PHYLOGENETIC ANALYSIS OF THE CUCULIDAE (AVES, CUCULIFORMES) USING BEHAVIORAL AND ECOLOGICAL CHARACTERS

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ABSTRACT.—A cladistic analysis of 21 genera of cuckoos (Aves, Cuculidae) using 28 behavioral and ecological characters produces one shortest-length tree (L = 80 steps, CI = 0.52, RI = 0.79, RC = 0.42) that differs from traditional classifications of the Cuculidae. My results suggest that two cuculid subfamilies, the terrestrial Neomorphinae and the Phaenicophaeinae, are polyphyletic. The obligate brood parasite *Tapera* (Neomorphinae) and the facultative brood parasite *Coccyzus* (Phaenicophaeinae) are removed from otherwise nonparasitic subfamilies and placed among the Old World obligate parasites in the Cuculinae. This suggests that: (1) brood parasitism arose only once in the Cuculidae rather than three times as previously thought; and (2) that terrestrial habitat use in *Tapera* has evolved secondarily. The placement of *Coccyzus* among the obligate parasites implies that the immediate ancestor of this genus was an obligate brood parasite. Therefore, the facultative behavior of *Coccyzus* represents a loss of obligate parasitism, rather than the development of facultative parasitism from a nonparasitic ancestor. In life, *Coccyzus* shares a number of life-history traits with the obligate brood parasites that support this hypothesis. Based on my analysis, I propose changes to the classification of the cuckoos that are consistent with the opinions of many early systematists, and the results of an unpublished phylogeny of the cuckoos based on postcranial osteological characters. In addition, my findings suggest that the Hoatzin (*Opisthocomus hoatzin*) is a cuckoo most closely related to the communally breeding anis (Crotophaginae). *Received 12 May 1994, accepted 27 January 1995.*

THE CUCKOOS are best known for obligately parasitic breeding habits, whereby a female will lay eggs in the nests of host species and, hence, relinquish the responsibilities of parenthood. However, this diverse family of birds, comprised of 129 species in 38 genera (Morony 1975), contains at least 4 species of facultative brood parasites (*Coccyzus* spp.; Nolan and Thompson 1975, Ralph 1975, Sick 1993) and 74 nonparasitic species, 4 of which are communal breeders (Wyllie 1981). The family is global in distribution and occupies nearly all temperate and tropical biomes with the exception of some remote oceanic islands. A few cuckoos are predominantly terrestrial, foraging and nesting on or near the ground; however, most species are arboreal and many are long-distance migrants (Rowan 1983). Food habits range through varying degrees of herbivory and carnivory with many species relying almost entirely on toxic aposomatic caterpillars. Egg color, clutch size, and incubation periods show little consistency throughout the family (Wyllie 1981). Furthermore, some parasitic genera, such as *Cuculus* and *Chrysococcyx*, exhibit egg polymorphism, egg mimicry and egg crypsis—traditionally attributed to an extended coevolutionary relationship with their hosts—that serves to minimize detection and destruction of cuckoo eggs (Hamilton and Orians 1965, Payne 1977, Davies and Brooke 1989). However, recent studies by Brooker and Brooker (1989, 1990) have suggested that these adaptations to parasitism may have evolved due to intraspecific competition between parasitic females that remove an egg from the host nest just prior to the deposition of their own egg. In addition, most cuckoo chicks will eject the host eggs or young from the nest within a few days of hatching. The nestling Striped Cuckoo (*Tapera naevia*) uses mandibular hooks to kill host chicks in a manner similar to that of the parasitic honeyguides of the genus *Indicator* (Piciformes; Morton and Farabaugh 1979). These adaptations ensure that the parasite chick is the sole occupant of the host nest, thereby improving its chances of fledging successfully.

The diversity of the Cuculidae may be the result of a long evolutionary history. Although the earliest known cuculid fossil dates from the Eo-Oligocene of France (Weigel 1963), some workers suggest that the cuckoos diverged from ancestral stock during the Late Cretaceous (Sibley and Ahlquist 1990). Fundamental differ-

ences in external and internal morphology within the group have perplexed systematists for decades and, although problematic, the most accepted classification of the cuckoos is that of Peters (1940), which is based predominantly on breeding habits and geographic distribution (Table 1). Several alternate classifications of the Cuculidae have been proposed in past decades following the anatomical studies of Berger (1952, 1954, 1960) and Verheyen (1956a), and more recently by Sibley and Monroe (1990) based on DNA-DNA hybridization of Sibley and Ahlquist (1990). However, these studies have not gained wide acceptance and, as a result, most current classifications still adhere to the sequence in Peters (1940). Phylogenetic systematics had not been used to construct a hypothesis of evolutionary relationship among the cuckoos until Seibel (1988) addressed the family in a cladistic analysis of postcranial osteological characters. Not surprisingly, his results did not entirely support traditional classifications of the group. Regrettably, this work remains in dissertation form only and, hence, has not received critical attention from the scientific community.

The consideration of behavior and ecology has often been used to evaluate the evolutionary relationships among birds (e.g. Whitman 1899, Heinroth 1911, Davis 1942, Mayr and Bond 1943, Tinbergen 1959, Strauch 1985, Prum and Johnson 1987, Prum 1990). More specifically, Baker (1927), Bannerman (1933), and Delacour (1947) suggested that the cuckoos could be subdivided based on their breeding habits. In addition, Delacour and Mayr (1946) noted that habitat use may be a valid systematic character for determining some degree of relationship within the family. In the present study, I use 28 behavioral and ecological characteristics to reconstruct the evolutionary relationships of the Cuculidae by phylogenetic systematics. The resulting topologies differ significantly from traditional classifications of the cuckoos in both placement and membership of subfamilies. Based my results and other evidence, I propose a new hypothesis for the evolution of brood parasitism in this taxon.

METHODS

Data.—Twenty-eight behavioral and ecological characters were used (see Appendix 1 for character descriptions). As suggested by De Queiroz and Wimberger (1993), behavioral characters were defined

TABLE 1. Classification of the Cuculiformes sensu Peters (1940). Obligately parasitic genera indicated with asterisk (*). Facultatively parasitic genus indicated with diamond ($\Diamond$).

Order Cuculiformes
Family Musophagidae
Family Cuculidae
Subfamily Cuculinae
Genus *Clamator**
Genus *Pachycoccyx**
Genus *Cuculus**
Genus *Cercococcyx**
Genus *Penthoceryx**
Genus *Cacomantis**
Genus *Rhamphomantis**
Genus *Misocalius**
Genus *Chrysococcyx**
Genus *Chalcites**
Genus *Caliechthrus**
Genus *Surniculus**
Genus *Microdynamis**
Genus *Eudynamys**
Genus *Urodynamis**
Genus *Scythrops**
Subfamily Phaenicophaeinae
Genus *Coccyzus*$\Diamond$
Genus *Hyetornis*
Genus *Piaya*
Genus *Saurothera*
Genus *Ceuthmochares*
Genus *Rhopodytes*
Genus *Taccocua*
Genus *Rhinortha*
Genus *Zanclostomus*
Genus *Rhamphococcyx*
Genus *Phaenicophaeus*
Genus *Dasylophus*
Genus *Lepidogrammus*
Subfamily Crotophaginae
Genus *Crotophaga*
Genus *Guira*
Subfamily Neomorphinae
Genus *Tapera**
Genus *Morococcyx*
Genus *Dromococcyx**
Genus *Geococcyx*
Genus *Neomorphus*
Genus *Carpococcyx*
Subfamily Couinae
Genus *Coua*
Subfamily Centropodinae
Genus *Centropus*

broadly as those representing movement of all or part of the external anatomy of the bird and, therefore, encompass a number of functional categories such as social interaction, courtship, nest building, egg laying, and incubation. Several ecological characters comprising diet and habitat use also were included. Data were collected for 38 genera of cuckoos, the turacos (Musophagidae), and the Hoatzin (*Opisthocomus hoatzin*) through an extensive literature search

TABLE 2. Data matrix of behavioral and ecological characters for Musophagidae, *Opisthocomus hoatzin*, and 21 genera of Cuculidae (see Appendix 2 for character definitions). Missing data indicated by "?". Genera marked with asterisks (*) are obligate parasites; genus marked with diamond (◊) is facultatively parasitic.

Taxon	Character																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Musophagidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opisthocomus	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
*Clamator**	0	1	1	1	1	1	1	1	1	1	0	3	3	1	0	1	1	1	3	1	0	0	1	0	0	0	1	0
*Pachycoccyx**	0	1	1	0	1	0	3	1	0	1	0	3	3	0	1	1	1	1	3	1	1	1	1	0	0	0	1	0
*Cuculus**	0	1	1	1	1	0	2	1	0	0	1	3	3	0	1	1	3	2	3	1	1	1	1	0	0	1	1	0
*Cacomantis**	0	1	1	1	0	0	1	1	0	?	?	3	3	0	1	1	2	1	3	1	1	1	0	0	0	1	1	0
*Chrysococcyx**	0	1	1	1	1	0	1	1	0	1	1	3	3	0	1	1	1	2	3	1	1	1	1	0	0	1	1	0
*Misocalius**	0	1	1	1	0	0	1	1	0	?	?	3	3	0	1	1	2	1	3	1	1	1	0	1	0	0	1	0
*Chalcites**	0	1	1	1	1	0	1	1	0	1	1	3	3	0	1	1	3	2	3	0	1	1	0	0	0	1	1	0
*Eudynamys**	0	1	0	1	0	0	0	1	?	0	0	3	3	1	0	1	1	1	3	1	1	0	0	0	0	0	1	0
*Scythrops**	0	1	0	1	0	0	0	1	0	?	?	3	3	0	0	1	1	1	3	1	1	0	0	0	0	0	1	0
Coccyzus◊	0	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	1	2	1	0	1	0	0	0	0	0	1	0
Piaya	0	1	2	0	0	1	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Saurothera	1	0	3	0	0	0	0	0	?	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crotophaga	0	0	2	0	0	2	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
Guira	0	0	2	0	1	2	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
*Tapera**	1	0	2	0	0	0	0	?	?	1	1	3	3	0	0	1	2	2	3	0	0	0	0	1	0	0	1	0
Morococcyx	1	0	2	0	0	0	0	?	?	0	?	1	2	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Neomorphus	1	0	3	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Geococcyx	1	0	3	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Carpococcyx	1	0	3	0	0	0	0	0	?	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Coua	1	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centropus	1	0	3	0	1	1	2	0	1	0	1	2	1	0	0	0	0	0	2	0	0	0	1	0	0	0	0	1

(Appendix 2). Many cuculid species demonstrate a high degree of endemism and often are secretive in nature. As a result, they may be poorly studied, and the available literature is lacking in accurate descriptions of their behavior and natural history. Therefore, as suggested by Prum (1990), I have deleted taxa for which there is insufficient information (considering 20% or more missing data adequate grounds for omission). This resulted in the exclusion of the following 17 genera; *Caliechthrus, Cercococcyx, Ceuthmochares, Dasylophus, Dromococcyx, Lepidogrammus, Microdynamis, Penthoceryx, Phaenicophaeus, Rhamphococcyx, Rhamphomantis, Rhinortha, Rhodopytes, Surniculus, Taccocua, Urodynamis,* and *Zanclostomus*. Despite the exclusion of these taxa, all six cuculid subfamilies recognized by Peters (1940) are represented in the analysis by at least three genera, except those which are monotypic (e.g. Centropodinae and Couinae) or ditypic (Crotophaginae).

The analysis included 20 binary characters and 8 nonadditive multistate characters (Table 2). Unknown characters for particular taxa were coded as missing (?). Coding inappropriate characters was problematic. Because many of the behaviors considered in my study are linked to breeding strategy, several were not applicable to either nonparasitic or parasitic genera. Wherever possible, characters were defined to avoid exclusion of genera solely due to breeding strategy (e.g. character 15 and 16). Inappro-

priate characters were coded in one of two ways according to Maddison (1993). Binary characters inappropriate to nonparasitic genera, such as laying mimetic eggs (character 20), were assigned the pleisomorphic state to restrain the algorithm from selecting a state applicable only to a parasitic genus. Multistate characters that were not applicable to both breeding strategies, such as host specialization (character 17) and nest architecture (character 12) were assigned an additional state (e.g. no host usage, does not build nest), that would allow the inclusion of all taxa.

Outgroups.—Characters were polarized into primitive and derived states through outgroup comparison with the turacos (Musophagidae) and the Hoatzin. The turacos traditionally have been considered the sister taxon to the Cuculidae (e.g. Pycraft 1903, Stegmann 1978, Cracraft 1981) and are commonly classified with the cuckoos in the Cuculiformes (e.g. Peters 1940, Howard and Moore 1991). However, DNA-DNA hybridization evidence of Sibley and Ahlquist (1990) suggests that these two taxa may not be one another's closest living relatives. Furthermore, they propose that the Hoatzin, often classified in the Galliformes (e.g. Stresemann 1934, Verheyen 1961, Cracraft 1981), is a cuckoo that is most closely related to the communally breeding anis (Crotophaginae; Sibley and Ahlquist 1972, 1973, 1990). This conclusion has been questioned by Bock (1992), who indicated that fundamental differences in foot morphology should ex-

clude the Hoatzin from the cuckoos. Although not unequivocal, the DNA sequencing results of Avise et al. (1994) suggest that the Hoatzin and the cuckoos may indeed be sister taxa, but do not support the inclusion of the Hoatzin within the small clade of seven cuckoos examined in their study. Despite the controversy, the alliance of the Hoatzin with the cuckoos in some capacity justifies its selection as an outgroup.

Phylogenetic analyses.—All phylogenetic analyses were performed using PAUP version 3.1 (Phylogenetic Analysis Using Parsimony; Swofford 1993) on an Apple Macintosh Quadra 660AV. An initial branch-and-bound search proved too time consuming. Therefore, I employed the heuristic-search option, as suggested by Swofford (1993) for use with data sets larger than 20 taxa and with moderate levels of homoplasy. To find the optimal tree, 36 heuristic searches were performed exhausting all possible combinations of the following search options: (1, optimization) accelerated transformation (ACCTRAN), delayed transformation (DELTRAN), and minimum *F*-value (MINF); (2, branch swapping) tree bisection-reconnection (TBR), subtree pruning-regrafting (SPR), and nearest-neighbor interchanges (NNI), and (3, stepwise addition sequence) simple, closest, as-is, and random with 10 replications. The MULPARS option was in effect. MAXTREES was set to 1,000 trees with automatic increase. Zero-length branches were collapsed to yield polytomies. The consistency index (*CI*), retention index (*RI*), and rescaled consistency index (*RC*) were calculated. Suboptimal trees were calculated by "keeping" all trees a specified number of steps longer than the minimum length tree.

Due to the distinct behavioral dimorphism of the Cuculidae (parasitic vs. nonparasitic genera), it was difficult to select and code enough characters independent of brood parasitism to produce well-resolved trees. Despite my efforts to avoid nonindependence, 12 characters remained in the initial analysis that were partially or fully dependent on parasitic behavior. Therefore, to verify that the resulting clades were not merely due to clustering of nonindependent characters, a second analysis (heuristic, ACCTRAN optimization, TBR branch swapping, and simple stepwise addition sequence) was performed including only those characters that were fully independent of brood parasitism (characters 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 23, 25, 26, 27, 28).

Finally, the behavioral and ecological data were compared to the postcranial osteological data of Seibel (1988). Taxa not included in both analyses were deleted from the data sets in order to facilitate comparison. Nine genera were removed from the osteological data matrix: *Ceuthmochares, Coccycua, Dromococcyx, Hyetornis, Penthoceryx, Phaenicophaeus, Rhinortha, Surniculus,* and *Urodynamis. Opisthocomus hoatzin* was deleted from the behavioral and ecological data set. Optimal trees for the osteological data were estimated using a heuristic search, ACCTRAN optimization, TBR

branch swapping, and simple stepwise addition. Following a visual comparison of the resulting trees, the behavioral and ecological data were constrainted on the optimal osteological trees to determine the number of additional steps required to reproduce the topologies. A total-evidence analysis (heuristic, ACCTRAN, TBR, simple stepwise addition) was performed by combining the osteological, behavioral, and ecological data (total = 76 characters). Since there were nearly twice as many osteological characters as there were behavioral and ecological characters included in this data set, the latter were given a weight of 2 to equalize the influence each type of data would have on the resulting topologies.

RESULTS

The phylogenetic analysis of behavioral and ecological characters yielded one shortest-length tree of 80 steps (*CI* = 0.52, *RI* = 0.79, *RC* = 0.42; Fig. 1). This tree resulted from 24 heuristic searches using all optimization and stepwise addition options with the TBR and SPR algorithms. Only four characters showed no homoplasy: characters 8 (sunbathing), 16 (>1 female), 27 (incubation period), and 28 (vocal duetting). Four characters had high levels of homoplasy, with consistency indices equal or
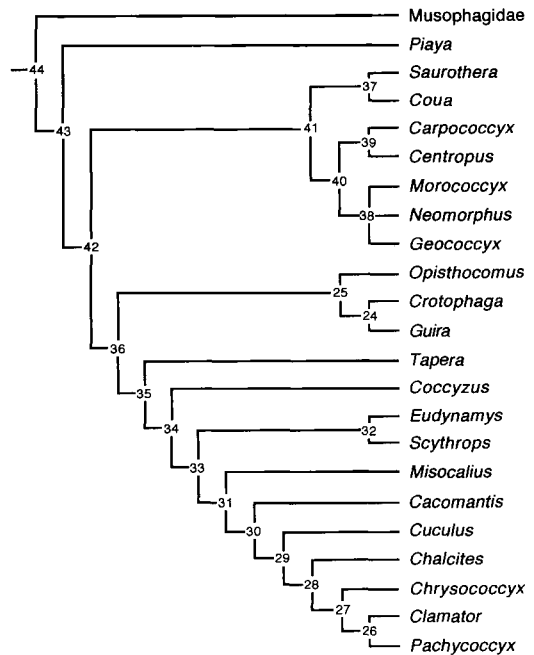

Fig. 1. Optimal tree based on behavioral and ecological data (*L* = 80 steps, *CI* = 0.52, *RI* = 0.79, *RC* = 0.42). Internal nodes are numbered. See Appendix 3 for character-change list corresponding to internal nodes.

less than 0.33: characters 5 (pair bond), 9 (allopreening), 11 (song posts), and 21 (egg removal). See Appendix 3 for a character-change list, as well as character consistency and retention indices. The heuristic NNI algorithm found the optimal tree (MIN-F, random), as well as eight trees of 81 steps ($CI = 0.52$, $RI = 0.79$, $RC = 0.41$) that differed only in the arrangement of taxa within the major clade of parasitic cuckoos (*Clamator*, *Pachycoccyx*, *Cuculus*, *Cacomantis*, *Chrysococcyx*, *Chalcites*, and *Misocalius*).

The trees based on behavioral and ecological characters differ significantly from traditional classifications of the cuckoos. Most importantly, two cuculid subfamilies sensu Peters (1940) were severed. The Neomorphinae (previously comprised of *Geococcyx*, *Neomorphus*, *Carpococcyx*, *Morococcyx*, *Dromococcyx*, and *Tapera*) was divided into two groups. *Morococcyx*, *Geococcyx*, and *Neomorphus* form a clade with *Centropus* and *Carpococcyx*. However, the neomorphine obligate brood parasite *Tapera* is positioned basally in a clade comprised of the obligately parasitic Cuculinae and the facultative-parasitic genus *Coccyzus*. Five additional steps would be required to unite *Tapera* with the nonparasitic neomorphine clade. This suggests that terrestrial habitat use by *Tapera* has evolved secondarily.

The Phaenicophaeinae, represented in my analysis by *Saurothera*, *Coccyzus*, and *Piaya*, has been partitioned into three parts. *Saurothera* forms a clade with *Coua* that is the sister group to the nonparasitic neomorphine cuckoos and *Centropus*. *Coccyzus* is clustered among the parasitic Cuculinae. *Piaya* occupies the basal position on the trees. Seven and 10 additional steps are needed to join *Coccyzus* with the other phaenicophaeine cuckoos, *Piaya* and *Saurothera*, respectively. If these topologies are accepted, the Neomorphinae and Phaenicophaeinae sensu Peters (1940) are not monophyletic.

In addition, my results suggest that brood parasitism evolved only once in the cuckoos, rather than three times as advocated by traditional classifications. In my analysis, the *Tapera*-*Coccyzus*-Cuculinae clade is the best supported clade, being united by six character-state changes on the optimal tree. All suboptimal trees examined—one step longer (81 steps; $n = 22$) and two steps longer (82 steps; $n = 359$) than the shortest tree—supported the position of *Coccyzus* and *Tapera* among the Cuculinae, despite the loss of resolution within the cuculine clade

itself. The position of the facultative parasite *Coccyzus* within a clade of obligate parasites implies that this genus is exhibiting a loss of obligate parasitism. Three additional steps would be required to reverse the positions of *Coccyzus* and *Tapera*; a topology that would support the hypothesis that facultative parasitism represents an intermediate stage in the evolution of obligate brood parasitism in the cuckoos.

The results of my second analysis, including only those characters independent of brood parasitism, upheld the strength of the *Tapera*-*Coccyzus*-Cuculinae clade. As in the first analysis, *Coccyzus* clustered among the obligate parasites when 12 characters partially or fully dependent on brood parasitism were deleted from the data set (16 trees of 42 steps; $CI = 0.50$, $RI = 0.78$, $RC = 0.39$). *Tapera* occupied a position at the base of the neomorphine-*Saurothera*-*Coua* clade on all shortest-length trees, but could be returned to its basal position in the Cuculinae with the addition of only one step. By deleting character 1 (generalized habitat use), the primary characteristic traditionally used to define the neomorphine cuckoos, *Tapera* resumed its position in the Cuculinae (156 trees of 40 steps; $CI = 0.50$, $RI = 0.77$, $RC = 0.39$) as depicted on the optimal tree.

On the shortest-length tree ($L = 80$ steps), the Hoatzin is the sister taxon to the crotophagine cuckoos, *Crotophaga* and *Guira*, despite its selection as an outgroup. This position is maintained on 17 of 22 suboptimal trees with a length of 81 steps. The remaining five trees place the Hoatzin as sister taxon to a clade containing the crotophagine and cuculine cuckoos. Two additional steps are required to constrain the Hoatzin to the outgroup. Deleting the Hoatzin from the analysis, using only the Musophagidae as the outgroup taxon, does not change the overall topology of optimal trees (three trees of 79 steps; $CI = 0.53$, $RI = 0.78$, $RC = 0.42$). However, there is a minimal loss of resolution within neomorphine cuckoos. Using the Hoatzin as the sole outgroup does not alter relationships within the major clades, but merely causes the crotophagine cuckoos to become the basal clade on the shortest-length topologies (12 trees of 79 steps; $CI = 0.53$, $RI = 0.79$, $RC = 0.42$).

The heuristic reanalysis of Seibel's (1988) 48 postcranial osteology characters resulted in 16 equally parsimonius trees that varied primarily in the arrangement of genera within the Cuculinae ($L = 66$, $CI = 0.86$, $RI = 0.94$, $RC = 0.81$).
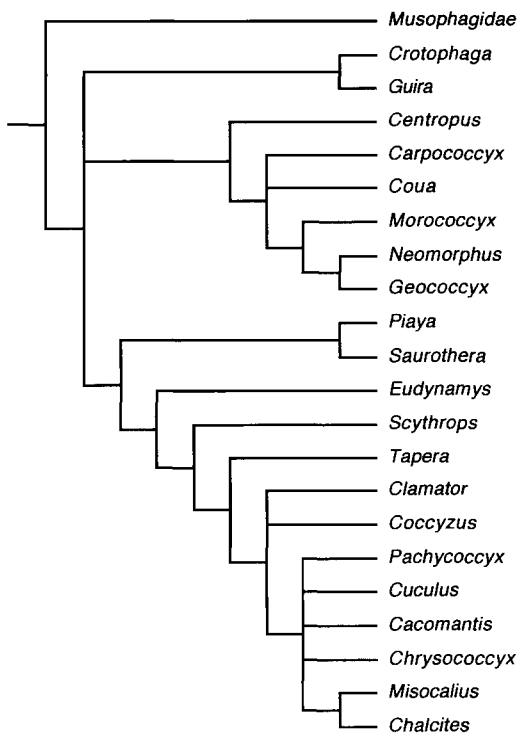
Fig. 2. Strict-consensus tree of 16 equally parsimonius trees based on postcranial osteological characters (after Seibel 1988; $L = 66$, $CI = 0.86$, $RI = 0.94$, $RC = 0.81$).
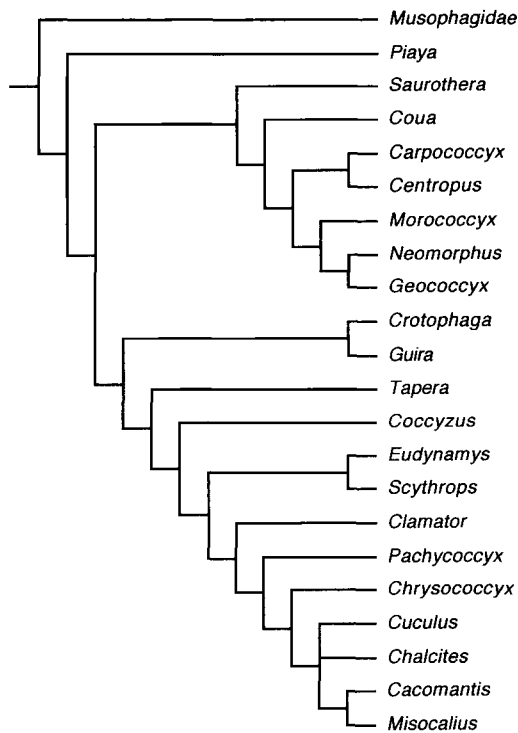
Fig. 3. Strict-consensus tree of three equally parsimonius trees based on combined osteological, behavioral and ecological data ($CI = 0.63$, $RI = 0.82$, $RC = 0.52$).

Figure 2 illustrates a strict-consensus tree of the resulting topologies. Perhaps the most striking similarity between Seibel's trees and those derived from the behavioral and ecological data is the placement of *Coccyzus* and *Tapera* within the Cuculinae. Also of importance is the inclusion of *Centropus* and *Coua* in the clade containing the neomorphine cuckoos. In traditional classifications, both *Centropus* and *Coua* form monotypic subfamilies (see Table 1). Forcing the behavioral and ecological characters onto the topology of Seibel's optimal trees requires 19 additional steps. However, 12 of these additional steps serve merely to provide resolution within the cuculine and neomorphine clades that may not be present in the behavioral data if suboptimal trees ($L = 81$ steps) are examined. Combining the behavioral and ecological data with the osteological data resulted in three equally parsimonius trees ($CI = 0.63$, $RI = 0.82$, $RC = 0.52$). Although, the CI, RI and RC for the combined data was lower than that of the osteological data alone, the addition of the

behavioral and ecological characters to Seibel's data provided more resolution within the cuculine and neomorphine clades. A strict-consensus tree for the combined data is illustrated in Figure 3.

DISCUSSION

The classification of the Cuculidae has remained virtually unchanged for decades, with taxonomies based on Peters (1940) still being widely accepted. However, the advent of phylogenetic systematics has allowed the reconstruction of phylogenies using a robust methodology unavailable to systematists like Peters and others. Therefore, it is imperative that it be used not only in the reevaluation of traditional classifications, but also in the proposal of new hypotheses of evolution (Brooks and McLennan 1991, Harvey and Pagel 1991). My reconstruction of the phylogeny of the cuckoos differs from many traditional classifications in two fundamental ways—the polyphyly of the Neomorphinae and of the Phaenicophaeinae.

The Neomorphinae.—Traditionally, the Neomorphinae are comprised of five genera of New World cuckoos and one genus of Old World cuckoos (Peters 1940; see Table 1), and contains both parasitic and nonparasitic species. Although this diverse subfamily differs significantly in life history and external morphology, in the past they have been grouped due to their distribution and their terrestrial habits (Berger 1960). Based on my results, I recommend the partitioning of the Neomorphinae into two groups. The subfamily Neomorphinae should be comprised of the traditional nonparasitic neomorphine genera *Carpococcyx, Geococcyx, Morococcyx, Neomorphus* plus *Centropus*. The position of *Coua* is less clear. Paired with *Saurothera*, it may represent the sister taxon to the Neomorphinae (Fig. 1). Alternatively, it could be included within the Neomorphinae (Figs. 2 and 3). The obligate parasite *Tapera* should be moved to the Cuculinae, the large subfamily that includes all 47 species of parasitic Old World cuckoos. *Dromococcyx*, another genus of parasitic New World cuckoos, traditionally seen as the sister genus of *Tapera* (e.g. Sclater and Salvin 1873, Shelley 1891, Verheyen 1956a), also should be included in the Cuculinae based on the postcranial osteological characters it shares with that group (Seibel 1988). This removal of *Tapera* and *Dromococcyx* from the Neomorphinae suggests that obligate brood parasitism arose only once among the Cuculidae rather than twice as proposed by Peters (1940). In addition, the polyphyly of the Neomorphinae demonstrates that terrestrial habitat use is a derived state among the cuckoos that has evolved at least twice in the family.

These modifications to the classification of the neomorphine cuckoos are supported in part by the literature. Prior to Peters (1940), many systematists had suggested the severance of the parasitic neomorphine cuckoos from the remainder of the group (Linnaeus 1766, Sclater and Salvin 1873, Beddard 1885, Shelley 1891, Gadow and Selenka 1891). Beddard (1885) and Gadow and Selenka (1891) classified *Tapera* as being within the Cuculinae based on musculature, pterylosis, and configuration of the syrinx. More recently, Verheyen (1956a) recognized a number of anatomical differences between parasitic and nonparasitic neomorphine cuckoos and, as a result, erected a new subfamily to contain *Tapera* and *Dromococcyx*. Berger (1960) found the appendicular muscles of *Tap-*

era to be unlike that of *Geococcyx, Morococcyx,* and *Carpococcyx.* In addition, Seibel (1988) found that *Tapera* and *Dromococcyx* differed from the nonparasitic neomorphine genera in 21 of 48 postcranial osteological characters.

Upon examining nonparasitic terrestrial cuckoos, Shufeldt (1886) placed *Geococcyx* and *Centropus* in the same subfamily based on anatomical characters. Berger (1960) noted similarities in the internal anatomy of *Morococcyx* and *Coua.* Although *Coua* traditionally has occupied a monotypic subfamily, Berger (1960) found little reason for this, suggesting such a designation likely was due to the restriction of the nine-species genus to Madagascar. Seibel's (1988) revised classification of the Cuculidae presented a new clade, Branch Centropodes, comprised of *Centropus, Coua* and the nonparasitic neomorphine cuckoos. Shelley (1891) placed *Coua* and *Saurothera* in the same subfamily.

The Phaenicophaeinae.—Peters (1940) was dissatisfied with his classification of the Phaenicophaeinae, calling it a "catch-all" (Berger 1960: 94) for genera that could not be allocated into other subfamilies. This is evidenced by the high morphological, behavioral, and distributional diversity among this group of Old World and New World cuckoos. In a study of nine phaenicophaeine genera, Berger (1960) found significant differences in pterylosis, appendicular muscular, and skeletal elements. Based on my analysis, I suggest the subdividing of Peters' Phaenicophaeinae into at least two groups by transferring *Coccyzus* to the Cuculinae.

In the past, *Coccyzus* was classified in the Phaenicophaeinae primarily on the basis of external morphology, distribution, and nonobligate parasitic nesting habits. However, many systematists have questioned this association. Beddard (1885) placed both *Coccyzus* and *Piaya* in the Cuculinae based on similarities in syrinx, musculature, and pterylosis. Shufeldt (1886) and Shelley (1891) also supported the inclusion of *Coccyzus* in the Cuculinae. Pycraft (1903) grouped *Coccyzus* with the obligately parasitic *Cuculus, Eudynamys,* and *Scythrops* based on his study of sternum configuration and appendicular musculature. In reviewing the musculature of *Coccyzus,* Berger (1952) concluded that this genus should not be included in the Phaenicophaeinae. Verheyen (1956a) erected a new subfamily for *Coccyzus* and two genera of obligately parasitic cuckoos (*Clamator* and *Pachycoccyx*), raising the parasitic cuckoos to the rank

of suborder based on similarities in their anatomy. Seibel (1988) found that *Coccyzus* differed from other phaenicophaeinae cuckoos by as many as 11 osteological characters.

The evolution of brood parasitism in the cuckoos. — The placement of *Coccyzus* and *Tapera* within a clade of obligate parasites suggests a new hypothesis for the evolution of brood parasitism in the Cuculidae. In traditional classifications, parasitism was thought to have evolved three times: obligate parasitism in the Neomorphinae and Cuculinae, and facultative parasitism in the Phaenicophaeinae. This in itself is counterintuitive since it is unlikely that so rare a behavior would originate many times in one family. Only about 1% of all avian species are obligate parasites (Payne 1977). If the conclusions of my analysis are accepted, the facultative parasite *Coccyzus* shared an ancestor with the Cuculinae that was an obligate parasite and, therefore, must be demonstrating a loss of obligately parasitic habits rather than de novo development of parasitism from a nonparasitic ancestor. Several studies have illustrated the propensity of *Coccyzus* for occasional intraspecific and interspecific parasitism (Nolan and Thompson 1975, Ralph 1975, Fleischer et al. 1985, Sick 1993). Although their most common hosts are conspecific or congeneric, the Yellow-billed Cuckoo (*Coccyzus americanus*) and the Black-billed Cuckoo (*C. erythropthalmus*) have parasitized at least 13 species of North American birds, including the American Robin (*Turdus migratorius*), Northern Cardinal (*Cardinalus cardinalis*), Gray Catbird (*Dumetella carolinensis*), and Wood Thrush (*Hylocichla mustelina*; Darwin 1859, Attwater 1892, McIlwraith 1894, Bendire 1895, Herrick 1910, Forbush 1927, Bent 1940, Sprunt and Chamberlain 1949, Nolan and Thompson 1975).

Unlike nonparasitic cuckoos, *Coccyzus* shares many life-history traits with the obligate parasites of the Cuculinae that are adaptive to a parasitic lifestyle. Kendeigh (1952), after Herrick (1910), noted that some cuckoos exhibited a characteristic "disassociation" of egg laying from the "normal" nesting sequence of courtship, nest building, egg laying, incubation, and care of young. In *Coccyzus*, this disassociation is manifested in the laying of eggs at irregular intervals, or before the nest is completed (Spencer 1943, Ralph 1975, Potter 1980). Like the obligate parasites, *Coccyzus* has an extremely short incubation period of 10 or 11 days (Spencer

1943, Hamilton and Hamilton 1965). This generally is considered to be an adaptation for successful parasitism since it allows the parasitic chick to hatch first and, therefore, gain a size advantage over the host young (Hamilton and Orians 1965, Payne 1977). Consequently, parasitic cuckoos have incubation periods between 10 and 15 days, with nonparasitic cuckoos having incubation periods greater than 15 days. Also, *Coccyzus* chicks have a very short nestling period of only seven to nine days. In contrast, the nestlings of many nonparasitic cuckoos fledge after about 18 to 20 days in the nest (Wyllie 1981). Although early fledging likely would reduce survival in a nonparasitic species, it could increase survival in a nestling that is being cared for by host parents, since it lessens the time during which recognition and rejection of the foreign offspring may occur. In addition, many parasitic species breed later in the season than nonparasites presumably to ensure a supply of clutches in varying stages of incubation in which to deposit an egg without detection (Hamilton and Orians 1965). Late breeding may also add stability to the parasite-host relationship by allowing the host to successfully raise their first brood unaffected by parasitism (May and Robinson 1985). Although the North American species of *Coccyzus* winter in the tropics, their breeding season does not generally begin until June and extends into September (Nolan and Thompson 1975, Cadman et al. 1987), long after many migratory species have departed the breeding grounds. In addition, the obligate parasites exhibit a constant readiness to breed (within season) to exogeneous stimuli, such as host availability. Similarly, the onset of breeding in *Coccyzus* appears to be regulated externally by resource availability rather than by endogeneous cues (Hamilton and Hamilton 1965, Ralph 1975). In parasitic cuckoos, egg mimicry is a common adaptation to host defenses. When parasitizing interspecifically, *Coccyzus* spp. may lay mimetic eggs (unpubl. data). Since it is unlikely that egg mimicry would evolve in a generally nonparasitic species that only rarely lays its eggs in other birds' nests (Davies and Brooke 1988, 1989, Rothstein 1990), egg mimicry by *Coccyzus* could be an artifact of an intense, and perhaps obligate, relationship that once existed between these parasites and their hosts. Therefore, these life-history traits that *Coccyzus* shares with the Cuculinae are not preadaptations to a future obligately parasitic life style (Hamilton

and Orians 1965), but the selectively neutral artifacts of an ancestral breeding strategy.

The Hoatzin.—The taxonomic position of the Hoatzin has perplexed systematists for more than two centuries. In an excellent review of its classification, Sibley and Ahlquist (1990) noted that the systematists had allied the Hoatzin with the Galliformes in 17, the turacos in 4, and the cuckoos in 8 classifications. In addition, the Hoatzin has been placed in a monotypic order 12 times. They suggested that many studies classifying the Hoatzin with the Galliformes have been biased by the original description of the species (Müller 1776) and the blind adherence to tradition by the systematists that followed (e.g. Huxley 1867, Gadow 1893, Peters 1934, Howard 1950, Cracraft 1981). However, in the past 40 years, several molecular and morphological studies have placed the Hoatzin outside of the Galliformes (Verheyen 1956b, Hudson et al. 1959, Streseman 1965, Sibley and Ahlquist 1972, 1973, 1990, De Queiroz and Good 1988). Like Sibley and Ahlquist (1972, 1973, 1990), my results include the Hoatzin in a clade with the communally breeding crotophagine cuckoos (*Crotophaga* and *Guira*). Beebe (1909) and others have noted the behavioral similarities between the Hoatzin and the Crotophaginae. Although my results support the Hoatzin's inclusion in the Cuculidae, it is possible that the characters aligning the Hoatzin with the cuckoos may be convergent adaptations to communal breeding rather than synapomorphies of the clade. Further molecular and morphological analyses are needed to resolve this enigma.

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APPENDIX 2. Behavioral and ecological character descriptions.

1. Generalized habitat use: (0) arboreal; (1) terrestrial. **2. Flying ability:** (0) weak flyer; (1) strong flyer. **3. Primary diet:** (0) fruits and foliage; (1) primarily caterpillars; (2) insects and other arthropods; (3) invertebrates and vertebrates. **4. Migration:** (0) sedentary; (1) migratory. **5. Pair bond:** (0) monogamous; (1) some polygamy or promiscuity. **6. Degree of social interaction during breeding season:** (0) solitary; (1) small flocks; (2) gregarious. **7. Territoriality during breeding season:** (0) territory defended by both; (1) territory defended predominantly by male; (2) territory defended predominantly by female; (3) not territorial. **8. Adults sunbathe by dropping wings and exposing back to sun:** (0) yes; (1) no. **9. Allopreening in mated pair during courtship:** (0) no; (1) yes. **10. Ritualized display flights by male or female during courtship:** (0) no; (1) yes. **11. Male or female call from song posts during courtship:** (0) no; (1) yes. **12. Nest architecture:** (0) poorly constructed saucerlike platform; (1) open cup; (2) well constructed enclosed dome; (3) does not build nest. **13. Nest location:** (0) placed in trees above 4 m; (1) placed in shrubs, bushes or grass between 1–4 m; (2) placed on or near ground; (3) does not build nest. **14. Parasitic male lures host female away from nest prior to parasitic egg deposition by mate:** (0) no; (1) yes. **15. Individual females lay more than one egg in nest:** (0) yes; (1) no. **16. Eggs laid in nest by more than one female:** (0) no; (1) yes. **17. Degree of host specialization:** (0) no host usage; (1) specific-host specialists; (2) generalist; (3) individual-host specialists. **18. Color of egg:** (0) monomorphic, immaculate white; (1) monomorphic nonwhite, or white with markings; (2) polymorphic within a species. **19. Sex incubating eggs:** (0) both; (1) predominantly female; (2) predominantly male; (3) does not incubate. **20. Parasitic female lays egg that mimics host egg:** (0) no; (1) yes. **21. Removal of egg from nest by adult:** (0) no; (1) yes. **22. Removal of eggs and/or young from nest by juvenile:** (0) no; (1) yes. **23. Chick excretes foul-smelling liquid from cloaca when disturbed:** (0) no; (1) yes. **24. Adult bird feeds fledglings:** (0) yes; (1) no. **25. Adult produces bill-clacking vocalization by snapping mandibles together:** (0) no; (1) yes. **26. Adults participate in mixed-species-flock feeding:** (0) no; (1) yes. **27. Incubation period:** more than 15 days (0); 15 days or less (1). **28. Mated pair participates in vocal duetting:** (0) no; (1) yes.

APPENDIX 3. Character-change list for behavioral and ecological characters on shortest-length tree (Fig. 1). Double-lined arrows indicate that changes occurred on all possible reconstructions. Single-lined arrows indicate that changes occurs only under some reconstructions. CI = consistency index. RI = retention index.

Character 1 ($CI = 0.50$; $RI = 0.86$) 0 [node 35] $\Rightarrow$ 1 [node $Tapera$]; 0 [node 42] $\Rightarrow$ 1 [node 41]. **Character 2** ($CI = 0.50$; $RI = 0.90$) 0 [node 35] $\Rightarrow$ 1 [node 34]; 0 [node 43] $\Rightarrow$ 1 [$Piaya$]. **Character 3** ($CI = 0.50$; $RI = 0.75$) 0 [node 44] $\rightarrow$ 2 [node 43]; 2 [node 25] $\Rightarrow$ 0 [$Opisthocomus$]; 2 [node 35] $\Rightarrow$ 1 [node 34]; 1 [node 33] $\Rightarrow$ 0 [node 32]; 2 [node 42] $\Rightarrow$ 3 [node 41]; 3 [node 38] $\Rightarrow$ 2 [$Morococcyx$]. **Character 4** ($CI = 0.50$; $RI = 0.88$) 0 [node 35] $\Rightarrow$ 1 [node 34]; 1 [node 26] $\Rightarrow$ 0 [$Pachycoccyx$]. **Character 5** ($CI = 0.25$; $RI = 0.57$) 0 [node 24] $\Rightarrow$ 1 [$Guira$]; 0 [node 30] $\Rightarrow$ 1 [node 29]; 0 [node 34] $\Rightarrow$ 1 [$Coccyzus$]; 0 [node 39] $\Rightarrow$ 1 [$Centropus$]. **Character 6** ($CI = 0.50$; $RI = 0.60$) 1 [node 43] $\Rightarrow$ 0 [node 42]; 0 [node 36] $\Rightarrow$ 2 [node 25]; 0 [node 26] $\Rightarrow$ 1 [$Clamator$]; 0 [node 39] $\Rightarrow$ 1 [$Centropus$]. **Character 7** ($CI = 0.60$; $RI = 0.50$) 0 [node 33] $\rightarrow$ 1 [node 31]; 1 [node 26] $\Rightarrow$ 3 [$Pachycoccyx$]; 1 [node 29] $\rightarrow$ 2 [$Cuculus$]; 1 [node 30] $\rightarrow$ 0 [$Cacomantis$]; 0 [node 39] $\Rightarrow$ 2 [$Centropus$]. **Character 8** ($CI = 100$; $RI = 100$) 0 [node 34] $\Rightarrow$ 1 [node 33]. **Character 9** ($CI = 0.33$; $RI = 0.33$) 0 [node 25] $\Rightarrow$ 1 [node 24]; 0 [node 26] $\Rightarrow$ 1 [$Clamator$]; 0 [node 40] $\rightarrow$ 1 [node 39]. **Character 10** ($CI = 0.50$; $RI = 0.75$) 0 [node 29] $\Rightarrow$ 1 [node 28]; 0 [node 35] $\Rightarrow$ 1 [$Tapera$]. **Character 11** ($CI = 0.25$; $RI = 0.57$) 0 [node 36] $\Rightarrow$ 1 [node 35]; 1 [node 27] $\Rightarrow$ 0 [node 26]; 1 [node 33] $\Rightarrow$ 0 [node 32]; 0 [node 41] $\Rightarrow$ 1 [node 40]. **Character 12** ($CI = 0.50$; $RI = 0.75$) 0 [node 26] $\Rightarrow$ 1 [node 24]; 0 [node 36] $\rightarrow$ 3 [node 35]; 3 [node 34] $\rightarrow$ 0 [$Coccyzus$]; 0 [node 41] $\Rightarrow$ 1 [node 37]; 0 [node 38] $\Rightarrow$ 1 [$Morococcyx$]; 0 [node 39] $\Rightarrow$ 2 [$Centropus$]. **Character 13** ($CI = 0.60$; $RI = 0.80$) 0 [node 36] $\Rightarrow$ 3 [node 35]; 3 [node 34] $\Rightarrow$ 1 [$Coccyzus$]; 0 [node 41] $\Rightarrow$ 1 [node 40]; 1 [node 38] $\Rightarrow$ 2 [$Morococcyx$]; 0 [node 43] $\Rightarrow$ 1 [$Piaya$]. **Character 14** ($CI = 0.50$; $RI = 0$) 0 [node 28] $\rightarrow$ 1 [$Clamator$]; 0 [node 42] $\Rightarrow$ 1 [$Eudynamys$]. **Character 15** ($CI = 0.50$; $RI = 0.80$) 0 [node 33] $\Rightarrow$ 1 [node 31]; 1 [node 26] $\Rightarrow$ 0 [$Clamator$]. **Character 16** ($CI = 100$; $RI = 100$) 0 [node 42] $\Rightarrow$ 1 [node 36]. **Character 17** ($CI = 0.75$; $RI = 0.88$) 0 [node 36] $\Rightarrow$ 2 [node 35]; 2 [node 30] $\Rightarrow$ 3 [node 29]; 3[node 28] $\Rightarrow$ 1 [node 27]; 2 [node 33] $\Rightarrow$ 1 [node 32]. **Character 18** ($CI = 0.50$; $RI = 0.83$) 0 [node 42] $\Rightarrow$ 1 [node 36]; 1 [node 31] $\Rightarrow$ 2 [node 30]; 2 [node 27] $\Rightarrow$ 1 [node 26]; 1 [node 35] $\Rightarrow$ 2 [$Tapera$]. **Character 19** ($CI = 0.75$; $RI = 0.90$) 0 [node 36] $\rightarrow$ 3 [node 35]; 3 [node 34] $\rightarrow$ 0 [$Coccyzus$]; 0 [node 41] $\Rightarrow$ 1 [node 38]; 0 [node 39] $\Rightarrow$ 2 [$Centropus$]. **Character 20** ($CI = 0.50$; $RI = 0.88$) 0 [node 35] $\Rightarrow$ 1 [node 34]; 1 [node 28] $\Rightarrow$ 0 [$Chalcites$]. **Character 21** ($CI = 0.33$; $RI = 0.78$) 0 [node 25] $\Rightarrow$ 1 [node 24]; 0 [node 34] $\Rightarrow$ 1 [node 33]; 1 [node 26] $\Rightarrow$ 0 [$Clamator$]. **Character 22** ($CI = 0.50$; $RI = 0.80$) 0 [node 33] $\Rightarrow$ 1 [node 31]; 1 [node 26] $\Rightarrow$ 0 [$Clamator$]. **Character 23** ($CI = 0.50$; $RI = 0.67$) 0 [node 28] $\Rightarrow$ 1 [node 27]; 0 [node 39] $\Rightarrow$ 1 [$Centropus$]. **Character 24** ($CI = 0.50$; $RI = 0$) 0 [node 31] $\Rightarrow$ 1 [$Misocalius$]; 0 [node 35] $\Rightarrow$ 1 [$Tapera$]. **Character 25** ($CI = 0.50$; $RI = 0.67$) 0 [node 40] $\Rightarrow$ 1 [node 38]; 0 [node 43] $\Rightarrow$ 1 [$Piaya$]. **Character 26** ($CI = 0.50$; $RI = 0.67$) 0 [node 31] $\Rightarrow$ 1 [node 30]; 1 [node 27] $\Rightarrow$ 0 [node 26]. **Character 27** ($CI = 100$; $RI = 100$) 0 [node 36] $\Rightarrow$ 1 [node 39]. **Character 28** ($CI = 100$; $RI = 100$) 0 [node 40] $\Rightarrow$ 1 [node 39].