{0-1}; T — 57^{1-0}, 61^{1-0}, 63^{0-1}; U — 36^{1-2}.

matrix, as there are errors in the matrix as published (Drewes, pers com.) This analysis is presented below.

Drewes' data: Relationships of the mainly African genera of treefrogs (Hyperoliidae)

The family Hyperoliidae *sensu* Drewes (1984) includes 15 genera: *Acanthixalus, Afrixalus, Callixalus, Chrysobatrachus. Cryptothylax. Heterixalus, Hyperolius, Kassina, Kassinula, Leptopelis, Semnodactylus (Notokassina* of Drewes 1985), *Opisthothylax, Phylictimantis, Tachycnemis, Paracassina. Heterixalus* is found on Madagascar, and *Tachycnemis* occurs on the Seychelles.

Drewes' (1984) data set was used as the basis for this analysis. The character states have been slightly modified and recoded where necessary to serve as input for PAUP.

Transformation series

1. Dorsal exposure of the sphenethmoid. (Based on Drewes 1984, Character 1). State 0: Sphenethmoid invisible dorsally or exposure not exceeding 0,2 of length of frontoparietals. State 1: Exposure of sphenethmoid greater than 0,3 of frontoparietals. Ranids commonly show a slight exposure of the sphenethmoid (Liem 1970; Drewes 1984). Polarity 0 → 1.

2. Ventral configuration of the sphenethmoid. (Unchanged from Drewes 1984, Character 2). State 0: Ventroanterior portion of sphenethmoid a single bony plate. State 1: Ventroanterior portion of sphenethmoid unfused, consisting of two elements. State 0 was present in most ranids examined by Liem (1970) and Drewes

(1984). Polarity 0 → 1.

3. Quadratojugal. (Based on Drewes 1984, Character 3). State 0: Quadratojugal contacts maxilla. State 1: Quadratojugal not contacting maxilla. Most ranids share State 0 (Drewes 1984). Polarity 0 → 1.

4. Prevomerine dentigerous processes. (Unchanged from Drewes 1984, Character 4). State 0: Prevomerine odontophore present, teeth present or absent. State 1: Prevomerine odontophore absent, prevomerine teeth always present. Dentigerous processes are widespread among ranids (Liem 1970).
Polarity 0 → 1.

5. Vertebral centra. (Unchanged from Drewes 1984, Character 5). State 0: Vertebrae diplasiocoelous. State 1: Vertebrae procoelous. Most ranids are diplasiocoelous (Drewes 1984). Polarity 0 → 1.

6. Neural arch. (Unchanged from Drewes 1984, Character 6). State 0: Neural arches of at least the anterior presacral vertebrae are imbricate, concealing the neural canal. State 1: Neural arches non-imbricate. State 0 is broadly distributed among anurans and ranines (Drewes 1984). Polarity 0 → 1.

7. Relative length of vertebral column. (Unchanged from Drewes 1984, Character 7). State 0: Ratio of vertebral column length to eighth transverse process length 1,6 to 2,4. State 1: Ratio of 2,5 to 3,5. State 2: Ratio greater than 3,6. State 0 is possessed by the majority of ranids (Liem 1970; Drewes 1984). Polarity 0 → 1 → 2.

8. Orientation of transverse processes of eighth presacral vertebra. (Unchanged from Drewes 1984, Character 8). State 0: Transverse processes of eighth

presacral vertebra essentially perpendicular to longitudinal axis of the vertebral column. State 1: Transverse processes of eighth presacral vertebra angled markedly forward, at least 70°. Most ranid species surveyed by Drewes exhibited State 0 (Drewes 1984). Polarity 0 → 1.

9. Cartilaginous stalk of thyrohyal. (Unchanged from Drewes 1984, Character 10). State 0: Thyrohyals abut directly on hyoid plate, not on cartilaginous stalks. State 1: Thyrohyals borne on cartilaginous stalks. Most ranids display State 0 (Drewes 1984). Polarity 0 → 1.

10. Anterior horn of hyoid. (Based on Drewes 1984, Character 11). State 0: Anteriormost process of anterior horn present, lateral process absent. State 1: Anterior horn composed of two elements, an anteromedial and a lateral process. State 2: Anterior horn entire, forming a complete arch. State 0 is exhibited by the majority of ranids (Drewes 1984). Polarity 0 → 1.

11. Palmaris musculature. (Unchanged from Drewes 1984, Character 12). State 0: Aponeurosis palmaris present, none of the tendenes superficialis is able to slide through it. State 1: Aponeurosis palmaris present, but thin and diaphanous, proximal ends of third and fourth tendenes superficialis are able to slide through it. State 2: Aponeurosis palmaris absent. State 0 was observed in all ranids examined by Liem (1970) and Drewes (1984). Polarity 0 → 1 → 2.

12. Digital sesamoids. (Based on Drewes 1984, Character 13). State 0: Sesamoids absent. State 1: Sesamoids present in subarticular regions of distal ends of phalanges of some or all fingers and toes. State 0 is widespread in the Ranidae (Drewes 1984). Polarity 0 → 1.

13. Terminal phalanx of third finger. (Based on Drewes 1984, Character 14). State 0: Terminal phalanx tapered, or peniform, or short and obtuse, but always unbifurcate. State 1: Terminal phalanx bifurcate. State 0 is present among the ranids (Drewes 1984). Polarity 0 → 1.

14. Coracoids. (Unchanged from Drewes 1984, Character 15). State 0: Medial margins of coracoids entire. State 1: Medial margins of coracoids centrally perforated. State 0 is present in most ranids (Drewes 1984). Polarity 0 → 1.

15. Omosternum. (Unchanged from Drewes 1984, Character 16). State 0: Base of omosternum unforked, usually forming a flat or slightly convex plane. State 1: Omosternum notched, (greatest space between arms less than half width of a single arm) or moderately forked, (interarm space one to two times width of one arm). State 2: Omosternum greatly forked, space between arms more than twice width of one arm. The unforked condition is found widely in the ranines (Liem 1970). Polarity 0 → 1 → 2.

16. Mineralization of metasternum. (From Drewes 1984, Table 1). State 0: Metasternum mineralized, at least in part. State 1: Metasternum not mineralized. The metasternum in ranids is bony (Drewes, 1984). Polarity 0 → 1.

17. Gular gland. (Based on Drewes 1984, Character

18). State 0: Gular gland absent. State 1: Gular gland present but moderately developed. State 2: Gular gland extensive. Gular glands were absent in the ranids examined by Drewes (1984). Polarity 0 → 1.

18. Forearm glands. (Based on Drewes 1984, Table 2). State 0: Forearm glands absent. State 1: Forearm glands present. Although topical glands are known in many ranoids, forearm glands appear to be absent in the Ranidae (Duellman & Trueb 1986). Polarity 0 → 1.

19. Pectoral glands. (Based on Drewes 1984, Table 2). State 0: Pectoral glands absent. State 1: Pectoral glands present. Although topical glands are known in many ranoids, pectoral glands appear to be absent in the Ranidae (Duellman & Trueb 1986). Polarity 0 → 1.

20. Digital glands. (Based on Drewes 1984, Table 2). State 0: Digital glands absent. State 1: Digital glands present. Although topical glands are known in many ranoids, digital glands appear to be absent in the Ranidae (Duellman & Trueb 1986). Polarity 0 → 1.

21. Nature of vocal sac openings. (Unchanged from Drewes 1984, Character 19). State 0: Vocal sac openings are posterior sphincters. State 1: Vocal sac openings not sphincters. Sphincteral vocal sac openings are present in most of the ranines studied (Drewes 1984). Polarity 0 → 1.

22. Position of vocal sac openings. (Unchanged from Drewes 1984, Character 20). (Note the printing error in Drewes, Appendix B: Character 20, transpose States 1 and 2). State 0: Vocal sacs open posteriorly. State 1: Vocal sacs open laterally. State 2: Vocal sacs open anteriorly. State 3: Vocal sac openings absent. Posterior spincter openings are present in most ranines (Drewes 1984). Polarity 0 → 1 → 2 → 3.

23. Anterior development of the interhyoideus. (Based on Drewes 1984, Character 21). State 0: Anterior interhyoideus simple. State 1: Anterior interhyoideus well developed. State 2: Vocal sac absent. Most ranids possess a simple interhyoideus (Drewes 1984). Polarity 0 → 1 → 2.

24. Posterior development of the interhyoideus. (Based on Drewes 1984, Character 21). State 0: Posterior interhyoideus simple. State 1: Posterior interhyoideus well developed. State 2: Vocal sac absent. Most ranids possess a simple interhyoideus (Drewes 1984). Polarity 0 → 1 → 2.

25. Spines. State 0: Spines absent. State 1: Spines present. Spines are absent in ranids. Polarity 0 → 1.

26. Eggs. State 0: Deposited in water or associated with ground or vegetation. State 1: Deposited between glued leaves. Ranids generally possess typical oviposition behaviour, depositing eggs in water or on moist soil. Polarity 0 → 1.

27. Male advertisement calls. State 0: Call present. State 1: Call absent (frogs mute). Male advertisement calls are present in the majority of ranids. Polarity 0 → 1.

The species possessing the most pleisiomorphies were selected to represent each genus from Appendix B of Drewes (1984) (Drewes' taxon codes in parentheses): *Acanthixalus spinosus* (A1), *Afrixalus brachycnemis* (B1), *Callixalus nictus* (C1), *Chrysobatrachus cupreoni- tens* (D1), *Cryptothylax gresshoffi* (E1), *Heterixalus*

madagascariensis (F1), *Hyperolius castaneus* (G3), *Kassina cassinoides* (H1), *Kassinula wittei* (I1), *Leptopelis karrisimbensis* (J7), *Opisthothylax immaculatus* (L1), *Phlyctimantis leonardi* (M1), *Semnodactylus wealei* (H18), *Tachycnemis seychellensis* (K1), *Paracassina kouniensis* (N1).

The data matrix is presented in Table 3.

Table 3 Data matrix modified from Drewes (1984). See text for details of species selected and character states

Acanthixalus	0111110011101010010001322101
Afrixalus	0111011111110001010001211110
Callixalus	0111111011100020110013 22001
Chrysobatrachus	0111010011200091111101201009
Cryptothylax	0110000011100010211012 00000
Heterixalus	0101010011100010100012 01000
Hyperolius	0111010111100010111112 10000
Kassina	0001001011011010110112 11000
Kassinula	0111011111100111100012 11000
Leptopelis	1010010000000000011100 01000
Tachycnemis	1111010011000010100011 01000
Opisthothylax	0101010111000010110112 01010
Phlyctimantis	0000001011000010110111 11000
Semnodactylus	1001002111010010110112 11000
Paracassina	0001002012110121110112 11000

Table 4 Consistency indices for the characters used in the analysis of Drewes' data

1.	Sphenethmoid exposure	0,500
2.	Sphenethmoid ventral configuration	0,500
3.	Quadratojugal	0,500
4.	Prevomerine dentigerous process	0,333
5.	Vertebral centra	1,000
6.	Neural arch	0,500
7.	Relative length of vertebral column	0,500
8.	Eighth presacral vertebra	0,250
9.	Thyrohyal stalk	1,000
10.	Hyoid anterior horn	1,000
11.	Palmaris musculature	0,667
12.	Digital sesamoids	1,000
13.	Terminal phalanx of third finger	0,500
14.	Coracoids	0,500
15.	Omosternum	0,667
16.	Mineralization of metasternum	0,333
17.	Gular gland	1,000
18.	Forearm glands	0,333
19.	Pectoral glands	0,500
20.	Digital glands	0,333
21.	Nature of vocal sac openings	1,000
22.	Position of vocal sac openings	0,750
23.	Development of interhyoideus (1)	0,500
24.	Development of interhyoideus (2)	1,000
25.	Spines	0,500
26.	Oviposition	0,500
27.	Advertisement call	1,000

Data analysis

The matrix was analysed using PAUP. The following options were set: MULPARS, SWAP = GLOBAL, HOLD = 5. All other options remained at the default values.

The resulting tree was rooted using *Leptopelis* as the sister group. The cladogram based on Liem's data (Figure 1), and Drewes' analysis (1984) both indicated that *Leptopelis* is the sister group to the other hyperoliids.

The analysis produced one tree of 63 steps with a consistency index of 0,571. The consistency indices for each character are listed in Table 4. The cladogram (Figure 2) will be discussed below.

Results and Discussion

The relationships of all the rhacophorid genera are illustrated by the cladogram in Figure 3. This tree is a composite of Figures 1 and 2. The phylogeny of the Hyperoliinae *sensu* Drewes, based on fifteen genera (Drewes' data) is preferred to the incomplete tree based on only ten genera (Liem's data).

The present study is best understood in terms of the preceding attempts at phylogeny construction. Liem proposed a phylogeny based on a comparative study of 112 species (1970), recognizing two families, Rhacophoridae and Hyperoliidae. The Hyperoliidae were reanalysed by Drewes (1984), with the addition of genera not examined by Liem. Drewes proposed a new phylogeny based on his analysis. Laurent subsequently (1986) disagreed with Drewes, presenting another interpretation of the relationships within the African treefrogs.

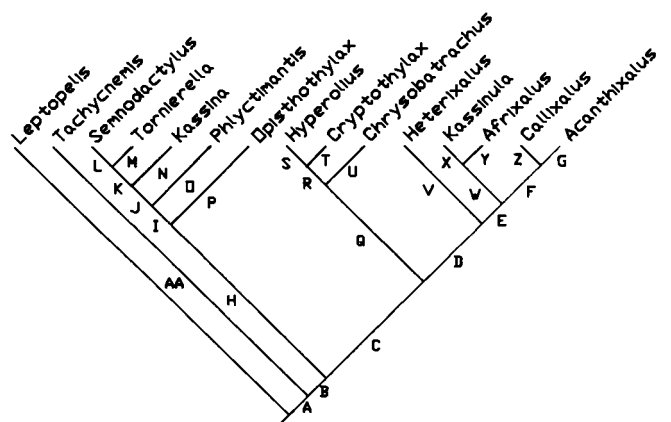One of the reasons for the differences in proposed

Figure 2 Cladogram of hyperoliid genera of Old World treefrogs, based on Drewes (1984). Character state changes are represented as in Figure 1. AA — $18^{1–0}$; A — $2^{0–1}$, $4^{0–1}$, $9^{0–1}$, $10^{0–1}$, $15^{0–1}$, $17^{0–1}$, $19^{1–0}$, $20^{1–0}$, $21^{0–1}$, $22^{0–1}$; B — $1^{1–0}$, $22^{1–2}$; C — $11^{0–1}$; D — $18^{1–0}$; E — $7^{0–1}$, $23^{0–1}$; F — $5^{0–1}$, $22^{2–3}$, $23^{1–2}$, $24^{1–2}$, $27^{0–1}$; G — $7^{1–0}$, $13^{0–1}$, $25^{0–1}$; H — $3^{1–0}$, $20^{0–1}$; I — $2^{1–0}$, $6^{1–0}$, $7^{0–1}$, $23^{0–1}$; J — $12^{0–1}$; K — $7^{1–2}$; L — $1^{0–1}$, $8^{0–1}$; M — $10^{1–2}$, $11^{0–1}$, $14^{0–1}$, $15^{1–2}$, $16^{0–1}$; N — $13^{0–1}$; O — $4^{1–0}$, $22^{2–1}$; P — $8^{0–1}$, $26^{0–1}$; Q — $19^{0–1}$; R — $24^{1–0}$; S — $8^{0–1}$, $20^{0–1}$, $23^{0–1}$; T — $4^{1–0}$, $6^{1–0}$, $17^{1–2}$; U — $11^{1–2}$, $16^{0–1}$; V — $3^{1–0}$; W — $8^{0–1}$; X — $14^{0–1}$, $16^{0–1}$; Y — $25^{0–1}$, $26^{0–1}$; Z — $15^{1–2}$, $18^{0–1}$.
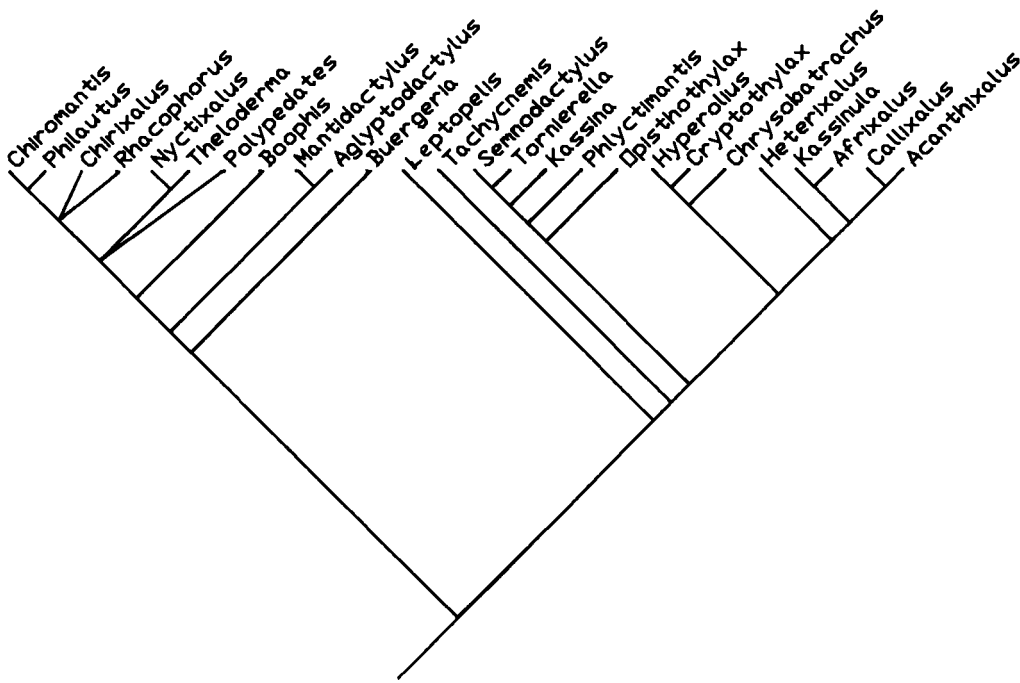
Figure 3 Cladogram of the genera of Old World treefrogs. This is a composite of Figures 1 and 2.

phylogenies, is that these authors applied different philosophies and methodologies to the analysis of their data. Liem mixed a cladistic method with a phenetic interpretation, but remarks that the computer available to him was unable to complete the analysis owing to lack of core memory (1970:55).

Laurent (1976, 1986) appears to be practising evolutionary taxonomy, (*sensu* Wiley 1981) using an explanatory approach to construct his hypotheses, despite labeling the figure of his proposed phylogeny as a cladogram. Laurent's (1986) cladogram is presented without the data matrix used to construct it, or the methodology applied. For example, he places 'skin smooth' (his Character 16) near the base of the Kassinini, yet makes no mention of the fact that the same character state applies to *Hyperolius* (placed in a sister group, the Hyperoliinae).

Drewes (1984) used a cladistic approach, but his analysis was completed by hand. The complexities of discovering the shortest tree for even moderate data sets are such that computers have become essential for phylogenetic analysis.

The analyses presented here are based mostly on the original data of Liem and Drewes. Unfortunately Laurent (1986) did not offer a data matrix to support his cladogram, so I was unable to evaluate his proposed phylogeny. The differences between the present cladograms and the preferred cladograms of Liem (Liem 1970; figs. 60 and 70) and Drewes (Drewes 1984; fig. 25) may be explained by the superior resolving power of PAUP.

Some of the relationships proposed by Liem and Drewes are supported by my analysis: Liem proposed the *Paracassina* (as *Tornierella*) and *Semnodactylus* sister groups, and the basal position of *Buergeria* and *Boophis* within the rhacophorid tree. The position of *Leptopelis*

as the sister group to the rest of the hyperoliinae *sensu* Drewes, proposed by both Liem and Drewes, is corroborated by the present study. Likewise Drewes placed *Acanthixalus* and *Callixalus* as sister groups, and *Kassina* as the sister group to both *Paracassina* and *Semnodactylus* (and *Kassinula*), with *Phlyctimantis* as the sister group to all three. These relationships are confirmed by my study, except that I find no support for the position of *Kassinula* as the sister group to *Paracassina* when all 15 hyperoliid genera are included in the analysis.

Relationships of Old World treefrogs

Species relationships

The relationships of species within the often large genera of Old World treefrogs are mostly unknown. Very few changes have been made to the status of species since the publication of the Amphibian Species of the World (Frost 1985).

The work of Blommers-Schlösser on Madagascar showed that *Hyperolius* does not occur on the island, and that most of the specimens of '*Hyperolius*' on Madagascar could be referred to *Heterixalus* (Blommers-Schlösser 1982). She has also examined the taxonomy of the species comprising the Mantellinae of the Ranidae (Blommers-Schlösser 1979a) and the genus *Boophis* (1979b). Drewes (1984) demonstrated that *Kassina wealii* was generically distinct and erected *Notokassina* (Drewes 1985). Dubois (1986) pointed out that *Notokassina* is a junior synonym of *Semnodactylus* Hoffman 1939. Perret (1988) recognizes *Nesionixalus* and erects three new genera (*Alexeroon, Arlequinus,* and *Chlorolius*) for West African species previously placed in *Hyperolius*. The most complete account of species

affiliations may be found in Frost (1985) and the references therein.

Generic relationships

Laurent (1943) separated the Hyperoliinae from the Rhacophorinae on the third carpal (free in hyperoliines, fused to the fourth and fifth in Rhacophorinae), and the cartilaginous metasternum (bony in Rhacophorinae). Liem (1970:57) listed a number of other differences between the groups, and considered each to be of family rank.

Blommers-Schlösser (1979a) removed *Aglyptodactylus* from the Mantelline ranids and considered it close to *Boophis*, on the basis of the absence of male femoral glands and the presence of male nuptial pads, and cytogenetic data (Blommers-Schlösser 1978). My analysis indicates that *Aglyptodactylus* is the sister group of *Mantidactylus*, and confirms its position close to *Boophis* within the Rhacophoridae. Liem had included *Aglyptodactylus* (as *Mantidactylus madagascariensis*) in the Rhacophoridae.

Monophyly of Old World treefrogs

This study supports the view that the 'Mantellinae' is a monophyletic group, but suggests that they be included within the Rhacophoridae, rather than the Ranidae. Further work is required to establish the relationships of the mantellines.

Two monophyletic lineages were found (Figure 1). The Rhacophoridae and Hyperoliidae are sister groups. This supports the current concept (Frost 1985) that the Old World treefrogs form two natural groups. This view is widely credited to Liem (1970), although Laurent (1943) had earlier suggested a similar split. However, although Liem (1970) proposed two families to accomodate the treefrogs, he presented only two lines of evidence: (i) phenetic evidence for the split (species of each family have 18 or more character states shared 1970:55); (ii) geographic evidence (hyperoliids primarily African, rhacophorids primarily Asian).

The derivation of the two families is uncertain. Liem proposed that the Rhacophoridae were derived from Asiatic ranid stock, while the Hyperoliidae originated from African ranid stock. Laurent suggested that the rhacophorids were derived from the Mantellinae (1951).

Figure 3 shows that the following monophyletic generic subgroups can be discerned within the hyperoliids: Kassininae, consisting of five genera, and Hyperoliinae, consisting of eight genera. The four genera discussed by Perret (1988), *Arlequinus, Alexeroon, Chlorolius,* and *Nesionixalus*, would appear to fit within the Hyperoliinae. The present cladogram will serve as a starting point to determine the relationships of these four genera.

Taxonomic proposals

Although the taxonomy of higher groups has traditionally been based largely on opinions rather than proven phylogenetic relationships, I have accepted familial and subfamilial status only for monophyletic groups. The

exception is the Rhacophorinae, which was retained rather than dividing the family into a number of redundant subfamilies each containing one genus.

I propose the following taxonomy, based on the cladogram shown in Figure 3 which is in turn derived from Figures 1 and 2. This scheme agrees substantially with the arrangement of subfamilies in Frost (1985).

Family Rhacophoridae (6 synapomorphies), monophyletic, including two monophyletic subfamilies and one subfamily (Rhacophorinae) which is paraphyletic.

> Subfamily Buergeriinae. I erect this subfamily to accomodate the four species of the genus *Buergeria*, which is the sister group to the rest of the Rhacophoridae. This genus of primitive rhacophorids is restricted to eastern Asia (Taiwan and the Japanese islands).

> Subfamily Mantellinae. This subfamily was erected by Laurent in 1946, and placed in the Ranidae. Liem indicated that that it belonged in the Rhacophoridae (1970), although currently it is still regarded as a member of the ranid group. This study shows that *Mantidactylus* and *Aglyptodactylus* share nine synapomorphies with, and are the sister group to the other rhacophorids, excluding *Buergeria*. Includes *Aglyptodactylus, Mantella, Mantidactylus* and *Laurentomantis*. The monotypic *Pseudophilautus* of Laurent (1943) is ignored here, as it appears to be a *Philautus* (Frost 1985).

> Subfamily Rhacophorinae. This is a polyphyletic group, but rather than confuse established usage by creating a series of categories and new names to reflect the phylogenetic relationships, I retain the subfamily, while presenting the relationships within it (Figure 3). Further work is required to test the generic groupings of the large number of little known Asian species. Includes *Boophis, Chirixalus, Chiromantis, Nyctixalus, Philautus, Polypedates (Rhacophorus* according to Dubois (1986)), *Rhacophorus,* and *Theloderma*. Dubois (1981) recognized the subfamily Philautinae to accommodate *Philautus,* here shown to be the sister group to *Chiromantis*.

Family Hyperoliidae (13 synapomorphies), monophyletic, with four monophyletic subfamiles recognized.

> Subfamily Hyperoliinae (corroborated by one synapomorphy; Table 1, Character 11, State 1), includes *Acanthixalus, Afrixalus, Callixalus, Chrysobatrachus, Cryptothylax, Heterixalus, Hyperolius,* and *Kassinula. Alexteroon, Arlequinus, Chlorolius,* and *Nesionixalus* are provisionally referred to this subfamily.

> Subfamily Kassininae (corroborated by two synapomorphies; Table 2, Character 20 State 1), includes *Kassina, Opisthothylax, Phlyctimantis, Semnodactylus,* and *Paracassina*.

> Subfamily Tachycneminae. Sister group to Hyperoliinae and Kassininae, with which it shares 8 synapomorphies, but is separated from them by the

reversal of Character 18 (Table 1). Includes only *Tachycnemis*.

Subfamily Leptopelinae (Sister group to the Hyperoliinae, Kassininae and Tachycneminae, with which it shares five synapomorphies, separated from them by one autapomorphy (Figure 2). Includes only *Leptopelis*.

Biogeography

The distribution of these treefrogs by subfamily is as follows (taken from Frost 1985):

Hyperoliidae

Hyperoliinae

Acanthixalus. Southern Nigeria and Cameroon to eastern Zaire.
Afrixalus. Subsaharan Africa.
Alexteroon. Southern and south-western Cameroon.
Arlequinus. South-western Cameroon.
Callixalus. Highlands of eastern Zaire and western Ruanda.
Chlorolius. Forests of south Cameroon to Gabon.
Chrysobatrachus. Itombwe highlands, eastern Zaire.
Cryptothylax. Forest swamps and waterways of the Congo basin, north to Uele Province, Zaire and west to Cameroon.
Heterixalus. Madagascar.
Hyperolius. African savanna and forest, south of the Sahara.
Kassinula. Southern Zaire and northern Zambia.

Kassininae

Kassina. Subsaharan Africa.
Nesionixalus. São Tomé Island, Gulf of Guinea.
Opisthothylax. Cap Saint-Jean, Gabon.
Phlyctimantis. Southern Tanzania; Liberia east to Ivory coast and in eastern Nigeria, western Cameroon, and Fernando Po, and rainforest in western Zaire.
Semnodactylus. Southern and eastern South Africa.
Paracassina. Central Ethiopia.

Tachycneminae

Tachycnemis. Seychelles.

Leptopelinae

Leptopelis. Subsaharan Africa.

Rhacophoridae

Buergeriinae

Buergeria. Taiwan; Ryuku Islands to Honshu Island (Japan).

Mantellinae

Aglyptodactylus. Madagascar.
Laurentomantis. Madagascar.
Mantella. Madagascar.
Mantidactylus. Madagascar.

Rhacophorinae

Boophis. Madagascar.

Chirixalus. South-east Asia.
Chiromantis. African tropics.
Nyctixalus. Philippines; India; Malaya; Sumatra; Java; Borneo.
Philautus. India and Sri Lanka through Burma and Thailand to China, the Philippines, and the greater Sunda Islands.
Polypedates. Japan and China, throughout tropical Asia to Borneo, Java, and Philippines.
Rhacophorus. India, Japan, and China to Celebes.
Theloderma. Burma and southern China through Indochina to Malaya and Sumatra.

Similar cosmopolitan distributions are shown by the frog families Bufonidae, Hylidae, and Raninae (Ranidae) (Savage 1973).

There are currently three hypotheses explaining the distribution of the Old World treefrogs, proposed by Liem (1970), Savage (1973) and Duellman & Trueb (1986). I will briefly outline them, and then use the present phylogeny to test these alternatives.

Liem (1970), following Laurent (1951), suggested that the rhacophorids (*sensu* Liem) were derived from Asian ranids. The Orient was suggested as the centre of origin, since the greatest diversity of the rhacophorines occurs there, and the relatively primitive *Buergeria* is at its periphery. *Mantidactylus* was regarded as a relict of an ancestral stock isolated in Madagascar. Liem suggested that *Mantidactylus* reached Madagascar directly from the Orient by waifing, as there are no closely related groups in Africa. *Chiromantis* was likewise argued to have very recently reached Africa from the Orient, because of its great similarities with *Rhacophorus*. *Boophis* was believed to have derived from *Mantidactylus*. Liem also followed Laurent (1951) by suggesting that the Hyperoliinae were derived from the Astylosterninae (Ranidae), and that they originated in Africa, dispersing to Madagascar and the Seychelles.

In a major work on the biogeography of anurans, Savage (1973), explained the distribution of the Old World treefrogs (as Rhacophorinae of the Ranidae, and Hyperoliidae) as follows:
The Rhacophorinae of the Oriental or Indo-Malayan region are derivatives from an Indian source. All recent families found in India today except the microhylids seem to be post-Eocene invaders from the northwest (ranoids). The primitive members of the Rhacophorines were probably somewhat like *Rhacophorus-Boophis* and may have originated in Africa and immigrated to Asia along with tropical ranines in the early Cenozoic. Apparently the basic stock in Africa has become extinct, but the specialized derivative genus *Chiromantis* occurs there. The elimination of rhacophorines in Africa is correlated apparently with the rise of the hyperoliid radiation. It remains possible, however, that the rhacophorines never had a major radiation in Africa.

He suggested that the Hyperoliidae represent a Cenozoic radiation of major proportions in Africa. The group was prevented from expanding into Asia by the arid barrier across north Africa, Arabia and Baluchistan. Such dispersal would have otherwise been possible while

the late Miocene to recent land connections between Africa and Asia existed.

He explained the distribution of treefrogs on Madagascar by the separation of Madagascar from Africa and eastern Gondwanaland in the Jurassic, before the origin of ranoids. Later Tertiary overwater immigration to Madagascar included the ancestors of *Boophis* and *Heterixalus*.

Savage believed that the rhacophorines dispersed from Africa to Madagascar by waifing and to south-east Asia by terrestrial dispersal, while the hyperolines dispersed from Africa to Madagascar and the Seychelles overwater.

The most recent synthesis of the distributional history of these frogs is that of Duellman & Trueb (1986). They proposed that the Hyperoliinae and Rhacophorinae were present on Gondwanaland, and associated with the Madagascar-Seychelles-Indian continent after the breakup of Gondwanaland. During its drift away from Africa, the Madagascar-Seychelles-Indian continent fragmented, with Madagascar moving northwards to its present position off the coast of Africa (100 my). The Seychelles broke off in the early Paleocene (64 my), and India finally collided with Asia in the Oligocene (35 my). This drifting land mass provided transportation for several groups of anurans represented on fragments left along its path. Once the land connection between India and Asia was effected, the rhacophorines (and others) migrated eastwards and then southwards into an area that fragmented in the late Oligocene into the Greater Sunda Islands. Rhacophorines subsequently waifed to the Philippines, which arose relatively late in the Oligocene.

The major differences among these three hypotheses concern the area of origin of the group, and the dispersal route from the origin. Both the hypotheses of Savage (1973) and Duellman & Trueb (1986) emphasize the importance of continental drift. Savage suggested that the major rhacophorine dispersal took place after the continents had separated, from Africa to south-east Asia by a terrestrial route, while the rhacophorines and hyperoliines which now occupy Madagascar and the Seychelles arrived by waifing. In contrast, Duellman & Trueb visualize the breakup of Gondwanaland as a major factor explaining the present distribution of the group. The rhacophorines and hyperoliines are believed to have originated in Gondwanaland, but dispersed on the Madagascar-Seychelles-Indian continent, leaving isolates on Madagascar and the Seychelles as these in turn broke from the drifting land mass that was to become India. After India collided with Asia, the rhacophorines dispersed from India north and then east to an area that subsequently fragmented, becoming the Greater Sunda Islands.

The cladogram presented in Figure 3 can be transformed to an area cladogram by substituting the names of the taxa by the area (continents or islands) where each occurs. This is further simplified by collapsing the tree to emphasize the sequence of evolution by area, by removing redundant branches from the same area. The result is an area cladogram which indicates the sequence of land
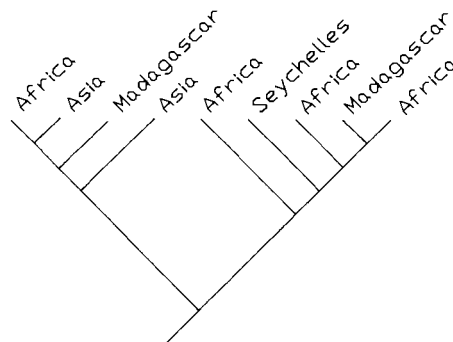

Figure 4 Simplified area cladogram of the Old World treefrog genera. This is constructed by replacing the generic OTUs with the name of the area where each occurs, and then collapsing redundant branches.

masses on which the hypothesized evolutionary events occurred (Figure 4).

The present distribution of the Rhacophoridae can be attributed to vicariance caused by tectonic plate movements. The stock leading to the Old World treefrogs would have been present on Pangaea. Fragmentation of that continent led to vicariance, with derivatives of the treefrog stock present on the Seychelles, Madagascar, Asia and Africa.

The simplified area cladogram shows that the Seychelles is unique to the hyperoliid branch of the area cladogram, while Asia is unique to the rhacophorid branch. Africa and Madagascar are represented on both branches. The most parsimonius vicariance hypothesis is the following: The ancestral stock existed on a supercontinent, Asia+Africa+Madagascar+Seychelles. The Seychelles separated first, leaving Asia+ Africa + Madagascar. Then Asia separated, and finally Africa and Madagascar split. This hypothesis postulates three fragmentation events. An alternate hypothesis would be similar, except for one dispersal event (*Heterixalus*) from Africa to Madagascar. This alternate hypothesis requires three fragmentation events plus one dispersal. The first hypothesis best fits the data by making the least assumptions. Both hypotheses await testing in the form of comparative analyses of other groups.

This vicariance hypothesis makes fewer assumptions (is more parsimonius) than the three hypotheses described above. Liem's proposals require two dispersals from the Orient (waifing of *Mantidactylus* to Madagascar, and movement of *Chiromantis* to Africa). Savage proposed four dispersal events. Liem's belief that the Rhacophoridae originated independently of the Hyperoliidae is not supported by my study, as these two families share seven synapomorphies.

The biogeographic proposals of Duellman & Trueb (1986) are contradicted by the cladogram (Figure 3) which shows that the branch leading from *Tachycnemis* (Seychelles) is not ancestral to the rhacophorids of the Orient.

Age of the group

This interpretation suggests that the Rhacophoridae and

Hyperoliidae are much older than has previously been believed. The preferred biogeographic hypothesis suggests that the stocks leading to the present genera already existed before Pangaea broke up, probably 200 my ago. This would explain the existence of primitive and derived stocks on various fragments of Pangaea. The presence of primitive rhacophorids and derived hyperoliids on Madagascar is most simply explained by assuming that they were there before Madagascar separated from the rest of Gondwanaland. There is geophysical evidence that Madagascar has been in place for about 90 my (Fooden 1972; McElhinny 1970; McElhinny & Luck 1970) and that it moved southwards from Africa to its present position (Tarling & Kent 1976; Rabinowitz, Coffin & Falvey 1983). All the fragmentation events would therefore have happened by 90 my. The Seychelles+India raft split about 75 my ago (Davies 1968) leaving the Seychelles island group with its interesting fauna and flora (Stoddart 1984).

Although such an early origin appears to be a radical suggestion for treefrogs, it has been presumed for at least one other frog family. Leiopelmatids are believed to have been widely distributed before the breakup of Pangaea, with fossil or extant frogs known from Argentina, North America and New Zealand (Duellman & Trueb 1986). Špinar & Hodrová (1986) proposed that *Indobatrachus* reached India from a south American origin, before the breakup of Gondwanaland, prior to the lower Cretaceous.

Unlike the Leiopelmatids, no treefrog fossils are known. Treefrogs are not likely candidates for fossilization, however, so future treefrog phylogenies will probably not be able to rely on corroborative evidence from fossils.

Acknowledgements

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