

Plumage-based phylogenetic analyses of the *Merops* bee-eaters

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I review previous systematic work on the family Meropidae and present phylogenetic hypotheses derived from my analyses of colour, pattern and shape variation in 30 plumage regions among species and subspecies in this family. Consistent patterns are seen across shallow portions of the trees. Uncertainty remains concerning the placement of several deep branches within this group's phylogeny. In particular, the phylogenetic placement of *Meropogon forsteni* and *Merops breweri*, *M. ornatus*, *M. hirundineus* and *M. boehmi* remains uncertain. The biogeographical patterns in the resultant trees are similar with either a Southeast Asian or African origin for the family, with most of the early diversification occurring in Africa, and with multiple independent subsequent invasions of non-African areas.

The bee-eaters, family Meropidae, are a group of 26 species of brightly coloured coraciiform birds. They are distributed throughout the palaeotropics and southern Eurasia (Fry 2001). Bee-eaters display a great range of diversity in several ecological and behavioural traits, including breeding systems, migratory habits, foraging behaviours and nest-site preferences (Fry 1969, 1984, Fry & Fry 1992, Burt 1996). These traits could be subjects of productive comparative studies. However, to make a valid comparative study of any of these traits, we must first know the phylogenetic relationships within the group.

The relationships among families in the Order Coraciiformes are uncertain because of early and rapid diversification of these lineages (Cracraft 1981, Sibley & Ahlquist 1990). Few systematic studies of the family have been completed previously and no studies of the family have utilized molecular data. Von Boetticher (1951) primarily used plumage colour and shape characters to derive a classification for the family. Fry (1969) used behavioural, biogeographical, ecological and plumage colour/shape characters to derive a phenetic classification and tree. Fry (1984) later modified the placement of certain lineages using information from geographical distributions of subspecies

and further behavioural observations. The major areas of disagreement between the conclusions of these two researchers concern the placement of four forest species. Fry's *Merops gularis* and *M. muelleri* are placed in a separate genus (*Meropiscus*) in Boetticher's classification. Fry's *Merops breweri* and *Meropogon forsteni* are placed into the genus *Nyctyornis* in Boetticher's classification. Furthermore, Fry (1969) places the African forest-dwelling *M. breweri* among African savanna *Merops* species whereas Boetticher places this species with Asian forest species. Fry later revised his views, agreeing that *M. breweri*'s closest relative may be *Meropogon forsteni* (Fry 1984, p. 203). Relationships among bee-eater species from these previous systematic studies were based primarily on each author's intuitive feel for the characters considered. The analyses reported here are the first to reconstruct the phylogenetic relationships within the family using explicit, cladistic methods.

In this study, I reconstruct the evolutionary relationships among the species in the family Meropidae using data on variation in plumage colour, pattern and shape (see Appendix). Results are presented from two maximum parsimony-based analyses with either species or subspecies as terminal taxa. I then examine the biogeographical distribution of each lineage to uncover potential patterns of geographical origin and dispersal. Finally, I compare the results of my analyses with the previous phenetic studies of this group by Fry (1969, 1984).

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METHODS

Specimens and plumage characters

Two data matrices were used in the study: one with species as terminal taxa and one with subspecies as terminal taxa. Single specimens from each of the nominate subspecies were first examined to document the basic plumage character patterns of each species. Multiple individuals of each sex from each of the geographically defined subspecies (Fry 2001) were then examined to document the extent of character variation within and among taxa.

Thirty plumage regions were scored for colour, pattern and shape using museum study skins and spirit specimens (see Appendix). Data from spirit specimens were excluded when specific plumage colours had evidently faded. Evidence of fading was derived by comparison of plumage colours from study skins and illustrations in Fry and Fry (1992). Detailed structural components of feathers consistently associated with carotenoid pigments suggest homology of these colours (Fry 1969). Plumage characters were retained only if they were invariant within subspecies in analyses. Subspecies identified as distinct by Fry (2001) were combined if they did not differ in plumage characters (*Nyctornis athertoni athertoni* = *N. a. brevicaudata*, *Merops hirundineus hirundineus* = *M. h. furcatus*, *M. pusillus meridionalis* = *M. p. argutus*, *M. bullockoides bullockoides* = *M. b. randorum*, *M. orientalis cyanophrys* = *M. o. muscatensis*, *M. o. viridissimus* = *M. o. flavoviridis*, *M. superciliosus superciliosus* = *M. s. alternans*). *M. nubicus* and *M. nubicoidea* are considered as distinct phylogenetic species owing to their disjunct breeding distributions and plumage differences. Sexual dichromatism is rare in bee-eaters, but in cases where it does occur, the dichromatic characters were coded as polymorphic for that taxon. Data matrices can be accessed at the TreeBASE website (www.treebase.org/treebase, S 1021). The subspecies data matrix and character descriptions are documented in the Appendix.

Character step matrices

Each plumage region typically has a large array of colours when examined across all geographically distinct subspecies. Each plumage region is represented here as a single character with several colour or shape character states. Each multistate character is linked to character-specific step matrices to retain additional information. Character step matrices assume

that transitions between similarly coloured character states are easier than they are to other coloured character states (e.g. orange-red to red easier than either is to blue).

Three basic levels of transition rules were used in construction of step matrices. It is assumed that each level represents an increasingly difficult transition between colours. The easiest level of transition was that between green and green with blue tips, chestnut and red chestnut, and between dark greenish-brown and light greenish-brown. The next level of transition linked all greens together and these to greens mixed with other colours. Also in this transition level were similar rules for blues, oranges and reds. The most difficult level of transition was that between more distant colours. No attempt was made to construct more detailed step matrices for relationships between colours of more distant spectral affinity. Although complex, these step matrices are actually quite conservative while still utilizing much of the information available in each multistate plumage character. Character step matrices can be accessed in the data files at the TreeBASE website (www.treebase.org/treebase, S 1021).

An alternative method of extracting the same information is to break each multistate plumage character into multiple, individual characters. That method was not used in this study because it would artificially inflate the number of independent characters in each data matrix. That is, certain characters would contain character states that could not exist, given any character state in certain other characters.

An example illustrates how this problem could occur. The step matrix for the forehead colour has three basic transition classes. The first transition class represents slight changes among species with green in the forehead. In some cases the basic green forehead is only slightly modified by the addition of faint blue tips and this slight difference is indicated by a cost of only a single step. Other transitions from the basic green involve more complex changes such as the addition of other colours (e.g. orange, brown) throughout the forehead region. These more complex changes result in an increased cost of two steps. Finally, some species have either a chestnut or reddish-chestnut forehead, probably indicating that these species are closely related, and therefore transitions between these two colours cost only a single step in the matrix. All other transitions are between colours of more distant spectral affinity and therefore cost three steps. It is possible to represent these basic colour changes in the forehead as different

characters (e.g. 'basic green or not', 'green with other colour or not', 'chestnut or not'), but the characters are not then independent. That is, if the forehead is chestnut, it cannot be green. Although the independence of characters in most phylogenetic analyses is typically assumed and not tested, one should not knowingly use non-independent characters (Farris 1983).

Plumage characters and bootstrap analysis

The nature of the characters used in this study provides one significant analytical problem. Bootstrap analyses are reliable estimates of the information content of data matrices and the relative probabilities of each node in resultant reconstructions representing those in the true phylogeny (Felsenstein 1988, Hillis & Bull 1993). Bootstrapping measures the variation present in the characters of a data matrix and how representative this subset of characters is of the larger distribution of all possible characters. Multiple bootstrap pseudoreplicate matrices are created by sampling characters with replacement from the original data matrix. Use of this technique assumes that characters are independent. In this study, a great deal of information is contained in each of the large multistate characters (and its relevant step matrix). The amount of information lost during the creation of each bootstrap replicate by leaving out any single, large, multistate character is therefore much greater than that lost when using more conventional characters. Bootstrap analyses in this case result in overly conservative bootstrap consensus trees with very little resolution. This problem can be corrected if each multistate plumage character is broken into multiple characters. However, we then have the problem of non-independence discussed above. Therefore, regardless of how characters are coded in this study, use of the bootstrap technique is not appropriate.

Phylogenetic analyses options

PAUP* (version 4.0b10, Swofford 2002) was used to carry out maximum parsimony phylogenetic analyses. I conducted heuristic searches because of the number of taxa in both the species and the subspecies data matrices. All the most parsimonious trees (MPTs) were retained. To increase the chance that the most parsimonious solution would be found, 1000 random addition sequence searches were conducted with tree bisection and reconnection (TBR)

branch swapping in each analysis. The starting trees for branch swapping were derived by stepwise addition of taxa. The number of TBR islands represented in the MPT set and the number of replicates in which they were found is reported to indicate the thoroughness of searches (Maddison 1991). Permutation tail probability test (PTP) results (using 1000 replicates), and consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) values are given to indicate the strength of structure and levels of homoplasy in both species and subspecies data matrices.

Relationships among the families of the order Coraciiformes are unclear because of long divergence times among the families (Cracraft 1981, Sibley & Ahlquist 1990). The choice and utility of outgroup taxa among these families are therefore questionable. Instead, the trees were rooted between the two species of the probable basal genus *Nyctyornis* and the remaining bee-eater lineages. Evidence for the basal placement of this genus is seen in the DNA-DNA hybridization data of Sibley and Ahlquist (1990: figure 359). Comparisons of the trees' fit to biogeographical patterns were examined by mapping geographical distributions on each phylogenetic hypothesis using MacClade (version 4.0, Maddison & Maddison 2000). Breeding distributions were taken from Fry (1984).

RESULTS

Phylogenetic reconstructions

The analysis using the subspecies matrix resulted in 2016 MPTs with 826 steps (PTP results: $P = 0.001$, CI = 0.652, RI = 0.7465, RC = 0.487, HI = 0.338). This single TBR island of trees was found in 558 of 1000 search replicates. The strict consensus tree from this MPT set is shown in Figure 1. The analysis using the species matrix resulted in four MPTs with 816 steps (Fig. 2; PTP results: $P = 0.001$, CI = 0.603, RI = 0.491, RC = 0.296, HI = 0.344). Two trees each were reconstructed in two TBR tree islands. These islands were found in 147 and 389 of 1000 search replicates.

Biogeographical patterns

Biogeographical patterns are similar for trees from analyses of both subspecies and species matrices (Fig. 3). Trees show the origin of the family as either Southeast Asia or Africa, with much of the early

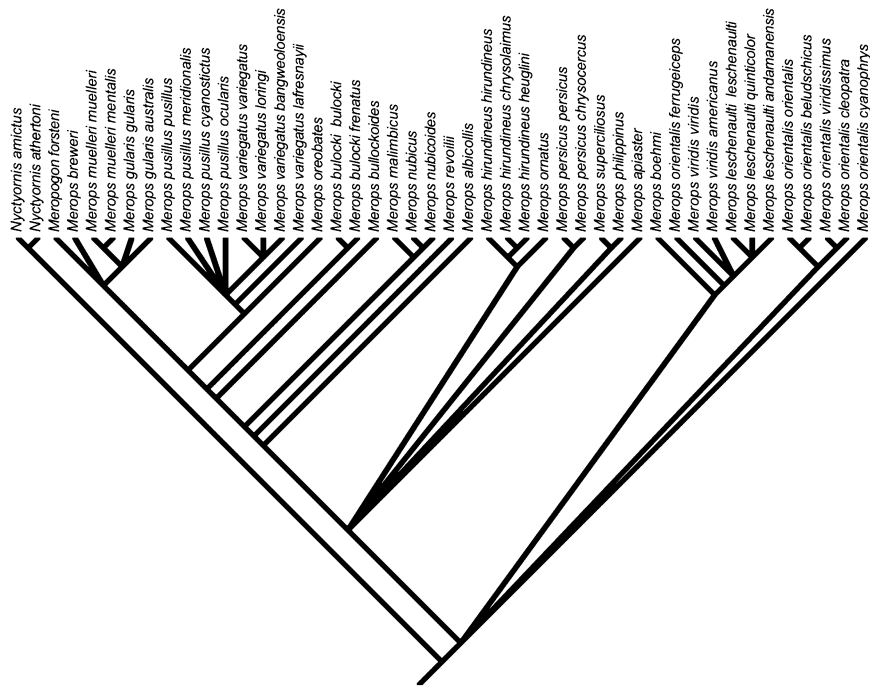


Figure 1. The strict consensus tree of 2016 most parsimonious trees from the analysis of the subspecies data matrix.

diversification of the family occurring in Africa. In all trees, *Meropogon forsteni* shows a pattern of invasion of Indonesia from African ancestors. Several additional invasions of non-African areas are seen in clades associated with basal branches in the genus *Merops*. Figure 3(a) shows more uncertainty in biogeographical patterns due to two deep polytomies. Assuming an African origin would show simultaneous diversification within Africa and invasion of non-African areas. However, it is also possible to show early diversification in Asia with a later invasion of Africa in this tree.

DISCUSSION

Several consistent patterns can be seen when trees from each analysis are examined. First, certain clades are consistent across the shallow portions of the trees (*Meropogon forsteni* – *Merops breweri* – *M. muelleri* – *M. gularis*, *M. pusillus* – *M. variegatus* – *M. oreobates*, *M. malimbicus* – *M. nubicus* – *M. nubicoides*, *M. hirundineus* – *M. ornatus*, *M. viridis* – *M. leschenaulti*). Furthermore, certain lineages consistently group together in sequential evolutionary patterns coming off the main backbone of the *Merops* clade (*M. bullocki* – *M. bullockoides*, *M. revoli* – *M. albicollis*). The close relationships among *M. persicus*, *M. superciliosus* and

M. philippinus are also apparent in most of the resultant trees. Subspecies group into species clusters, if not always clades, for all species except *M. orientalis*. This species has six subspecies of which one, *M. orientalis ferrugeiceps*, does not group with the other subspecies in the species (Fig. 1). Finally, *Meropogon forsteni* is placed within the *Merops* clade in all trees. Certain taxa, however, vary conspicuously in their placement among trees (i.e. *M. apiaster*, *M. boehmi*).

Comparing trees between analyses shows more uncertainty over the placement of certain deep branches of the tree. The branching order of lineages in the *Meropogon forsteni* to *M. albicollis* clade is consistent. However, the branching order of lineages involving *M. hirundineus* – *M. ornatus*, *M. viridis* – *M. leschenaulti* and *M. persicus* – *M. superciliosus* – *M. philippinus* and the problematic lineages *M. apiaster* and *M. boehmi* is less consistent.

Comparison with earlier systematic work

The only attempt to reconstruct explicit phylogenetic relationships within the family Meropidae prior to this study was that of Fry (1969). In that study, a combination of morphological, biogeographical, ecological and behavioural characters was used to derive a phenetic-based hypothesis of species relationships.

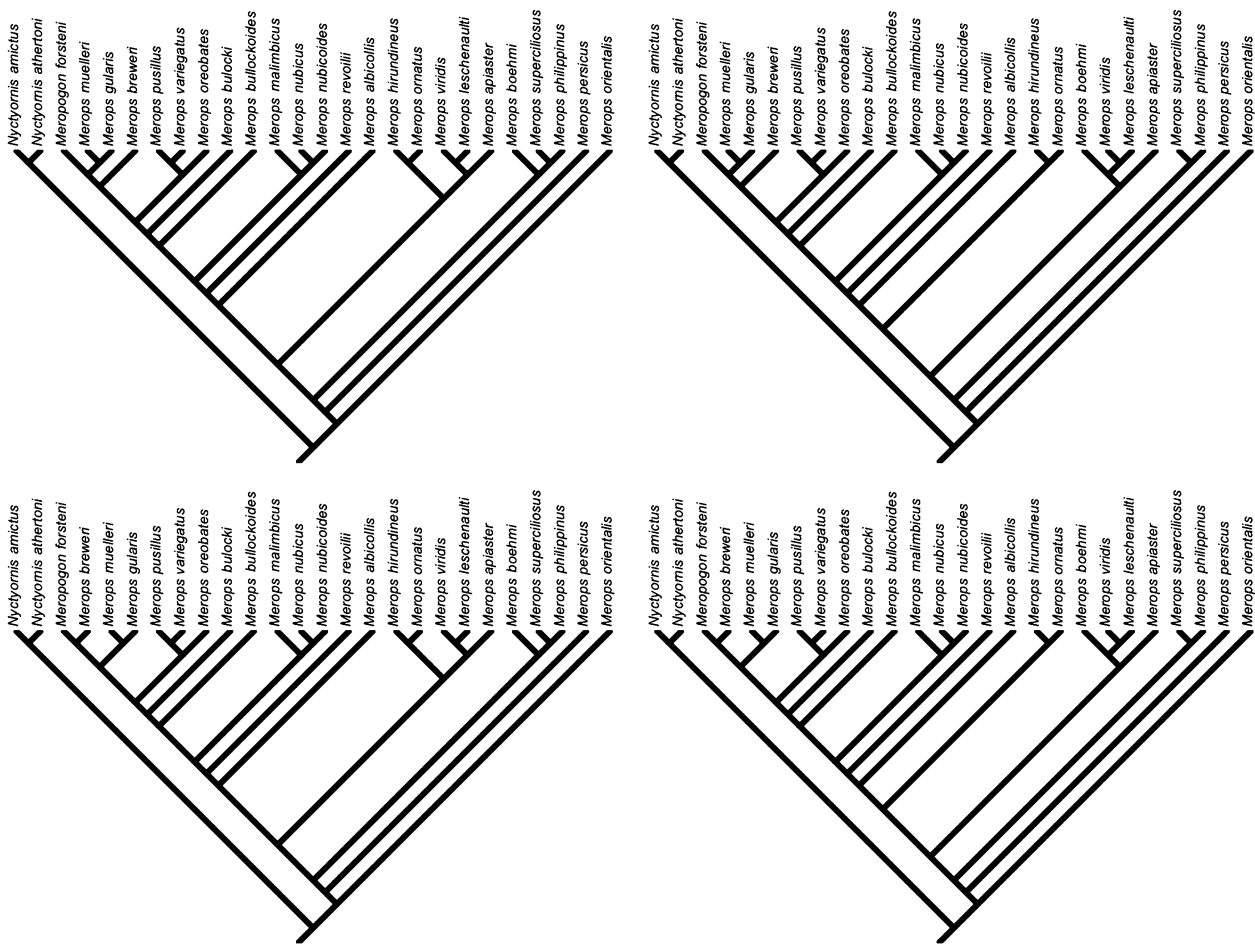


Figure 2. Four most parsimonious trees from the analysis of the species data matrix.

Fry's hypothesis is represented by a figure of a 'cross-section through the top of a phylogenetic tree' (Fry 1969: p. 587) reproduced in Figure 4.

Comparisons between trees in this study with Fry's species groups and superspecies show areas of agreement and conflict. Each tree in this study shows a sister species relationship between *M. philippinus* and *M. superciliosus*. Fry includes *M. ornatus* with each of these species in a species group. This study does not support a close relationship between *M. ornatus* and *M. philippinus* or *M. superciliosus*. In fact, each tree in this study supports a sister species relationship between *M. ornatus* and *M. hirundineus*. Fry places *M. hirundineus* in a species group with *M. pusillus* and the superspecies *M. variegatus* and *M. oreobates*. This study supports a strong relationship among the latter three species; however, each tree shows a sister relationship between *M. variegatus* and *M. pusillus*, not between *M. variegatus* and *M. oreobates*. The

subspecies analysis also suggests that *M. v. lafresnayii* might represent a distinct lineage just above *M. oreobates* and at the base of the *M. variegatus* – *M. pusillus* clade. Previous researchers have debated this possibility because of the relative colorations and sizes of individuals in these lineages (reviewed in Fry 1969). Fry also placed *M. boehmi* and *M. orientalis* in a species group. This arrangement is not supported by this study; however, neither is there any strong support for the placement of *M. boehmi* between any specific branches in this study. The close relationships between several other species in this study show additional general consistencies with Fry's hypothesis: *N. amictus* – *N. athertoni*, *M. gularis* – *M. muelleri*, *M. bulcocki* – *M. bullockoides*, *M. revoilii* – *M. albicollis*, *M. malimbicus* – *M. nubicus* – *M. nubicoides*, *M. viridis* – *M. leschenaulti* – *M. aplaster*.

The basal relationship of *Meropogon forsteni* to the *Merops* bee-eaters in Fry's hypothesis is quite different

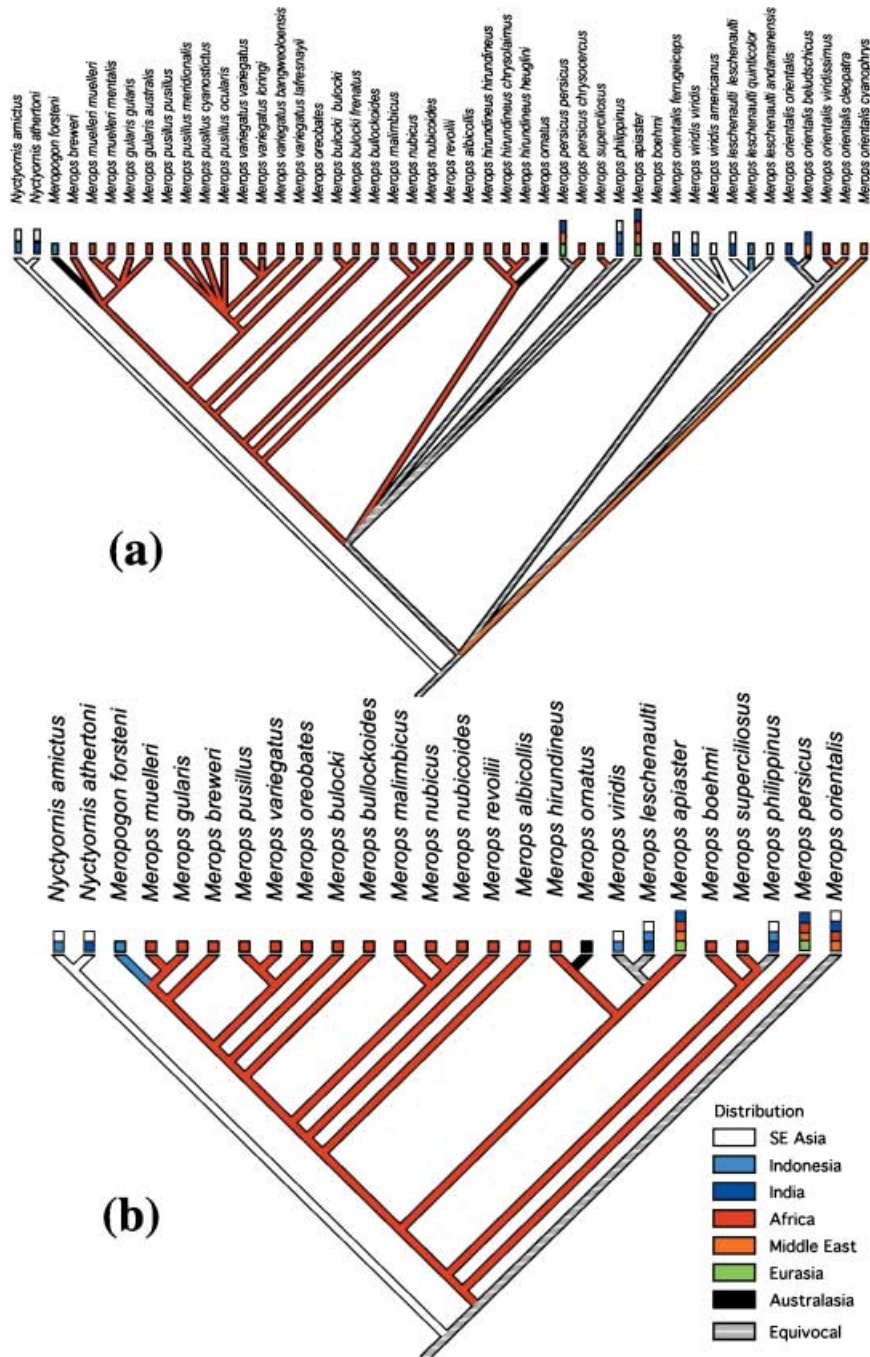


Figure 3. Reconstructions of biogeographical patterns. (a) Strict consensus tree from subspecies analysis. (b) Representative species tree. Biogeographical patterns are similar for each of the four species trees.

from the pattern seen in this study. The placement of the Indonesian *Meropogon forsteni* well within an African clade in my reconstructions seems biogeographically improbable. Branching of this species between the Asian/Indonesian *Nyctyornis* and the

primarily African *Merops* seems to be more intuitive and would further suggest an Asian origin for the family. Furthermore, differing rib numbers and structure are reported for this species, setting it apart from both *Merops* and *Nyctyornis* (Fry 1969, 1984).

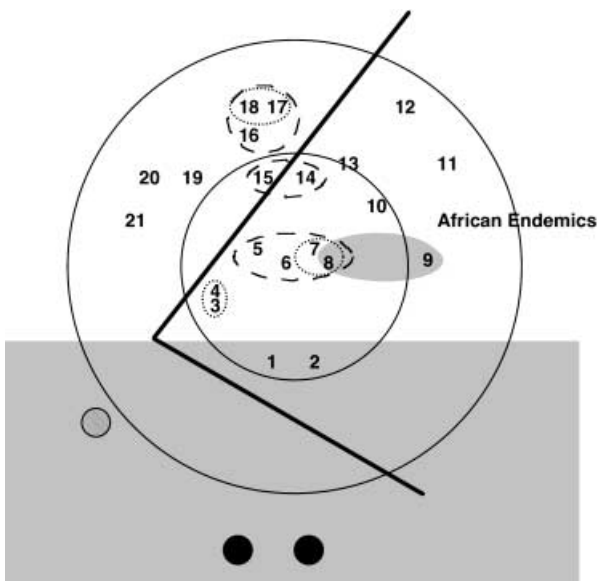


Figure 4. (a) Diagram of a cross-section of the top of a phylogenetic tree. Circles describe distance relationships with respect to *Merops pusillus* (6). Bottom to top of figure represents general advancement of characters from plesiomorphic states. Dashed-line circles represent species groups. Dotted-line circles represent superspecies. Shaded areas equal forest, unshaded equals savanna. Black dots = *Nyctyornis amictus* and *N. athertoni*; hatched dot = *Meropogon forsteni*; numbers = *Merops*: (1) *gularis*, (2) *muelleri*, (3) *bullockoides*, (4) *bullocki*, (5) *hirundineus*, (6) *pusillus*, (7) *variegatus*, (8) *oreobates*, (9) *breweri*, (10) *revouillii*, (11) *malimbicus*, (12) *nubicus*, (13) *albicollis*, (14) *boehmi*, (15) *orientalis*, (16) *ornatus*, (17) *superciliosus*, (18) *philippinus*, (19) *viridis*, (20) *leschenaulti*, (21) *apiaster*. Reproduced from Fry (1969).

Fry (1969) suggests *M. breweri* is most closely related to his *M. pusillus* species group. In this study, the forest-dwelling *M. breweri* is consistently associated in some manner with other forest species: *M. muelleri*, *M. gularis* and *Meropogon forsteni*. As mentioned in the introduction, Fry (1984: p. 203) revised his views, stating that *M. breweri*'s closest relative may be *Meropogon forsteni*. This sister-group relationship is supported in part by this study (several of the trees used to form Fig. 1, two trees in Fig. 2).

Additional phylogenetic data, particularly sequence data, are needed to test the phylogenetic hypotheses presented here. These data could be especially important for a better understanding of the phylogenetic placement of *Meropogon forsteni*, *M. breweri*, *M. ornatus*, *M. hirundineus* and *M. boehmi*.

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APPENDIX

Subspecies data matrix

Subspecies	Character number									
	1	2	3	4	5	6	7	8	9	10
<i>Nyctyornis amictus</i>	0	0	1	6	5	0	0	0	0	0
<i>Nyctyornis athertoni</i>	0	4	1	0	0	0	4	1	0	4
<i>Meropogon forsteni</i>	2	2	2	7	6	1	1	2	0	0
<i>Merops breweri</i>	3	3	3	8	7	2	2	2	0	0
<i>Merops muelleri muelleri</i>	0	4	4D	4	7	2	3	2	0	1
<i>Merops muelleri mentalis</i>	0	4	E	1	7	2	3	2	0	1
<i>Merops gularis gularis</i>	0	3	3	1	7	2	2	2	0	3
<i>Merops gularis australis</i>	B	3	3	5	7	2	2	2	0	3
<i>Merops hirundineus hirundineus</i>	5	5	1	0	3	3	0	2	1	0
<i>Merops hirundineus chrysolaimus</i>	0	5	1	1	3	3	0	2	1	0
<i>Merops hirundineus heuglini</i>	5	5	1	0	3	3	0	2	1	0
<i>Merops pusillus pusillus</i>	4	1	5	5	8	5	4	2	1	4
<i>Merops pusillus meridionalis</i>	4	1	5	3	8	5	4	2	1	4
<i>Merops pusillus cyanostictus</i>	0	1	5	1	8	5	4	2	1	4
<i>Merops pusillus ocularis</i>	4	1	5	3	8	5	4	2	1	4
<i>Merops variegatus variegatus</i>	4	1	5	5	9	4	4	2	1	4
<i>Merops variegatus loringi</i>	4	1	5	1	9	4	4	2	1	4
<i>Merops variegatus bangweoloensis</i>	4	1	5	5	9	4	4	2	1	4
<i>Merops variegatus lafresnayii</i>	0	1	5	1	9	4	4	2	1	4
<i>Merops oreobates</i>	B	1	5	1	9	4	4	2	1	4
<i>Merops bulocki bulocki</i>	4	1	5	05	04	6	5	2	1	4
<i>Merops bulocki frenatus</i>	0	1	5	1	1	7	5	2	1	4
<i>Merops bullockoides</i>	6	6	6	1	2	8	5	2	1	4
<i>Merops revollii</i>	7	A	A	1	2	4	A	2	1	4
<i>Merops albicollis</i>	6	7	7	2	2	4	6	2	1	4
<i>Merops boehmi</i>	9	8	8	9	1	9	4	2	1	4
<i>Merops orientalis orientalis</i>	C	C	F	0	1	A	6	2	1	4
<i>Merops orientalis viridissimus</i>	5	5	1	0	4	0	0	2	1	0
<i>Merops orientalis cleopatra</i>	5	5	1	0	4	0	0	2	1	4
<i>Merops orientalis cyanophrys</i>	0	4	1	1	1	A	0	2	1	4
<i>Merops orientalis beludschicus</i>	C	C	F	0	1	A	6	2	1	4
<i>Merops orientalis ferrugeiceps</i>	9	8	8	0	1	A	7	2	1	1
<i>Merops persicus persicus</i>	D	4	5	4	3	B	4	2	1	4
<i>Merops persicus chrysocercus</i>	D	4	1	4	3	B	0	2	1	0
<i>Merops superciliosus superciliosus</i>	6	B	B	2	2	C	B	2	1	6
<i>Merops philippinus</i>	A	D	G	1	1	9	C	2	1	6
<i>Merops ornatus</i>	4	1	0	0	1	D	5A	2	1	4
<i>Merops viridis viridis</i>	E	E	H	A	1	A	D	2	1	7
<i>Merops viridis americanus</i>	9	8	8	9	1	A	7	2	1	1
<i>Merops leschenaulti leschenaulti</i>	9	8	8	9	8	5	7	2	1	1
<i>Merops leschenaulti quinticolor</i>	9	8	8	9	8	5	7	3	2	1
<i>Merops leschenaulti andamanensis</i>	9	8	8	9	8	5	7	3	3	1
<i>Merops apiaster</i>	61	1	8	4	3	E	7	2	1	1
<i>Merops malimbicus</i>	8	9	9	B	2	8	8	2	1	5
<i>Merops nubicus</i>	F	F	C	C	B	F	9	2	1	2
<i>Merops nubicoides</i>	F	F	C	C	A	6	E	2	1	8

Subspecies data matrix continued

Subspecies	Character number									
	11	12	13	14	15	16	17	18	19	20
<i>Nyctyornis amictus</i>	0	0	0	0	0	0	0	0	0	0
<i>Nyctyornis athertoni</i>	1	3	3	0	2	1	0	1	4	1
<i>Meropogon forsteri</i>	0	0	0	0	2	2	2	0	2	2
<i>Merops breweri</i>	1	0	0	0	2	2	2	0	3	3
<i>Merops muelleri muelleri</i>	2	1	5	2	0	4	3	2	5	3
<i>Merops muelleri mentalis</i>	2	7	5	6	?	4	?	3	5	3
<i>Merops gularis gularis</i>	3	6	2	2	0	4	3	4	5	0
<i>Merops gularis australis</i>	3	6	2	2	?	4	?	4	5	0
<i>Merops hirundineus hirundineus</i>	0	6	2	1	2	5	6	1	6	4
<i>Merops hirundineus chrysolaimus</i>	0	2	1	4	?	5	?	1	6	4
<i>Merops hirundineus heuglini</i>	0	2	1	4	?	5	?	1	6	4
<i>Merops pusillus pusillus</i>	1	3	3	0	1	6	3	1	6	4
<i>Merops pusillus meridionalis</i>	1	3	3	0	2	6	3	1	6	4
<i>Merops pusillus cyanostictus</i>	1	3	3	0	?	6	?	1	6	4
<i>Merops pusillus ocularis</i>	1	3	3	0	?	6	?	1	6	4
<i>Merops variegatus variegatus</i>	1	3	3	0	2	6	3	1	6	4
<i>Merops variegatus loringi</i>	1	3	3	0	?	6	?	1	6	4
<i>Merops variegatus bangweoloensis</i>	1	3	3	0	?	6	?	1	6	4
<i>Merops variegatus lafresnayii</i>	1	3	3	0	?	6	?	1	6	4
<i>Merops oreobates</i>	1	3	3	0	0	6	3	1	6	4
<i>Merops bullocki bullocki</i>	1	3	3	0	1	7	6	1	5	0
<i>Merops bullocki frenatus</i>	1	3	3	0	?	7	?	1	5	0
<i>Merops bullockoides</i>	1	3	1	7	2	7	6	1	7	0
<i>Merops revoilii</i>	1	6	2	7	1	8	5	1	7	5
<i>Merops albicollis</i>	1	3	2	8	0	9	1	5	7	5
<i>Merops boehmi</i>	1	3	3	8	2	9	1	1	1	7
<i>Merops orientalis orientalis</i>	1	3	3	9	2	9	1	1	4	68
<i>Merops orientalis viridissimus</i>	0	0	0	9	?	9	?	1	9	9
<i>Merops orientalis cleopatra</i>	1	3	3	9	?	9	?	1	9	9
<i>Merops orientalis cyanophrys</i>	1	3	3	9	?	9	?	1	4	1
<i>Merops orientalis beludschicus</i>	1	3	3	9	?	9	?	1	4	6
<i>Merops orientalis ferrugeiceps</i>	1	3	3	9	?	9	?	1	8	6
<i>Merops persicus persicus</i>	1	3	3	9	1	8	5	1	6	7
<i>Merops persicus chrysocercus</i>	0	0	0	9	1	8	?	1	6	7
<i>Merops superciliosus superciliosus</i>	1	3	3	0	1	8	5	6	A	7
<i>Merops philippinus</i>	7	2	2	48	1	8	1	6	6	7
<i>Merops ornatus</i>	1	2	2	A	2	7	4	1	6	4
<i>Merops viridis viridis</i>	1	2	2	3	1	7	1	1	4	8
<i>Merops viridis americanus</i>	1	2	2	3	?	7	?	1	8	6
<i>Merops leschenaulti leschenaulti</i>	0	2	2	07	1	7	1	0	6	4
<i>Merops leschenaulti quinticolor</i>	0	2	2	3	?	7	?	0	6	4
<i>Merops leschenaulti andamanensis</i>	0	2	2	04	?	7	?	0	6	4
<i>Merops apiaster</i>	4	4	3	7	1	8	5	87	6	4
<i>Merops malimbicus</i>	5	5	4	5	2	7	5	9	7	0
<i>Merops nubicus</i>	6	2	2	B	2	3	5	A	B	A
<i>Merops nubicoides</i>	8	2	2	B	2	3	5	A	5	0

Subspecies data matrix continued

Subspecies	Character number										
	21	22	23	24	25	26	27	28	29	30	31
<i>Nyctornis amictus</i>	0	0	0	A	0	0	0	0	0	1	01
<i>Nyctornis athertoni</i>	0	A	1	1	1	0	0	0	0	1	02
<i>Meropogon forsteni</i>	0	2	2	2	2	1	1	1	1	0	1
<i>Merops breweri</i>	1	3	3	B	9	1	1	1	1	1	3
<i>Merops muelleri muelleri</i>	0	2	4	4	6	0	2	2	2	2	3
<i>Merops muelleri mentalis</i>	0	2	4	4	6	1	2	2	2	2	3
<i>Merops gularis gularis</i>	0	4	9	C	8	0	3	3	3	3	3
<i>Merops gularis australis</i>	0	B	9	C	8	0	3	3	3	3	3
<i>Merops hirundineus hirundineus</i>	2	7	7	5	3	2	1	1	1	1	3
<i>Merops hirundineus chrysolaimus</i>	2	7	7	5	3	2	1	1	1	1	3
<i>Merops hirundineus heuglini</i>	2	7	7	5	3	2	1	1	1	1	3
<i>Merops pusillus pusillus</i>	3	5	5	B	4	3	0	0	0	1	3
<i>Merops pusillus meridionalis</i>	9	5	5	B	4	3	0	0	0	1	3
<i>Merops pusillus cyanostictus</i>	A	5	5	B	4	3	0	0	0	1	3
<i>Merops pusillus ocellaris</i>	9	5	5	B	4	3	0	0	0	1	3
<i>Merops variegatus variegatus</i>	5	5	5	6	4	3	0	0	0	0	3
<i>Merops variegatus loringi</i>	5	5	5	6	4	3	0	0	0	0	3
<i>Merops variegatus bangweoloensis</i>	B	5	5	6	4	3	0	0	0	0	3
<i>Merops variegatus lafresnayii</i>	C	5	3	B	4	3	0	0	0	0	3
<i>Merops oreobates</i>	A	3	3	B	9	0	0	0	0	1	3
<i>Merops bullocki bullocki</i>	0	8	6	3	5	0	1	1	1	1	3
<i>Merops bullocki frenatus</i>	0	8	6	3	5	0	1	1	1	1	3
<i>Merops bullockoides</i>	0	8	6	3	5	0	0	0	0	1	3
<i>Merops revoilii</i>	0	8	6	3	3	0	0	0	0	1	3
<i>Merops albicollis</i>	6	6	A	7	3	1	0	0	4	1	3
<i>Merops boehmi</i>	0	7	0	0	3	1	0	0	0	1	3
<i>Merops orientalis orientalis</i>	D	C	C	5	B	1	0	0	0	1	2
<i>Merops orientalis viridissimus</i>	D	7	0	D	A	1	0	0	0	1	3
<i>Merops orientalis cleopatra</i>	D	C	C	5	B	1	0	0	0	1	4
<i>Merops orientalis cyanophrys</i>	6	C	C	5	3	1	0	0	0	1	4
<i>Merops orientalis beludschicus</i>	D	C	C	5	B	1	0	0	0	1	24
<i>Merops orientalis ferrugeiceps</i>	D	C	5	5	B	1	0	0	0	1	02
<i>Merops persicus persicus</i>	0	C	C	D	A	1	0	0	0	1	24
<i>Merops persicus chrysocercus</i>	0	C	C	D	A	1	0	0	0	1	3
<i>Merops superciliosus superciliosus</i>	0	7	C	D	A	1	5	5	6	1	3
<i>Merops philippinus</i>	0	7	C	D	3	1	4	4	5	1	01
<i>Merops ornatus</i>	8	7	0	58	3	1	0	0	0	1	6
<i>Merops viridis viridis</i>	0	C	C	5	3	1	0	0	0	1	01
<i>Merops viridis americanus</i>	0	C	C	5	3	1	0	0	0	1	0
<i>Merops leschenaulti leschenaulti</i>	4	D	1	8	C	0	1	1	1	1	02
<i>Merops leschenaulti quinticolor</i>	7	D	1	8	3	0	1	1	1	1	1
<i>Merops leschenaulti andamanensis</i>	4	D	1	8	C	0	1	1	1	1	0
<i>Merops apiaster</i>	7	1	7	5	3	1	1	62	72	0	23
<i>Merops malimbicus</i>	0	9	8	9	7	1	6	7	8	4	3
<i>Merops nubicus</i>	0	9	B	9	3	1	7	8	9	5	3
<i>Merops nubicoides</i>	0	9	B	9	3	1	7	8	9	5	3

Characters and character state

1. Forehead: 0. light blue, 1. yellow and white, 2. deep blue-purple, 3. black, 4. green with blue tips, 5. green, 6. white, 7. pied, 8. grey, 9. chestnut, a. light blue and green, b. little light blue, c. green with orange, d. white and light blue, e. red chestnut, f. greenish blue.
2. Forecrown: 0. lilac, 1. green with blue tips, 2. deep purple, 3. black, 4. light blue, 5. green, 6. white, 7. dark brown, 8. chestnut, 9. grey, a. pied, b. dark greenish-brown, c. green with orange, d. light greenish brown, e. red chestnut, f. greenish blue.
3. Hindcrown: 0. orange and green, 1. green, 2. deep purple and brown, 3. black, 4. light blue, 5. green with blue tips, 6. orange, 7. dark brown, 8. chestnut, 9. grey, a. pied, b. dark greenish-brown, c. greenish-blue, d. blue, e. purple, f. green with orange, g. light greenish brown, h. red chestnut.
4. Supercilium: 0. green, 1. light blue, 2. white, 3. small blue, 4. white and blue, 5. very little blue, 6. green and lilac, 7. deep purple, 8. black, 9. chestnut, a. red chestnut, b. grey, c. greenish-blue.
5. Infracilium: 0. green, 1. light blue, 2. white, 3. light blue and white, 4. very little blue, 5. green and red, 6. deep purple, 7. black, 8. yellow, 9. white and yellow, a. red, b. greenish blue.
6. Cheek: 0. green, 1. deep purple, 2. black, 3. white and blue, 4. white, 5. yellow, 6. red, 7. red and blue, 8. red and white, 9. blue and chestnut, a. blue, b. blue and green, c. white, yellow and chestnut, d. yellow and blue, e. white and yellow, f. greenish blue.
7. Nape: 0. green, 1. dark brown, 2. black, 3. deep purple, 4. green with blue, 5. orange, 6. orange-green, 7. chestnut, 8. grey, 9. red, a. green with blue over orange, b. dark greenish brown, c. light greenish-brown, d. red chestnut, e. orange red.
8. Lore: 0. lilac and red, 1. green, 2. black, 3. black and chestnut.
9. Eyestripe: 0. none, 1. black, 2. chestnut, 3. black and chestnut.
10. Mantle: 0. green, 1. chestnut, 2. red, 3. black, 4. green, blue tips, 5. grey, 6. light greenish-brown, 7. red chestnut, 8. orange red.
11. Back: 0. green, 1. green, blue tips, 2. chestnut, 3. black, 4. yellow and chestnut, 5. grey, slight red, 6. red, 7. light greenish-brown, 8. orange red.
12. Rump: 0. green, 1. chestnut-light blue, 2. blue, 3. green, blue tips, 4. yellow-green, 5. grey, slight red, 6. light blue, 7. blue-purple.
13. Upper tail coverts: 0. green, 1. blue, 2. light blue, 3. green, blue tips, 4. greyish red, 5. deep purple.
14. First rectrix, dorsal: 0. green, 1. light blue, white tip, 2. dark blue to black, 3. blue, 4. blue-green, white tip, 5. reddish black, 6. purple, 7. blue-green, 8. blue-green, black tip, 9. green, black tip, 10. blue, black tip, 11. red to black tip.
15. First rectrix rachis, dorsal: 0. black, 1. brown, 2. dark brown.
16. Outer rectrix, ventral: 0. proximal yellow, distal black, 1. yellow, 2. orange-brown to brown m to L, 3. darker light brown, 4. black, 5. brown, white tips, 6 p to d, orange-brown, black, white?, 7. brown, 8. light brown, 9. light brown, dark tip.
17. Outer rectrix rachis, ventral: 0. yellow, 1. off-white, 2. orange-brown, 3. tan to black distally, 4. off-white to brown distally, 5. tan, 6. brown.
18. Scapulars: 0. green, 1. green with blue, 2. chestnut, 3. chestnut-orange, 4. black, 5. green with orange, 6. greenish brown, 7. yellow-orange, 8. yellow-orange with green, 9. grey, slight red, a. red.
19. Chin: 0. blue then red, 1. chestnut, 2. black then purple, 3. black, 4. blue, 5. red, 6. yellow, 7. white, 8. bluish-green, 9. green, a. yellow and white, b. greenish blue.
20. Throat: 0. red, 1. blue, green sides, 2. deep purple, 3. black, 4. yellow, 5. white, 6. bluish-green, 7. chestnut, 8. blue, 9. green, a. greenish blue.
21. Gorget: 0. none, 1. chestnut, 2. light blue, dark blue, 3. light blue, black, chestnut, 4. chestnut, black, 5. white, light blue, dark blue, chestnut, 6. light blue, black, light blue, 7. black, 8. chestnut, black, blue, 9. white, light blue, black, chestnut, a. light blue, dark blue, black, chestnut, b. white, light blue, dark blue-black, chestnut, c. light blue, dark blue, chestnut, d. green-blue, black, green-blue.
22. Breast: 0. red, green sides, 1. greenish-blue, 2. deep purple, 3. yellow-orange, 4. black and iridescent blue, 5. orange-yellow-green, 6. light green, 7. green, 8. orange-brown, 9. red, a. blue, green sides, b. black and iridescent blue with red, c. green with blue, d. yellowish green.
23. Flank: 0. green, 1. green and yellow, 2. brown-grey, 3. yellow-orange, 4. blue, 5. orange-yellow-green, 6. orange-brown, 7. greenish-blue, 8. red, 9. iridescent blue and black, a. light green, b. orange-red, c. green with blue.

24. Belly: 0. green, 1. green and yellow, 2. brown-grey, 3. buff, 4. blue, 5. greenish-blue, 6. yellow-green, 7. greenish-white, 8. light green-blue, 9. red, a. light green, b. orange-yellow-green, c. iridescent blue, d. green with blue.
25. Undertail coverts and vent: 0. light green, 1. yellow, 2. burnt orange, green tips, 3. light blue, 4. buff, 5. blue-purple, 6. blue, 7. reddish-grey, 8. iridescent blue, 9. orange, green tips, a. green with blue, b. greenish blue, c. light green-blue.
26. Tail shape: 0. square, 1. streamer, 2. forked, 3. slight fork.
27. Marginal coverts: 0. green, blue tips, 1. green, 2. chestnut, 3. black, 4. light greenish-brown, 5. dark greenish-brown, 6. grey, 7. red.
28. Lesser coverts: 0. green, blue tips, 1. green, 2. chestnut, 3. black, 4. light greenish-brown, 5. dark greenish-brown, 6. green with chestnut, 7. grey, 8. red.
29. Median and greater coverts: 0. green, blue tips, 1. green, 2. chestnut, 3. black, 4. green with orange, 5. light greenish-brown, 6. dark greenish-brown, 7. green with chestnut, 8. grey, 9. red.
30. Tertiaries: 0. green, 1. green, blue tips, 2. chestnut, 3. black, 4. grey, 5. red, blue tips.
31. Distribution: 0. Southeast Asia, 1. Indonesia, 2. India, 3. Africa, 4. Middle East, 5. Eurasia, 6. Australasia.