The Systematic Status of Rhacophorid Frogs

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Abstract  The frog family Rhacophoridae recently underwent notable reorganization and taxonomic rearrangement. Several new genera were erected to reflect evolutionary history, including Ghatikalus, Gracicalus, Feihyla, Liuixalus and Raorchestes. Herein, we reviewed the systematics and phylogeny of the rhacophorids, the definition of the family Rhacophoridae and its tribes, and the taxonomic history and diagnoses of the genera of this family. Also, we suggest future directions for research.

Keywords  progress, prospect, faunal survey, systematics, amphibian, China

1. Introduction

Today, the family Rhacophoridae consists of 319 species in 14 genera (Biju et al., 2010; Frost, 2010). The group ranges across tropical Africa and Southern Asia, including India and Sri Lanka, the Himalayas, Myanmar, South China, eastward to Japan and the Philippine Islands, and southward across Indochina to Greater Sunda (Figure 1) (Frost, 2010; Liem, 1970). Most rhacophorids are treefrogs, with the majority of species exhibiting particularly vivid and pleasant coloration. The species are united morphologically in possessing intercalary elements between the two distal phalanges and expanded digit discs. These characters are shared with hylids, mantellids, and some ranid lineages (Frost et al., 2006; Liem, 1970; Manzano et al., 2007). Toe pads help in climbing due to their ectodermal morphology and secreted proteins which aid in their adherence to surfaces (Duellman and Trueb, 1986). Many treefrogs can change color, usually to match their surroundings. When the reproductive season has passed, treefrogs usually burrow into the humus on the forest floor. Rhacophorids range from being small to large, with SVL (snout-vent length, from tip of snout to vent) ranging from 15 to 110 mm. The habitats vary from living on soil to the forest canopy (Amphibian Web, 2010). Some interesting reproductive modes occur in rhacophorids. Several genera, including Philautus, Pseudophilautus and Raorchestes, are characterized by the aerial direct development of eggs into froglets (Bahir et al., 2005; Biju et al., 2010; Bossuyt and Dubois, 2001; Dring, 1979; Dutta, 1997). The genera Chiromantis, Feihyla, Rhacophorus and Polypedates either form aerial nests of foam or they lay their eggs in a jelly-like secretion filled with bubbles which hangs over water. Their eggs develop into tadpoles that drop into the water once they reach a certain size (Bain and Nguyen, 2004; Boulenger, 1903; Duellman and Trueb, 1986; Inger, 1966; Liem, 1970; Orlov et al., 2002, 2004). Treefrogs are known for their loud and diverse vocalizations, made only by the males, with flap consonant.

Rhacophorid taxonomy has been a matter of much recent debate. Previous classifications are based on either a single morphological character or a complex of characters (Channing, 1989; Jiang et al., 1987; Liem, 1970; Zhao and Adler, 1993). Historically, morphological studies played a central role in the development of rhacophorid systematics and taxonomy. Within this body of research, representative studies include Channing (1989), Jiang et al. (1987), Liem (1970) and Wilkinson and Drewes (2000). Nowadays, DNA sequences are commonly used for inferring phylogenetic relationships (Frost et al., 2006; Grosjean et al., 2008; Li et al., 2008, 2009; Meegaskumbura et al., 2002; Richards and Moore,
1998; Wilkinson et al., 2002; Yu et al., 2008, 2009) and making taxonomic revisions. Stemming from the recent changes, herein we review the phylogenetic systematics of rhacophorids, the definition of the family Rhacophoridae and its tribes, and the taxonomic history of the genera recognized within this family. We also provide suggestions for future research.

2. Systematics and Phylogeny of Rhacophorids

Ahl (1931), in the first major taxonomic revision of the family Rhacophoridae, recognized 12 genera and 527 species distributed in Africa, Madagascar, the Seychelles Islands, and Asia. Based on an extensive suite of osteological characters, Laurent (1943, 1946) erected a new subfamily, the Hyperoliinae, to include all of the African treefrog genera, except for Chiromantis. The subfamily was considered as the familial rank by Laurent (1951) without diagnosed characters. The placement of Afro-Asian species into the Rhacophoridae, and that of those from Madagascar into another family, the Mantellidae, have been widely accepted recently (e.g., Frost et al., 2006; Van der Meijden et al., 2005; Vences and Glaw, 2001).

Liem (1970) made the first phylogeny-based revision of the rhacophorids. His study used myological, skeletal, and external morphology of 420 species of Old World treefrogs. Liem defined the major evolutionary lines within the assemblage and made some taxonomic suggestions with respect to genera. He proposed that the Rhacophoridae probably evolved from an Asian ranid stock. One genus appeared to have reached Africa relatively recently. This conclusion was supported by Li et al. (2008, 2009) and Wilkinson et al. (2002).

Channing (1989) reanalyzed Liem’s data and obtained a different cladogram. His results suggested that the subfamily Mantellinae, including Mantella and Laurentomantis, should be moved from the Ranidae to the Rhacophoridae.

Other studies have focused on rhacophorid systematics. Jiang et al. (1987) constructed a phylogenetic hypothesis for Chinese species using morphological characters. They resolved Polypedates and Rhacophorus as sister taxa, and together these genera formed the sister clade of “Chirixalus”. Philautus rooted as the sister group to this clade and Buergeria being the most basal genus. Using allozyme data and the incorporation of Japanese species, Nishioka et al. (1987) also resolved Buergeria as the most basal genus and Polypedates and Rhacophorus as sister lineages. Yang and Lin (1997), and Wilkinson (1997) came to similar conclusions in that Rhacophorus and Polypedates were sister taxa followed downward on the tree by “Chirixalus” and then Buergeria.

Wilkinson and Drewes (2000) produced a comprehensive phylogenetic reconstruction for the Rhacophoridae based on the data largely taken from Liem’s (1970) and Channing’s (1989) studies. They identified synapomorphies for the major clades and all genera, and summarized intergeneric relationships. Their results resolved Rhacophorus as the sister group of Polypedates as opposed to “Chirixalus”. Nyctixalus and Philautus were resolved as sister taxa for the first time. All Asian genera, except Buergeria, formed a monophyletic group, and Polypedates and Rhacophorus were sister genera.

Phylogenetic hypotheses continued to differ. Using 1081 bp of nucleotide sequence data from the mtDNA 12S and 16S genes, Richards and Moore (1998) placed Chiromantis as the sister taxon to
Polypedates. Subsequently, Emerson et al. (2000) placed Chiromantis as the sister taxon to “Chirixalus”, and Richards et al. (2000) resolved it as the sister taxon to Rhacophorus. Also using DNA sequence data, Wilkinson et al. (2002) provided evidence for a sister group relationship of the Rhacophoridae and Mantellidae. They considered that these families should be subfamilies within Rhacophoridae. Mantellidae. They considered that these families a sister group relationship of the Rhacophoridae and taxon to data, Wilkinson et al. (2002) placed Chiromantis as the sister taxon to “Chirixalus” palpebralis was isolated phylogenetically from their representative rhacophorids. Further, “Chirixalus” was not monophyletic, Chiromantis and Polypedates had a close relationship, and Rhacophorus formed the sister clade to Philautus plus “Chirixalus”. Nyctixalus and Theloderma were resolved as sister taxa.

Delorme et al. (2005) constructed a phylogeny, and proposed a new taxonomy based on morphological and molecular data. However, they did not detail all the evidences supporting their phylogeny. Their phylogeny was similar to that of Channing (1989), Liem (1970), Jiang et al. (1987), Wilkinson and Drewes (2000), and Wilkinson et al. (2002) as follows: Buergeria was the sister taxon of all the remaining rhacophorids; Theloderma and Nyctixalus were sister taxa; and Chirixalus was not resolved as being monophyletic because of C. palpebralis. Surprisingly, Delorme et al. (2005) erected a non-monophyletic new genus Aquixalus with type species “Philautus” odontotarsus and divided Aquixalus into the subgenera Aquixalus (type species “Philautus” odontotarsus) and Gracixalus (type species “Philautus” gracilipes). Unfortunately, their morphological diagnosis of Aquixalus also applied to some species of Kurixalus. They assigned some species of “Philautus” to Aquixalus without reference to a phylogeny. Subsequently, Fei et al. (2009, 2010a) assigned all Chinese species of “Philautus” to Aquixalus.

Frost et al. (2006) supported Channing’s (1989) recognition of the subfamilies Buergeriinae and Rhacophorinae. In order to avoid the polyphyly of the genus Chirixalus, they erected the new genus Feihyla to contain “Chirixalus” palpebralis. They also placed Chirixalus into synonymy with Chiromantis and suggested that Kurixalus and Aquixalus were morphologically plesiomorphic. They recognized the putatively monophyletic subgenus Gracixalus whose type species, G. gracilipes, rooted at the base of their tree for the subfamily Rhacophorinae.

Using 1676 bp of mitochondrial and nuclear gene fragments (12S, 16S and rhodopsin) from 48 rhacophorids, including 16 undescribed Sri Lankan and southern Indian species, Grosjean et al. (2008) recognized both subfamilies Buergeriinae and Rhacophorinae and erected the new tribe Nyctixalini. The basal position of Buergeria within the Rhacophorinae was well supported, and Nyctixalus and Theloderma were sister taxa. The type species of Feihyla (Chirixalus palpebralis) nested at the base of the tree for Chiromantis, albeit, with low support. These authors did not believe Feihyla deserved recognition; they recognized “Chirixalus palpebralis” as belonging to Chiromantis. The following sets of relationships were congruent with those of Frost et al. (2006): (1) Chirixalus was a junior synonym of Chiromantis; (2) Kurixalus was closely related to Aquixalus; and (3) Kurixalus idiootocus and K. veruccosus were in the correct genus. Adding more data from India, Sri Lanka and the Sunda Islands, Philautus was not a monophyletic group. The clades of Philautus did not coincide with geographic distributions. Grosjean et al. (2008) also studied the evolution of reproduction in the Rhacophoridae and found that the ability to produce a foam nest emerged only once, as previously proposed (Wilkinson et al., 2002).

Li et al. (2008) employed maximum parsimony, maximum likelihood, and Bayesian inference analyses to investigate the molecular phylogenetic relationships of the Rhacophoridae. They used 2904 bp of sequences from both mitochondrial (12S rRNA, 16S rRNA, tRNA for valine) and nuclear (tyrosinase, rhodopsin) genes. Consistent with the studies by Delorme et al. (2005) and Frost et al. (2006), Aquixalus was not a monophyletic assemblage of species. Aquixalus (Aquixalus) formed a well-supported monophyletic group within Kurixalus, and Aquixalus (Gracixalus) was more closely related to the species of Rhacophorus, Polypedates and Chiromantis than to Aquixalus (Aquixalus). Consequently, they synonymized Aquixalus (Aquixalus) into Kurixalus, and elevated the subgenus Gracixalus to full generic rank. After moving R. hainanus to Kurixalus, the monophyly of Rhacophorus was strongly supported. Philautus did not form a monophyletic group because Philautus (Kurixalus) was the sister group to the clade comprised of Kurixalus and Aquixalus (Aquixalus). However, Li et al. (2008) did not make taxonomic changes in Philautus because of inadequate taxonomic sampling. Chiromantis romeri did not cluster with the other species of Chiromantis, but rather formed the sister group to all other rhacophorids save Buergeria. Because of the phylogenetic position of Chiromantis romeri, Li et al. (2008) erected the
new genus *Liixalus* to contain it. They suggested that mainland Chinese populations of *P. megacephalus* are likely a complex of at least two species, according to their phylogeny and the studies of Narins *et al.* (1998), Orlov *et al.* (2002), and Trépanier *et al.* (1999).

Yu *et al.* (2008) used 23 Chinese rhacophorid species in their phylogenetic analyses of mtDNA sequences. Their results were largely consistent with those of Frost *et al.* (2006), Li *et al.* (2008), and Yu *et al.* (2007). For example, “*Philautus* romeri” was the sister taxon to all other rhacophorines, and “*Chirixalus* doriae” nested within *Chiromantis*. In order to obtain a monophyletic *Philautus*, they transferred *P. rhododiscus* and *P. albopunctatus* into *Theiloderma*, which was also published by Yu *et al.* (2007). Adding several nuclear protein-coding genes, Yu *et al.* (2009) expanded on their hypothesis for the phylogenetic relationships within the Rhacophoridae. They resolved *Chiromantis* as the sister group to the clade formed by *Feihyla*, *Polypedates* and *Racophorus*, and confirmed that *Feihyla* was a valid genus. They also suggested that the Chinese *Rhacophorus* needed revision. *Rhacophorus pingbianensis* was considered to be a junior synonym of *R. omeimontis*. In order to maintain a monophyletic *Philautus*, Yu *et al.* (2009) elevated subgenus *Curixalus* to the rank of genus and placed *P. menglaensis* within it as *K. menglaensis*.

Most recently, Li *et al.* (2009) investigated the phylogenetic relationships among 12 genera of treefrogs based on a large DNA sequence data set, including five nuDNA (brain-derived neurotrophic factor, proopiomelanocortin, recombination activating gene 1, tyrosinase, and rhodopsin) and three mtDNA (partial 12S and 16S rRNA, and tRNA valine) genes. Analysis of the nuDNA data resolved three major clades. *Gracixalus*, *Philautus*, *Theiloderma moloch*, *Pseudophilautus*, and *Kurixalus* constituted the first group with the latter two being sister taxa. The second group consisted of *Nyctixalus* and *Theiloderma* exclusive of *T. moloch*. The third group contained *Feihyla*, *Polypedates*, *Rhacophorus* and *Chiromantis vitatus*. The elevation of *Kurixalus* to generic rank (Yu *et al.*, 2009) was justified, but the name *Kurixalus* Dubois, 1987 was replaced with *Pseudophilautus* Laurent, 1943 because of priority. In order to maintain the monophyly of *Philautus*, Li *et al.* (2009) transferred *P. ocellatus* and *P. hainanus* into *Liixalus*, *P. longchuanensis* and *P. gryllus* into *Pseudophilautus*, *P. banaensis* into *Kurixalus*, and *P. quyeti* into *Gracixalus*. Again, foam nesting was resolved to have evolved only once, as did lay eggs in a jelly-like matrix containing some bubbles. Terrestrial direct development evolved twice in the Rhacophoridae.

3. Definition of the Family Rhacophoridae and Its Tribes

The name Rhacophoridae Hoffman, 1932 takes the date of publication for Polypedatidae Günther, 1858, and thus has priority under the provisions of Article 40 of the International Code of Zoological Nomenclature (1999). The type genus is *Rhacophorus* Kuhl et Van Hasselt, 1822. Several studies consider rhacophorids to be a monophyletic subfamily, the Rhacophorinae, within the Ranidae (Dubois, 1981, 1987; Liem, 1970; Wilkinson and Drewes, 2000; Wilkinson *et al.*, 2002). Channing (1989) reanalyzed Liem’s data and divided the Rhacophoridae into two subfamilies, Buergeriinae and Rhacophorinae. Dubois (1992) proposed a major taxonomic revision, while considering the group to be a subfamily of the Ranidae. Marmayou *et al.* (2000) suggested that rhacophorids were deeply imbedded within the Ranidae. In their anatomical and molecular analyses, Frost *et al.* (2006) recognized the family Rhacophoridae and this usage was consistent with most other studies (Bossuyt and Roelants, 2009; Fei *et al.*, 2009; Grosjean *et al.*, 2008; Jiang *et al.*, 1987; Li *et al.*, 2008, 2009; Yu *et al.*, 2008, 2009; Zhao and Adler, 1993; Zhao *et al.*, 2000). Channing’s recognition of the two subfamilies has been strongly supported by several molecular studies (Bossuyt *et al.*, 2006; Frost *et al.*, 2006; Li *et al.*, 2008, 2009; Wilkinson *et al.*, 2002; Yu *et al.*, 2009).

Dubois (1992) recognized three rhacophorid tribes: Buergerini, Philautini, and Rhacophorini. Within these tribes, the Buergerini included only one genus, *Buergeria*. The Philautini contained “*Aquilixalus*”, *Curixalus*, *Nyctixalus*, *Philautus*, and *Theiloderma*, and the Rhacophorini included *Chirixalus*, *Chiromantis*, *Polypedates*, and *Rhacophorus* (Dubois, 2005). Using mitochondrial DNA (mtDNA) and nuclear DNA (nuDNA) sequence data, Grosjean *et al.* (2008) suggested that the Rhacophorinae should consist of two tribes, the Rhacophorini and Nyctixalini, the latter containing *Theiloderma* and *Nyctixalus*. Using an even larger DNA sequence dataset, Li *et al.* (2009) erected the rhacophorine tribe Liixalini, (type genus *Liixalus*) and recognized the Nyctixalini (*Theiloderma* and *Nyctixalus*) and Rhacophorini (*Chiromantis*, *Feihyla*, *Ghatixalus*, *Gracixalus*, *Kurixalus*, *Rhacophorus*, *Philautus*, *Polypedates*, and *Pseudophilautus*). The subfamily
Buergeriinae has been maintained without modification (Channing, 1989; Delorme et al., 2005; Frost et al., 2006; Grosjean et al., 2008; Li et al., 2008, 2009; Liem, 1970; Wilkinson et al., 2002; Yu et al., 2009).

4. Taxonomic History and Diagnoses of the Genera of Rhacophoridae

The subfamily Buergeriinae contains a single genus, Buergeria, which has Hyla burgeri as its type species. The species of the subfamily range from being moderately large to small in size (SVL = 40–80 mm). Unlike other rhacophorids, their general body form appears quite similar to that of Rana.

The diagnosis of Buergeria is as follows: skin of body and limbs smooth; no dorsal ornamentations; digital tips moderately dilated and transverse groove sometimes distinct; feet fully webbed; fingers up to half webbed (Liem, 1970). The subfamily is distributed in Hainan and Taiwan (China), and in Japan from the Ryukyu Islands to Honshu Island (Frost, 2010; Liem, 1970). Buergeria includes four species: B. buergeri, B. japonica, B. oxycephala, and B. robusta.

Chiromantis Peters, 1854, with type species Chiromantis xerampelina, is the only Asian rhacophorid genus that also occurs in Africa. Apart from Africa, the genus is distributed in East and Southeast Asia including Myanmar, Thailand, Viet Nam, Laos and China (Frost, 2010). The species in this genus are moderately large with a SVL of 35–80 mm (Liem, 1970). Wilkinson et al. (2003) provided a key to distinguish between ten species of Chiromantis. Asian species formerly assigned to Chiromantis are now assigned to Chiromantis to eliminate paraphyly (Frost et al., 2006; Grosjean et al., 2008; Li et al., 2008, 2009; Richards and Moore, 1998; Wiens et al., 2009; Wilkinson et al., 2002). After Fei et al. (2010 b) transferred Chiromantis vittatus into Feihyla, Chiromantis became monophyletic. Presently, Chiromantis cannot be diagnosed morphologically due to the recent inclusion of the species formally assigned to Chiromantis. Now, Chiromantis contains 15 species, including C. cherrapunjiaei, C. doriae, C. dudhwaensis, C. hansenae, C. kelleri, C. laevis, C. nongkhorensis, C. petersii, C. puctatus, C. rufescens, C. samkosenis, C. senapatiensis, C. shyamrupus, C. simus and C. xerampelina (Fei et al., 2010b; Frost, 2010).

Feihyla was erected by Frost et al. (2006) using Philautus palpebalis as the type species. This genus occurs in southern Annam (Viet Nam) and Yunnan (China), and it is expected to occur in Laos and elsewhere in northern Viet Nam (Frost, 2010). This reproductive mode, laying eggs in a jelly containing some bubbles, serves as a behavioral synapomorphy to diagnose Feihyla (Li et al., 2009). It presently contains F. palpebalis, F. fuhua, and F. vittatus (Fei et al., 2010 b; Frost, 2010).

Ghatixalus was described by Biju et al. (2008) using Polypedates variabilis as the type species. Biju et al. (2008) considered the genus to be the sister taxon of Polypedates. They assigned two species to the genus: G. asterops and G. variabilis. Ghatixalus was morphologically diagnosed as follows: medium-sized adults (male SVL 38.8–51.3 mm, female 58.1–66.7 mm); a dorsal color pattern with dark brown prominent blotches; a free swimming tadpole stage, and the habitat associated with mountain streams. Its distribution was restricted to high altitudes in the Western Ghats of southern India (Biju et al., 2008; Frost, 2010).

Gracixalus was erected as a new subgenus of Aquixalus by Delorme et al. (2005) and its type species was Philautus gracilipes. Li et al. (2008) suggested that Aquixalus (sensu stricto) should be placed within Kurixalus and Gracixalus was phylogenetically distant from Kurixalus. Thus, Gracixalus was elevated to a full genus. It was distinguished morphologically as follows: spines on the upper eyelid; rictal gland connected to mouth; foot very thin; two outer palmar tubercles; white spot on snout tip of tadpole, and five pairs of prelingual papillae and crescent shaped crest on the tadpole (Frost et al., 2006). This genus, which ranges from southern China southward to northwestern Thailand, central montane Viet Nam, and intervening Laos, has been considered to contain the following five species: G. jinxuensis, G. gracilipes, G. medogensis, G. quyet and G. supercornutus.

Kurixalus Ye, Fei and Dubois, 1999 has Rana eiffingeri as the type species. In the north, it is widely distributed in the Himalayan front ranges from eastern India to montane southern China and southward to southern Cambodia, central Viet Nam, western and northern peninsular Thailand, northern Myanmar, Taiwan (China), and the Ryukyu Islands of Japan (Frost, 2010). Compared with the species of Chiromantis, Kurixalus eiffingeri and K. idiootocus do not have opposable phalanges and an arch shaped anterior horn. In addition, vomerine teeth are present in K. eiffingeri and K. idiootocus. Kurixalus presently includes ten species: K. ananjevae, K. baliogaster, K. banaensis, K. bisacculus, K. carinensis, K. eiffingeri, K. idiootocus, K. naso, K. odontotarsus, and K. verrucosus (Frost, 2010; Yu et al., 2010). Using two mtDNA genes, Yu et al. (2010) reconstructed the
phylogeny of the *K. odontotarsus* species group, and suggested that *K. hainanus* was a junior synonym of *K. bisacculus*.

A new genus, *Liuixalus*, with type species *Philautus romeri*, was erected by Li et al. (2008) due to the phylogenetic relationships of *L. hainanus*, *L. ocellatus* and *L. romeri* (Frost, 2010; Li et al., 2008, 2009). No diagnostic morphological characters have been proposed for this genus, which is restricted to Hong Kong, Hainan and Guangxi (China).

*Nyctixalus* Boulenger, 1882, with type species *N. margaritifer*, is widely distributed in the Philippines, Malaysia, Sumatra, Java, Borneo, and southern Viet Nam (Frost, 2010). Smith (1931) considers that *Nyctixalus* should be placed in *Philautus*; Dubois (1981) removed it from the synonymy of *Philautus*. Recent molecular studies suggest that *Nyctixalus* is the sister taxon of *Thelododera* and is distantly related to *Philautus* (Grosjean et al., 2008; Li et al., 2008, 2009; Wilkinson et al., 2002; Yu et al., 2009). All the species of *Nyctixalus* share the following morphological characters: a medium-sized adult being 30–40 mm in SVL; skin of head ossified to skull; body and limbs with numerous spiny tubercles; fingers free or webbed at base; and vocal sacs always absent (Liem, 1970). It contains three species: *N. margaritifer*, *N. pictus*, and *N. spinosus*.

*Philautus* Gistel, 1848, with type species *Hyla aurifasciata*, includes 48 species. It ranges from central India through Myanmar and Thailand, south to the Philippines and the Greater Sunda Islands (Frost, 2010). Previous morphological studies indicate that all rhacophorids having aerial direct development of eggs into froglets should be assigned into *Philautus* (Dring, 1979; Bossuyt and Dubois, 2001). However, this form of development is not documented for most species and the assignment to *Philautus* is usually based on overall morphological similarity alone. Dubois (1987) divides *Philautus* into three subgenera: *Philautus*, *Goerixalus*, and *Kirtixalus*. Bossuyt and Dubois (2001) revise this taxonomy, transferring several Indian species from the subgenus *Kirtixalus* to *Philautus*. Recent molecular studies suggest that *Philautus* is not monophyletic, and some species are now transferred to other genera (Delorme et al., 2005; Frost et al., 2006; Grosjean et al., 2008; Li et al., 2008, 2009; Meegaskumbura et al. 2002; Yu et al., 2008, 2009). Many Indian and Sri Lankan species are in *Pseudophilautus* (Li et al., 2009). Several new genera and species are now recognized and some subgenera are elevated to generic rank, such as *Feihyla*, *Gracixalus*, *Liuixalus*, *Pseudophilautus* and *Raorchestes* (Biju and Bossuyt et al., 2009; Biju et al., 2010; Delorme et al., 2005; Grosjean et al., 2008; Li et al., 2008, 2009).

*Pseudophilautus* Tschudi 1838, with type species *P. leucomystax*, contains 23 species. The genus ranges across eastern India, Southeast Asia, Philippines, Indonesia, and Borneo (Frost, 2010). Due to similar morphologies, the species of *Pseudophilautus* are easily confused with those of *Rhacophorus*. Liem (1970) splits the largely-sized rhacophorids into the genera *Pseudophilautus* and *Rhacophorus*. Channing (1989) agrees with this assignment and does not consider *Rhacophorus* and *Pseudophilautus* to be sister taxa. Jiang et al. (1987) also consider these genera to be distinct. Rao et al. (2006) recognize *Pseudophilautus* as a distinct genus and suggest it is paraphyletic with respect to *Rhacophorus*, yet some studies recognize *Rhacophorus* only (e.g., Dubois, 1987; Fei, 1999; Fei et al., 2005). Matsui and Wu (1994) cannot distinguish between *Rhacophorus* and *Pseudophilautus* on the basis of vocalizations. Molecular phylogenetic studies consistently support the recognition of both genera (Frost et al., 2006; Grosjean et al., 2008; Li et al., 2008, 2009; Wilkinson et al., 2002; Yu et al., 2008, 2009) and this assignment is widely accepted (Fei et al., 2009, 2010a; Frost et al., 2006; Grosjean et al., 2008; Li et al., 2008, 2009; Wilkinson et al., 2002; Yu et al., 2008, 2009). *Pseudophilautus* and *Rhacophorus* have several synapomorphic characters, including “Y”-shaped terminal phalanges. Webbing between the fingers of *Pseudophilautus* separates it from *Rhacophorus* (Liem, 1970; Wilkinson and Drewes, 2000; Rao et al., 2006).

*Pseudophilautus* Laurent, 1943 has *Ixalus temporalis* as its type species. Li et al. (2009) resurrect the genus from the synonymy of *Philautus*. They recognize the species within the Sunda shelf as *Philautus sensu stricto*, and the group with its centre of diversification on the Indian Subcontinent as *Pseudophilautus*. This arrangement is consistent with Grosjean et al. (2008), Li et al. (2008), Meegaskumbura et al. (2002), and Yu et al. (2008, 2009), and accepted by Frost (2010). Most recently, Biju et al. (2010) have erected the new genus *Raorchestes* out of *Pseudophilautus*. Many new species of Sri Lankan shrub-frogs are now known (Gururaja et al., 2007; Manamendra-Arachchi and Pethiyagoda, 2005; Meegaskumbura and Manamendra-Arachchi, 2005), all of which are assigned to *Pseudophilautus* (Biju et al., 2010).

*Raorchestes* has *Ixalus glandulosus* as its type species (Biju et al., 2010). The genus is diagnosed by the following suite of characters: (1) relatively small frogs, SVL of adult 1.5–4.5 cm; (2) vomerine teeth
absent; large gular pouch transparent while calling; (3) primarily nocturnal; and (4) direct development without free-swimming tadpoles (Biju et al., 2010). According to the trees made by Li et al. (2009) and Yu et al. (2009), Chinese Pseudophilautes menglaensis and *P. longchuanensis* and Vietnamese *P. gryllus* should be assigned to *Raorchestes* (Biju et al., 2010). Thus, *Raorchestes* ranges at least from the Western Ghats of India through mainland Southeast Asia to southern China, and the genus is not documented to occur in Sri Lanka (Biju et al., 2010).

Containing 80 species, *Rhacophorus* Kuhl et Van Hasselt, 1882 occurs widely across India, China, Japan, mainland Southeast Asia, the Greater Sunda Islands, and the Philippines (Frost, 2010). The genus is diagnosed by the following morphological characters: procoelous vertebrae, anal folds that are usually present, typically extensive dermal forearm and tarsal folds (Bordoloi et al., 2007; Jiang et al., 1987; Liem, 1970; Wilkinson and Drewes, 2000). Dubois (1987) resurrects *Leptomantis* Peters, 1867 as a subgenus and he subdivides the subgenus *Rhacophorus* into ten groups. However, this division is not followed by many researchers (e.g., Harvey et al., 2002). Iskandar and Colijn (2000) raise the subgenus *Leptomantis* to full generic rank. This genus now contains *R. appendiculatus*, the species of *Philautus* in Dubois’ (1987), and the species of the subgenus *Gorhixalus* in Bossuyt and Dubois’ (2001) (the *Philautus hosii* group of Dring, 1987). However, *Leptomantis* cannot be diagnosed morphologically because its defining characters are shared with some species of *Rhacophorus* sensu stricto, such as *R. kajau*, *R. bisacculus* and *R. everetti* (Dring, 1983; Inger et al., 1999; Liem, 1970). Recent molecular studies (Grosjean et al., 2008; Li et al., 2008, 2009; Wilkinson et al., 2002; Yu et al., 2008, 2009) resolve two main groups of *Rhacophorus*. Regardless, the validity of the subgenera remains largely untested because previous studies do not include the type species *L. bimaculata* of the subgenus *Leptomantis*.

*Thelodera* Tschudi, 1838, with type species *T. leporosa*, is widely distributed in mainland Southeast Asia, including Sri Lanka, northeastern India, Myanmar and southern China, and also Malaysia, and Sumatra (Frost, 2010). Frost et al. (2006) consider *Thelodera* to be the sister taxon of *Philautus*, but their analysis does not include true *Philautus*. Li et al. (2008, 2009) and Yu et al. (2009) resolve *Thelodera* as the sister taxon of *Nyctixalus*; this clade forms the sister group of all other rhacophorids excluding *Liuxialus* and *Buergeria*. The diagnostic characters are as follows: medium to large adults (SVL = 30–60 mm); numerous warts on body and limbs, fingers webbed at base or up to half webbed. The inclusion of *Thelodera moloch* renders the genus paraphyletic and this species may represent a new genus (Li et al., 2009). Notwithstanding, at present the genus *Thelodera* contains 17 species: *T. andersoni*, *T. asperum*, *T. baibengensis*, *T. bicolor*, *T. corticale*, *T. gordonii*, *T. horridum*, *T. kwangsiense*, *T. lateriticum*, *T. leporosum*, *T. licin*, *T. moloch*, *T. nagalandense*, *T. phrynodermata*, *T. rhododiscus*, *T. ryabovi* and *T. stellatum* (Frost, 2010).

5. Suggestions for Future Research

5.1 Taxonomic representation Previous studies provide an initial resolution to the systematics and phylogeny of rhacophorids. A far more comprehensive investigation should be pursued and this should include as many species as possible. A densely-sampled tree is very important and necessary to gain an understanding of the rhacophorids. Many Southeast Asian taxa remain to be evaluated, including many species from the Philippines, Borneo, and Malaysia. The same is true for Indian and Sri Lankan species.

A comprehensive phylogeny of *Rhacophorus* needs to be reconstructed. Previous studies focus on species from India, China and Viet Nam (Frost et al., 2006; Grosjean et al., 2008; Li et al., 2008, 2009; Meegaskumbura et al., 2002; Richards and Moore, 1998; Wilkinson et al., 2002; Yu et al., 2008, 2009). Most of the species from Malaysia, mainland Southeast Asia and the Philippines are not represented in existing data sets. Their phylogenetic positions remain unknown.

The phylogenetic placement of most putative species of *Philautus* should be examined. Due to their small size and cryptic habits, some species of *Philautus* are represented in few studies. Many species are tentatively assigned to *Philautus* based largely on their observed or inferred direct developmental reproductive mode. Field data are lacking for many species and thus, some former species of *Philautus* are now placed in other genera, such as *Kurixalus* and *Rhacophorus* (Bossuyt and Dubois, 2001). Recent molecular studies suggest the existence of much confusion. For example, many Chinese *Philautus*, such as *P. ocellatus* and *P. hainanus* are now assigned to *Liuxialus*. *Philautus longchuanensis* and *P. gryllus* are now placed in *Pseudophilautes* (Grosjean et al., 2008; Li et al., 2008, 2009). Further, *Philautus banaensis* now resides within *Kurixalus*, and *P. quyeti* within *Gracixalus* (Grosjean et al., 2008; Li et al., 2008, 2009). The new genera *Pseudophilautes* and *Raorchestes*, have close
phylogenetic relationships with *Philautus*, to the extent that morphological diagnosis remains problematic. Future studies should focus on the phylogeny and taxonomy of the complicated genera *Philautus*, *Pseudophilautus* and *Raorchestes*.

5.2 Discovery of morphologically diagnostic characters
A robust molecular phylogeny should be used to identify potential morphological characters that can serve to diagnose higher taxa. Future studies should also focus on the discovery of morphological characters that can lead to the construction of a total evidence morphological and molecular analysis.

5.3 The study of character evolution
Given a robust molecular phylogeny, future research can center on the mechanisms of adaptation to the surrounding environment. Extensive adaptive radiations involving parallel and convergent evolution occur in the Caudata and Anura (e.g., Wake, 1966, 1987; Zhang et al., 2006). Bossuyt and Milinkovitch (2000) provide a nice example of what is possible to achieve. Future research on morphological character evolution will be valuable. For example, the evolution of toe webbing is a remarkable feature in rhacophorids and it may represent adaptive parallelism within different lineages.

5.4 Biogeography of widely distributed species
Most rhacophorids live on trees, but some inhabit smaller plants, and a few species are ground-dwellers. Regardless, all rhacophorids live in very moist habitats mostly in association with forests. Most treefrogs seem to have lower dispersal abilities than many other anurans, such as ranids and dicroglossids. These attributes lend themselves to biogeographic investigations, such as whether vicariance or dispersal is the dominant biogeographic driver. For example, Brown et al. (2010) presented some geographic scenarios for the *Polypedates leucomystax* complex, Kuraishi et al. (2009) estimated the origin of *Polypedates leucomystax* introduced to the Ryukyu Archipelago, and Yang et al. (1994) did studies for *Rhacophorus taipeianus*, and so on.

5.5 The biogeography of the Rhacophoridae
The biogeographic history of the rhacophorids remains to be determined. The “out-of-India” hypothesis (Bossuyt and Milinkovitch, 2001; Roelants et al., 2004) deals with higher taxa on a global scale, including South America, Africa, Madagascar, peninsular India and Australia. Fine-scale biogeographic patterns can explain how the rhacophorids dispersed out of India to East and Southeast Asia. Rhacophorids may have a history typical of other taxa. Previous studies (Grosjean et al., 2008; Li et al., 2008, 2009; Meegaskumbura et al., 2002; Yu et al., 2008, 2009) suggest that multiple taxa have their origins on the Indian subcontinent, and that some genera disperse out of Indian multiple times to East and Southeast Asia. Some may have returned back to India. Further investigation is highly desirable.

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