Phylogenetics and Systematics of Animal Life

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Abstract Phylogenetics is the study of evolutionary relationships among groups of organisms, and systematics the study of the diversity of organisms and the relationships among them. The relationships are presented in evolutionary trees. In addition to morphological data, gene-enzyme systems were used extensively in earlier days for phylogenetic and systematic studies. Currently, molecular sequencing data are commonly used for phylogenetics and systematics. Cytogenetic data in some cases also serve as good parameters for differentiating sibling/cryptic species. In general, sound systematics and phylogenetics are important and relevant to various fields of biology. This review discusses selected taxonomic groups in which identification has proven problematic based on morhphological characters. The role of phylogenetics and systematics is illustrated by nematode parasites of the genus *Angiostrongylus*, stingless bees of the genus *Tetragonilla*, tephritid fruit flies of *Bactrocera caudata* complex, crab-eating frogs of *Fejervarya cancrivora* complex, and murid rats of the genera *Hapalomys* and *Maxomys*.

1 Introduction

Phylogenetics is the study of evolutionary relationships among groups of organisms. Systematics may be defined as "the entire field dealing with the kinds of animals [organisms], their distribution, classification, and evolution" (Blackwelder and Boyden 1952), and "the scientific study of the kinds and diversity of organisms and

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of any and all relationships among them" (Simpson 1961). It includes taxonomy, "the theoretical study of classification, including its bases, principles, and rules", and classification, "the ordering of animals [organisms] into groups (or sets) on the basis of their relationships" (Simpson 1961).

Both phylogenetics and systematics concern the study of relationships among taxa. The relationships are presented in evolutionary trees. In addition to morphological data, gene-enzyme systems were used extensively in earlier days for phylogenetic and systematic studies. Currently, molecular sequencing data are commonly used for phylogenetics and systematics. Cytogenetic data in some cases also serve as good parameters for differentiating sibling/cryptic species. In general, sound systematics and phylogenetics are important and relevant to various fields of biology, including biodiversity and conservation, and other scientific disciplines.

This review discusses selected taxonomic groups in which identification has proven problematic based on morphological characters. They are cryptic or sibling species (referred to as species complex), i.e. closely related species that appear as a single species based on morphological characters. The role of phylogenetics and systematics is illustrated by nematode parasites of the genus *Angiostrongylus*, stingless bees of the genus *Tetragonilla*, tephritid fruit flies of *Bactrocera caudata* complex, crab-eating frogs of *Fejervarya cancrivora* complex, and murid rats of the genera *Hapalomys* and *Maxomys*.

2 Nematode Parasites Genus *Angiostrongylus*

The *Angiostrongylus* lungworms are of public health and veterinary concerns in many countries. They are bursate nematodes of the family Angiostrongylidae, superfamily Metastrongyloidea. Of the *Angiostrongylus* lungworms, the rat lungworm, *A. cantonensis* (Chen 1935) is a food-borne zoonotic parasite of public health importance in many countries of the tropics and subtropics (Eamsobhana and Tungtrongchitr 2005; Eamsobhana 2006).

A related species, *A. malaysiensis* Bhaibulaya and Cross 1971 in Southeast Asia and Japan, has not been confirmed to infect humans but human infection from the species remains a possibility. When first documented, it was referred to as *A. cantonensis* (Bhaibulaya and Cross 1971). With taxonomic revision, the taxa in Sarawak, Sabah and Peninsular Malaysia, earlier attributed to *A. cantonensis* have been shown to be *A. malaysiensis* (Eamsobhana 2006).

Another congenric species, *A. costaricensis* (Morera and Céspedes 1971) in the Americas (from southern United States to northern Argentina in South America), causes abdominal or intestinal angiostrongyliasis which mimics appendicitis, with eosinophilia (Graeff-Teixeira 2010; Graeff-Teixeira et al. 2009). This species does not occur in the Old World.

Apart from the species of human public health importance, the French heartworm *A. vasorum* (Baillet 1866) is of veterinary concerns. This parasite infects wild and domestic canids and causes canine angiostrongylosis (Conboy 2000; Morgan

et al. 2005). It is enzootic to Western Europe but has been found in many parts of the world.

Molecular differentiation of *A. cantonensis* and its phylogenetic relationship to other *Angiostrongylus* species have been achieved by polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) (Calderia et al. 2003) and DNA sequences of 66-kDa protein gene (Eamsobhana et al. 2010a), internal transcribed spacer 2 (ITS-2) (Jefferies et al. 2009; Foronda et al. 2010), cytochrome *c* oxidase subunit I (COI) (Eamsobhana et al. 2010b; Tokiwa et al. 2012), and small subunit (SSU) ribosomal RNA (Fontanilla and Wade 2008; van Megen et al. 2009; Tokiwa et al. 2012).

Based on SSU rDNA sequences (van Megen et al. 2009), 66-kDa protein gene (Eamsobhana et al. 2010a) and COI sequences (Eamsobhana et al. 2010b), *A. cantonensis* shows closest affinity to *A. malaysiensis* compared to other congeneric species.

Phylogenetic analyses of COI nucleotide sequences indicate two distinct genetic lineages each for *A. costaricensis* and *A. vasorum* (Jeffries et al. 2009, 2010; Eamsobhana et al. 2010b; Fig. 1). The genetic distances between these allopatric taxa are many folds larger than intraspecific distances (Table 1), indicating the component taxa are valid cryptic species.

The COI sequences of the georgraphic isolates of *A. cantonensis* (Fig. 1) indicate that the Thailand isolate is most likely not involved in dispersal to other areas. On the other hand, most of the Brazil isolates might have been introduced from Japan. The dispersal of the parasite from China (Fujian and Guangdong) and Taiwan to Japan (Honshu Island), and vice-versa, needs to be confirmed.

3 Stingless Bees of the Genus *Tetragonilla*

Stingless honey bees are members of the Apidae. There are some 30 species in Malaysia. The genus *Tetragonilla* was erected by Moure (1961) for the taxa of the *atripes* species group of stingless bees, comprising the taxa *atripes*, *collina*, *fuscibasis* and *rufibasalis*. Although the component taxa were accorded specific status, he was of the opinion that *fuscibasis* could be a Bornean subspecies of *collina*.

The four taxa of the *atripes* species group were regarded by Schwarz (1939) as varieties of *Trigona* (*Tetragona*) *atripes*. Schwarz was also of the opinion that "… it is possible that *fuscibasis* instead of being a variety of *collina* is merely the callow stage of that insect".

Taxonomic treatments had placed the *atripes* species group as members of the subgenus *Tetragona* of the genus *Trigona* (Schwarz 1939; Wille 1979), the subgenus *Tetragonilla* (Sakagami 1975) and the subgenus *Tetragonula* (Sakagami et al. 1985). At present the species group is accorded generic status, viz. *Tetragonilla* as originally proposed by Moure (1961). The phylogeny based on five genes (16S, ArgK, EF-1α, opsin and 28S) indicates close affinity of *Tetragonilla* to the genus *Tetragonula* (Rasmussen and Cameron 2010). Of the component taxa, *T. atripes* clusters with *T. rufibasalis* and *T. collina* with *T. fuscibasis*.

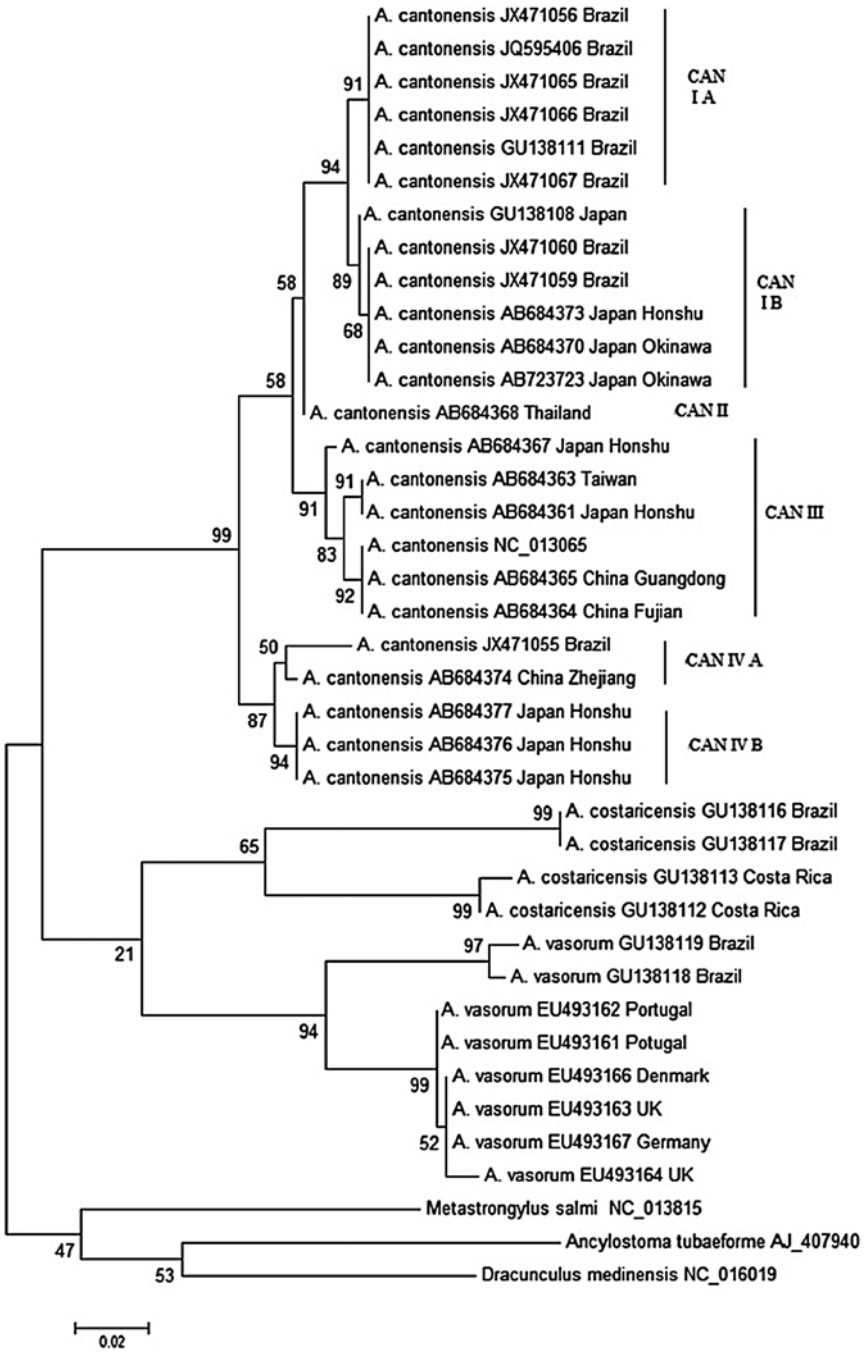

Fig. 1 Phylogenetic tree of *Angiostrongylus* lungworms (with *Metastrongylus salmi*, *Ancylostoma tubaeforme* and *Dracunculus medinensis* as outgroups) generated by the Maximum Likelihood method based on partial COI mtDNA nucleotide sequences conducted in MEGA5 (Tamura et al. 2011)

Table 1 Genetic distance (uncorrected 'p' distance) between taxa of *Angiostrongylus costaricensis* and *Angiostrongylus vasorum* (based on COI sequences listed in Fig. 1)

	A. costaricensis		*A. vasorum*	
Taxon	Brazil	Costa Rica	Brazil	Europe
A. costaricensis Brazil	0			
A. costaricensis Costa Rica	0.1316–0.0088	0.1423		
A. vasorum Brazil	0.1608	0.1605–0.1717	0.0118	
A. vasorum Europe	0.1528–0.1639	0.1639–0.1715	0.0810–0.0878	0.0000–0.0118

Table 2 Genetic idemntity (Nei's *I*, above diagonal) and genetic distance (*D*, below diagonal) among the component taxa of the genus *Tetragonilla* of Malaysian stingless bees based on 17 enzyme loci (After Yong 1991)

Species	*T. atripes*	*T. collina*	*T. fuscibasis*	*T. rufibasalis*
T. atripes	–	0.58	0.62	0.65
T. collina	0.54	–	0.66	0.76
T. fuscibasis	0.48	0.42	–	0.73
T. rufibasalis	0.43	0.27	0.31	–

The four component taxa of *Tetragonilla* (*Trigona atripes* species group in earlier literature) could be unequivocally separated from one another based on 17 enzyme loci (Yong 1991). The genetic identity values (Table 2) indicate closest affinity between *T. collina* and *T. rufibasalis* (I = 0.76, D = 0.27), and most distant between *T. collina* and *T. atripes* (I = 0.58, D = 0.54). It is noteworthy that *T. collina* and *T. fuscibasis* which are morphologically rather similar, are genetically more distant compared to *T. rufibasalis*.

4 Tephritid Fruit Flies of the *Bactrocera caudata* Complex

Tephritid fruit flies are of economic importance, with some 200 species considered as pests, causing direct losses to a wide variety of fruit, vegetable and flower crops (Carroll et al. 2002). The larvae of about 35 % of the species attack soft fruits, and about 40 % of species develop in the flowers of Asteraceae (White and Elson-Harris 1992). Among the species attacking Asteraceae flowers is *Bactrocera caudata*

Fig. 1 (continued) using the Tamura-Nei model (1993). The tree with the highest log likelihood (−1700.7916) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 39 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 342 positions in the final dataset

Table 3 Percentage of uncorrected 'p' distances between mainland Asia (Peninsular Malaysia) and Indonesia (Bali and Lombok) samples of *Bactrocera caudata* based on combined COI and 16S rDNA sequences (After Lim et al. 2012)

Taxon	1	2	3	4
1. *B. caudata* (UM, P. Malaysia)	–			
2. *B. caudata* (Carey Island, PM)	0.09	–		
3. *B. caudata* (Lombok)	4.45	4.46	–	
4. *B. caudata* (Lombok)	4.45	4.46	0.00	–
5. *B. caudata* (Bali)	4.45	4.46	0.00	0.00

(Fabricius). It has a Paleartic and Oriental distribution, occurring in India, Sri Lanka, Myanmar, Thailand, Vietnam, China, Malaysia, Brunei and Indonesia (Sumatra, Java, Bali, Lombok, Flores) (Carroll et al. 2002; Lim et al. 2012).

The partial DNA sequences of cytochrome *c* oxidase subunit I (COI) and 16S rRNA genes reveal distincet genetic lineages of *B. caudata* from mainland Asia and Indonesia (Bali and Lombok), without common haplotype between them (Lim et al. 2012). The uncorrected 'p' distances for COI, 16S and combined COI-16S sequences between *B. caudata* of Malaysia-Thailand-China and *B. caudata* of Bali-Lombok are distinctly different from intraspecific 'p' distance (Table 3). Both the *B. caudata* lineages are distinctly separated from related species in the subgenus *Zeugodacus* – *B. ascita*, *B. scutellata*, *B. ishigakiensis*, *B. diaphora*, *B. tau*, *B. cucurbitae*, and *B. depressa*. Molecular phylogenetic analysis indicates that the *B. caudata* lineages are closely related to *B. ascita* sp. B, and form a clade with *B. scutellata*, *B. ishigakiensis*, *B. diaphora* and *B. ascita* sp. A.

The taxon in Lombok (east of Wallace's Line) is most likely an alien introduction from neighboring island(s), such as through Bali.

5 Crab-Eating Frogs of the *Fejervarya cancrivora* Complex

The crab-eating frogs are widely distributed in Asia (Frost 2013). Gene-enzyme systems (17 enzymes, 26 loci) and mtDNA sequences (16S rRNA and cytochrome b genes) reveal the occurrence of three distinct genetic lineages: (1) Mangrove-type in Bangladesh, Thailand and Philippines; (2) Large-type in Malaysia and Indonesia (Sumatra, Java, Bangka); and (3) Sulawesi-type in West Java and Sulawesi (Kurniawan et al. 2010).

Genetic distances based on these enzyme loci and mitochondrial genes (Table 4) indicate that the three genetic lineages are valid cryptic species. Of the three taxa, the Large-type has closer affinty to the Sulawesi-type, in good agreement with geographical distribution. The Large-type is the nominal *F. cancrivora* and the Mangrove-type attributed to *F. moodiei* (Hasan et al. 2012). Indeed molecular markers indicate considerable numbers of cryptic species in many groups of amphibians (Hasan et al. 2012; Kurashi et al. 2012).

Table 4 Genetic distance of three taxa/types of *Fejevarya cancricora* complex based on 26 enzyme loci (Nei's D, above diagnoal) and mtDNA sequences (16S rRNA/cytb, uncorrected 'p' distance in percentage, below diagonal) (After Kurniawan et al. 2010)

Taxon/Type	Mangrove	Large	Sulawesi
Mangrove	–	0.510 ± 0.025	0.586 ± 0.036
Large	9.10 ± 0.25/14.64 ± 0.59	–	0.197 ± 0.012
Sulawesi	10.22 ± 0.24/16.38 ± 0.49	5.78 ± 0.21/12.88 ± 0.28	–

6 Murid Rodents

6.1 *Marmoset Rats Genus* Hapalomys

Marmoset rats are currently represented by two nominal species: *Hapalomys delacouri* Thomas (Lesser Marmoset Rat or Delacour's Marmoset Rat) and *Hapalomys longicaudatus* Blyth (Greater Marmoset Rat) (Musser and Carleton 2005). Two subspecies of *H. delacouri* were recognized based on tail pilosity and some cranial and dental dimensions: *H. d. delacouri* from C. Vietnam and *C. d. pasquieri* from Laos (Corbet and Hill 1992).

The karyotype of *H. delacouri* from Thailand consists of 2n = 48 chromosomes and Nfa = 92 (Badenhorst et al. 2009). On the other hand, the karyotype of the Vietnam *H. delacouri* is 2N = 38 and Nfa = 48 (Abramov et al. 2012). The significantly different karyotypes indicate the two taxa are distinct cryptic species. As the type locality of *H. delacouri* is S. Vietnam (Dakto), the northern Thailand taxon with 2N = 48 warrants a new specific rank. An available name is *H. pasquieri* Thomas described from Xieng Khouang, Laos (Corbet and Hill 1992; Abramov et al. 2012). However it remains to be confirmed if the two taxa are conspecific.

The usefulness of karyotype for species discrimination (Table 5) is also supported by the karyotype of a congeneric species *H. longicaudatus* which has 2N = 50 (Yong et al. 1982). Based on chromosome constitution, it appears that the Thailand *H.* '*delacouri*' has closer affinity to *H. longicaudatus*.

6.2 *Spiny Rats Genus* Maxomys

Spiny rats of the genus *Maxomys* are represented by some 18 species (Corbet and Hill 1992; Musser and Carleton 2005; Achmadi et al. 2012). Among them are two sibling species, *Maxomys rajah* Thomas and *Maxomys surifer* Miller (previously referred to the genus *Rattus*). Cytogentic, serological (albumin and hemoglobin) and ecological characters show that they are genetically distinct and are valid species (Yong 1969, 1972). *M. rajah* possesses 36 chromosomes and *M. surifer* 52 chromosomes (1969, 1972). Prior to that, these two species had been also regarded as colour phases of one species.

Table 5 Karyotypes of marmoset rats *Hapalomys* spp

Taxon	2N	X	Y	Ref
H. delacouri (Vietnam)	38	M	M	Abramov et al. (2012)
H. '*delacouri*' (Thailand)	48	M	M	Badenhorst et al. (2009)
H. lomgicaudatus	50	M	SA	Yong et al. (1982)

2N, diploid number; X and Y, sex chromosomes; M, metacentric; SA, subacrocentric

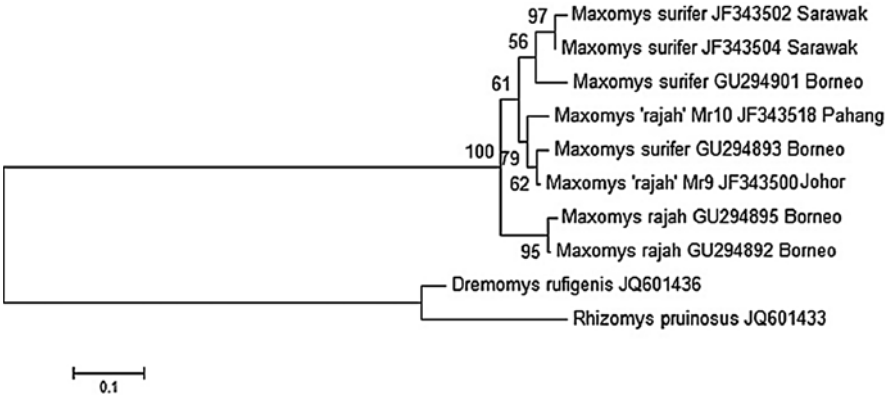

Fig. 2 Phylogenetic relationship of *Maxomys rajah* and *Maxomys surifer* (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Maximum Likelihood method based on partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011) using the Tamura-Nei model (1993). The tree with the highest log likelihood (−2202.5033) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 10 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 471 positions in the final dataset

Among the definitive hosts of the rat lungworm *A. cantonensis* in Thailand is a spiny rat of the genus *Maxomys*, reported as *Rattus raja* (Punyagupta et al. 1970). This taxon is probably *M. surifer* as based on cytogenetic evidence, *M. rajah* does not occur in Thailand (Marshall 1977).

Phylogenetic analysis based on partial sequences of cytochrome *c* oxidase subunit I (COI) gene could not confirm the taxonomic status of some specimens attributed to *M rajah* (Tamrin and Abdullah 2011). One specimen (Mr11, Kubah National Park, Sarawak) clustered with *Leopoldamys sabanus* and *Niviventer cremoriventer*. On the other hand, two specimens from Peninsular Malaysia (Mr9 from Johor; Mr10 from Pahang) clustered with *M. surifer*. Comparison of the COI sequences of these two specimens with those of *M. surifer* and *M. rajah* indicates close affinity of these two specimens with *M. surifer* and distinctly separated from *M. rajah* (Fig. 2). This dataset does not support the two specimens to be distinct from *M. surifer*. As

Table 6 Coefficient of genetic similarity (S, Roger's formula) of *Maxomys* rats in Peninsular Malaysia based on nine erythrocyte protein loci (Data from Chan et al. 1978)

Species	*M. surifer*	*M. whiteheadi*	*M. inas*
M. rajah	0.13	0.17	0.13
M. surifer		0.25	0.15
M. whiteheadi			0.69

these specimens were singletons, the inclusion of more individuals from the same locality, or the application of multiple genes (nuclear and mitochondrial), is needed for clarification of the systematic status.

Based on nine erythrocyte protein loci, *M. rajah* is distantly related to *M. surifer* compared to two other congeneric species (*M. whiteheadi* and *M. inas*) from Peninsular Malaysia (Table 6; Chan et al. 1978). Phylogenetic analyses using two COI nucleotide sequences of different length also unequivocally separate *M. rajah* and *M. surifer* (Figs. 3 and 4). The taxa of *M. surifer* from Laos and Vietnam show closer affinity compared to the taxon from Kalimantan; the unidentified *Maxomys* species from Johor clusters with *M. surifer* and distinct from *M. rajah* (Fig. 3). However, the genetic distance ($p = 0.1281$) between the Kalimantan taxon and the Laos-Vietnam taxon indicates distinct genetic lineage. Further studies using multiple genes and extensive geographic sampling are needed to resolve this issue.

Although different phylogenetic methods unequivocally differentiate the congeneric species, the phylogentic relationships resulting from different methods may not be concordant (Figs. 4 and 5). The topology of the phylogenetic trees is also affected by the number of taxa (Figs. 3 and 4).

7 Conclusion

Phylogenetic analyses form an essential component in researching the evolutionary tree of life. Proteins and nucleotide sequences, in particular, provide large numbers of characters for phylogenetic analysis. Phylogeography, based on phylogenetic analysis, can help in the prioritization of areas of high value for conservation. Systematics (particularly correct identification) is of paramount importance in phylogenetics as well as other disciplines for sound inference, decision or judgment. The contribution and importance/relevance of systematics to various fields of biology (including biodiversity and conservation) and other scientific disciplines are succinctly reflected by the following statement regarding ecology (Elton 1947): "The extent to which progress in ecology depends upon accurate identification, and upon the existence of a sound systematic groundwork for all groups of animals, cannot be too much impressed upon the beginner in ecology. This is the essential basis of the whole thing; without it the ecologist is helpless, and the whole of his work may be rendered useless".

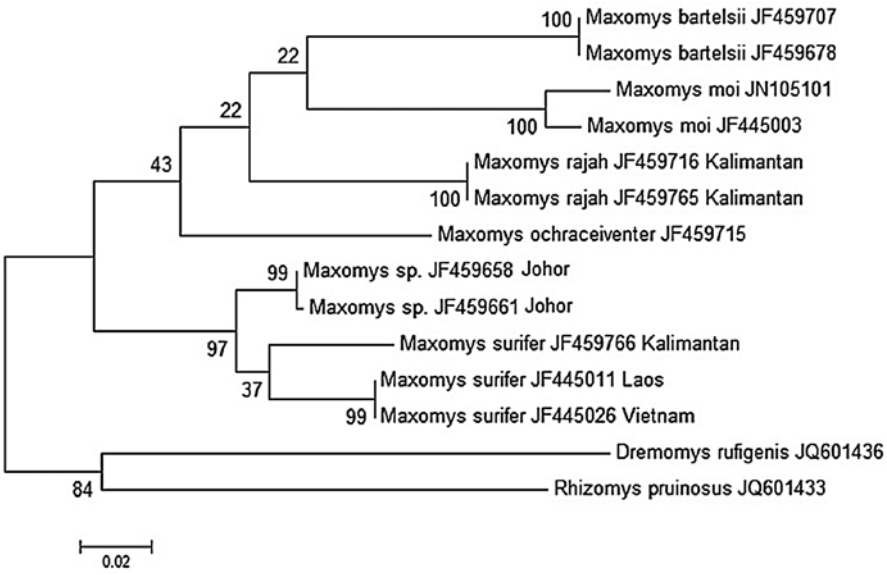

Fig. 3 Phylogenetic tree of *Maxomys* spiny rats (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Maximum Likelihood method based on relatively long partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011) using the Tamura-Nei model (1993). The tree with the highest log likelihood (−2692.1225) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 14 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd + Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 593 positions in the final dataset

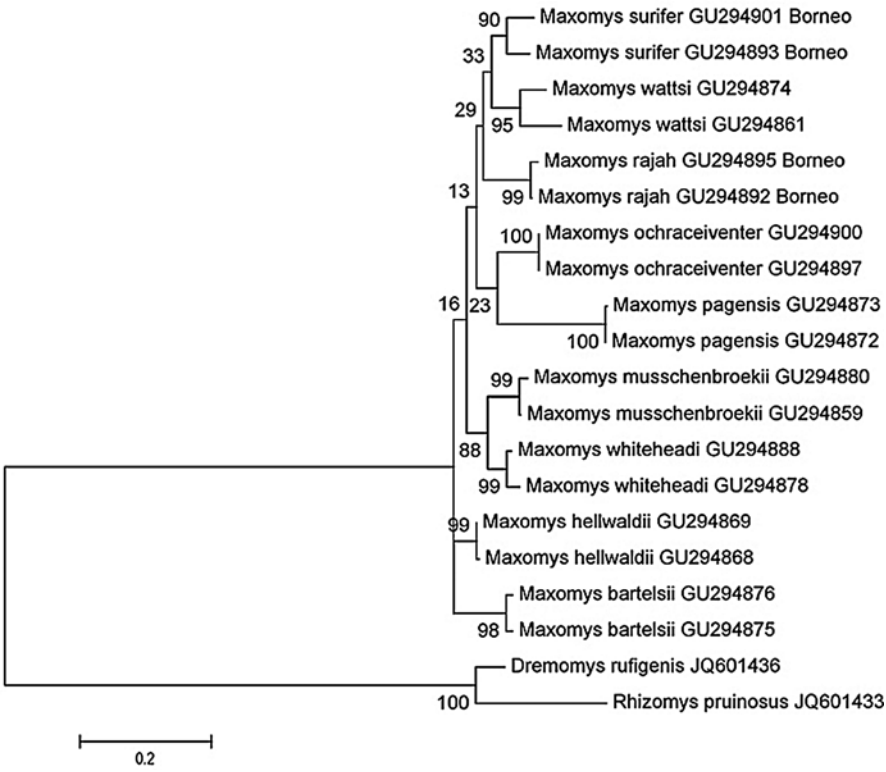

Fig. 4 Phylogenetic tree of *Maxomys* spiny rats (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Maximum Likelihood method based on relatively short partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011) using the Tamura-Nei model (1993). The tree with the highest log likelihood (−3452.2025) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 20 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 474 positions in the final dataset

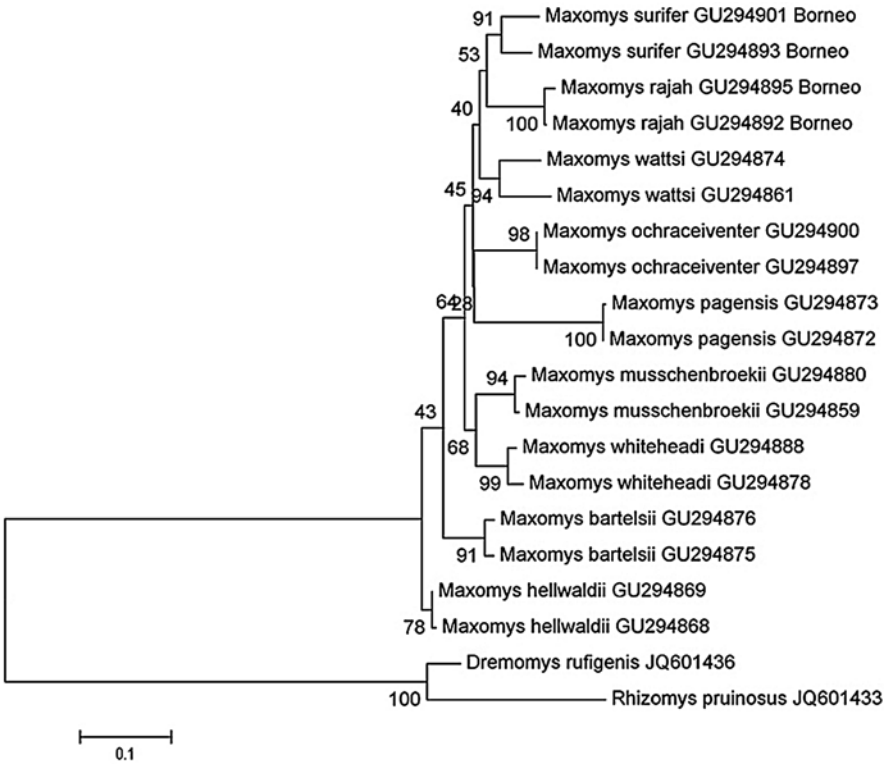

Fig. 5 Phylogenetic tree of *Maxomys* spiny rats (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Neighbor-Joining method (Saitou and Nei 1987) based on relatively short partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011). The optimal tree with the sum of branch length = 1.93656235 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) are shown next to the branches (Felsenstein 1985). The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Kimura 2-parameter method (Kimura 1980) and are in the units of the number of base substitutions per site. The analysis involved 20 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 474 positions in the final dataset

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