Article

Patterns of morphological and genetic variation in the *Mentocrex kioloides* complex (Aves: Gruiformes: Rallidae) from Madagascar, with the description of a new species

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Abstract

We examine patterns of morphological and molecular genetic differentiation in the endemic *Mentocrex kioloides* complex of Madagascar. This forest-dwelling rail (often placed in *Canirallus*) is known from two subspecies: *M. k. kioloides*, which occurs in the island's humid central and eastern forests; and *M. k. berliozi*, which occurs in the transitional dry deciduous-humid forests of the northwest. Two new specimens (an adult and a downy young) recently became available from lime-stone karst areas of the lowland central west, the adult of which is notably different in size and plumage coloration, as well as showing considerable genetic divergence, from the two recognized subspecies of *M. kioloides*. The central west animals are herein named as a species new to science, *Mentocrex beankaensis*, **sp. nov.**

Key words: Madagascar Wood Rail, Beanka Massif, *tsingy* forest

Résumé

Les différences morphologiques et génétiques entre les individus appartenant au complexe *Mentocrex kioloides*, endémique de Madagascar ont été examinées. Cette espèce forestière de râle était jadis séparée en deux sous-espèces: *M. k. kioloides* se rencontrant dans les forêts humides du Centre et de l'Est et *M. k. berliozi* dans la forêt de transition entre la forêt sèche caducifoliée et la forêt humide du Nord-ouest. De nouveaux spécimens, provenant des zones karstiques des plaines du Centre-ouest devenus récemment disponibles, montrent des différences de taille et de coloration du plumage. En outre, ils se distinguent par une divergence génétique considérable par rapport aux deux sous-espèces connues de *M. kioloides*. Les individus du Centre-ouest sont ici désignés comme une nouvelle espèce pour la science, *Mentocrex beankaensis*, **sp**. **nov**.

Introduction

The past few decades have seen considerable advances in knowledge of the highly endemic avifauna of Madagascar (Goodman & Hawkins 2008). Systematic advances include resolution of certain higher-level taxonomic questions and, to a lesser extent, refinements at the species level (Johnson *et al*. 2000; Cibois *et al*. 2001; Kirchman *et al*. 2001; Sorensen & Payne 2005). Numerous questions remain concerning intra-specific relationships of endemic taxa, and only a few studies using molecular genetics have examined patterns of geographic variation (e.g. Goodman *et al*. 2001; Goodman & Weigt 2002; Fuchs *et al*. 2007).

The Madagascar Wood Rail, *Mentocrex kioloides* (Pucheran) is a relatively poorly known endemic Malagasy forest-dwelling species. The nominate form of this highly secretive terrestrial bird is widely distributed across the

eastern humid forest from near sea level to 2,000 m (Rand 1936; Morris & Hawkins 1998). A second subspecies, *M. k. berliozi* (Salomonsen), occurs in lowland transitional humid-dry deciduous forest in the northwestern portion of the island (Salomonsen 1934), within a zone known as the Sambirano (Gautier & Goodman 2008). The principal differences between these geographical forms include plumage coloration and, to a lesser extent, external measurements (Langrand 1990; Taylor 1996; Morris & Hawkins 1998). Subsequently, birds referred to *M. kioloides* were found in the limestone karst formation of Bemaraha, in the central west (e.g., Nicoll & Langrand 1989; Langrand 1990; Bousquet & Rabetaliana 1992; Ramanitra 1997), a considerable distance from other known populations of *Mentocrex* (Fig. 1). As the Bemaraha population is distinctly colored, some authors have suggested it may be an undescribed subspecies (Morris & Hawkins 1998; Taylor 1996) or even a new species (Fishpool & Evans 2001; Brede *et al*. 2010). Until now, it has not been possible to resolve this question, as no specimens were available. We recently obtained material of *Mentocrex* from central western Madagascar, and herein use morphology and molecular genetics to resolve the taxonomic status of this population and patterns of geographic variation within *Mentocrex*, a genus endemic to Madagascar.
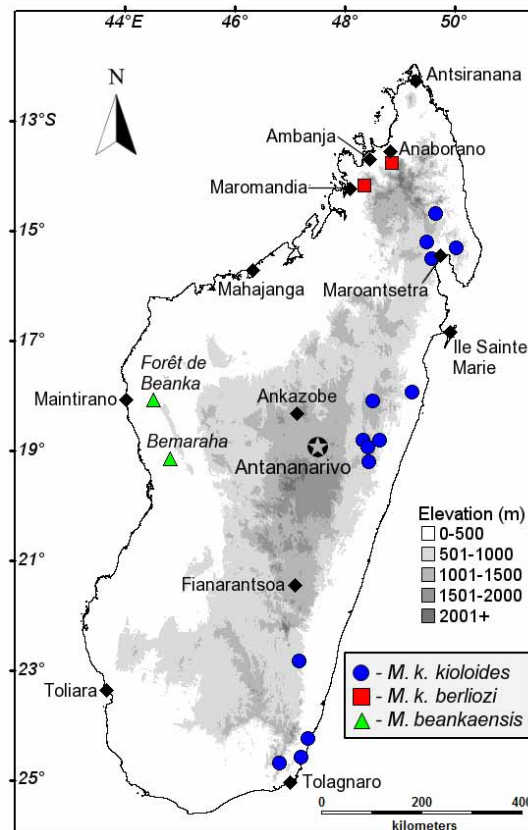

FIGURE 1. Map showing the distribution of *Mentocrex beankaensis*, **sp. nov.**, *M. k. kioloides* and *M. k. berliozi* based on specimen records. Sites mentioned in the text and other localities are also shown.

Material and methods

Morphology. We measured museum specimens (Table 1, Appendix 1) following the techniques described by Baldwin *et al*. (1931). Specimens were examined from the following museums: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); Muséum national d'Histoire naturelle, Paris (MNHN); The Natural History Museum, Tring, formerly British Museum (Natural History) [BMNH]; and Département de Biologie Animale, Université d'Antananarivo (UADBA). Color terminology (first letters capitalized) and codes (in parentheses) follow Smithe (1976).

    Generic designation. We follow Peters (1934), Olson (1973), and others, in placing members of the *kioloides* complex in the endemic Malagasy genus *Mentocrex,* rather than in the Afrotropical genus *Canirallus*.

TABLE 1. Descriptive statistics of external measurements (in mm) of *Mentocrex* from different portions of Madagascar. Samples are presented as mean ± standard deviation (minimum-maximum, sample size). For each geographic zone, t-tests were conducted to examine patterns of sexual dimorphism.

Region	Sex	Wing (flattened)	Tail length	Tarsus length	Exposed culmen	Bill from anterior nostril	Bill width at anterior nostril
Beanka (*M. beankaensis* **sp. nov.**, [UADBA 48179])	♂	142	65	46.1	27.1	17.0	4.6
Region of Maroantsetra in NE (*M. k. kioloides*)	♂♂	131.8 ± 3.08 (126–137, n=22)	56.1 ± 2.33 (52–61, n=20)	42.6 ± 1.80 (38.3–45.6, n=19)	26.4 ± 1.49 (24.2–30.1, n=22)	16.8 ± 0.97 (15.2–18.9, n=23)	4.3 ± 0.28 (4.0–5.0, n=22)
	♀♀	131.7 ± 1.41 (129–134, n=9) n.s.	55.5 ± 2.32 (52–59, n=8) n.s.	40.4 ± 1.12 (38.7–42.6, n=9) t=3.28, p=0.002	24.4 ± 1.49 (21.6–26.2, n=8) t=3.01, p=0.005	15.7 ± 0.52 (14.7–16.7, n=8) t=3.08, p=0.005	4.2 ± 0.29 (3.9–4.7, n=8) n.s.
Across the eastern humid forest (*M. k. kioloides*)	♂♂	132.2 ± 2.95 (126–137, n=30)	55.5 ± 2.46 (50–61, n=29)	42.1 ± 1.96 (37.9–45.6, n=28)	26.1 ± 1.45 (24.0–30.1, n=29)	16.6 ± 1.03 (14.4–18.9, n=30)	4.3 ± 0.31 (3.5–5.0, n=30)
	♀♀	131.3 ± 2.11 (128–136, n=17) n.s.	54.8 + 3.17 (51–63, n=16) n.s.	40.0 ± 1.61 (35.5–42.6, n=17) t=3.75, p=0.0005	24.3 ± 1.41 (21.6–26.9, n=16) t=3.88, p=0.0004	15.1 ± 1.01 (13.0–16.4, n=16) t=4.62 p=0.0003	4.2 ± 0.31 (3.5–4.7, n=16) n.s.
Region of Ambanja in NW (*M. k. berliozi*)	♂♂	134.2 ± 3.91 (130–141, n=13)	56.5 ± 3.18 (51–61, n=13)	43.2 ± 1.11 (41.6–45.1, n=13)	28.0 ± 1.07 (25.2–29.4, n=13)	17.6 ± 1.63 (15.6–20.7, n=13)	4.8 ± 0.37 (3.8–4.9, n=12)
	♀♀	133.8 ± 3.07 (130–140, n=9) n.s.	57.1 ± 3.37 (53–61, n=9) n.s.	40.9 ± 1.64 (38.6–43.6, n=10) t=3.85, p=0.0001	26.8 ± 1.23 (25.3–29.0, n=10) t=2.52, p=0.02	16.9 ± 0.77 (15.8–17.8, n=9) n.s.	4.1 ± 0.32 (3.6–4.2, n=9) n.s.

Molecular genetics. *Laboratory techniques*—Muscle from fresh samples was obtained for two specimens of *M. k. kioloides* (FMNH 345622, UADBA 48178) and two individuals from the new central west population (FMNH 431145, UADBA 48179). DNA was extracted from muscle samples using the DNeasy® Blood & Tissue Kit (Qiagen, Inc., Valencia, CA, USA) according to the manufacturer's protocol. For the muscle samples, we sequenced three mitochondrial DNA segments. Using the primers L10755 and H11151 (Chesser 1999), we amplified the entire NADH dehydrogenase subunit 3 gene (ND3) and 18 bp of the flanking tRNA-Gly gene. We used the primers A8PWL and CO3HMH (Seutin, G. & Bermingham, E., unpublished data) to amplify the ATP synthase F0 subunit 6 gene (ATP6). Finally, we used the primers L14990 (Kocher *et al.* 1989) and H15916 (Edwards *et al.* 1991) to obtain 917 bp of the cytochrome *b* gene (cytB). In total, we obtained 1943 bp of mtDNA for the tissue samples. For ND3, the polymerase chain reaction (PCR) followed the profile: 94°C for 2 min, 35 cycles of denaturation at 95°C for 15 sec, annealing at 60°C for 30 sec, extension at 72°C for 30 sec, and a final extension of 1 min. We used a similar profile for ATP6 and cytB, but the annealing step was at 50°C, the extension was for 1 min, and the final extension was for 2 min.

In addition to the muscle samples, we obtained toepads from three museum specimens of *M. k. kioloides* (FMNH 215460–215461, 404575) and four of *M. k. berliozi* (MNHN 1932.492, 1932.494, 1932.501, 1932.502). DNA was extracted from toepads using a modified protocol of the QIAamp® DNA Micro Kit (Qiagen, Inc.). All extractions were performed using equipment and lab space separate from that used for muscle samples. For toepad samples, amplification of ND3 (372 bp) was achieved using the protocol described above or, when necessary, by using species-specific internal primers designed for this study. Amplification difficulties with these toepad samples prevented sequencing of cytB and ATP6.

We purified PCR products using an ExoSAP protocol for ND3 and a GELase™ (Epicentre Technologies, Madison, WI, USA) protocol for ATP6 and cytB. The purified products were cycle sequenced using BigDye® Terminator v3.1 chemistry (Applied Biosystems, Foster City, CA, USA [AB]). We purified the cycle sequencing products using AB's recommended ethanol/EDTA precipitation method. The precipitated products were resuspended in Hi-Di™ Formamide and run on an AB 3730 DNA Analyzer. All resulting sequences were checked in BioEdit v7.0.9 (Hall 1999), and no stop codons or distinct double peaks were present in coding regions that would indicate the presence of nuclear pseudogenes. All sequences have been deposited in GenBank (HQ403653-403671).

Phylogenetic analyses—All sequences of *Mentocrex* were edited and aligned in BioEdit, along with relevant outgroup sequences from the *Rallina eurizonoides* genome in GenBank (Ozaki *et al.* 2010). We constructed molecular phylogenies separately for the ND3 dataset (372 bp) and the complete dataset (1943 bp for tissue samples, 372 bp for toepad samples) to assess the utility of amplifying only ND3 for the toepad samples. Phylogenies were constructed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) methods. For the latter two methods, the best substitution model parameters were chosen based on the Akaike Information Criterion calculated by MODELTEST (Posada & Crandall 1998). MP and ML analyses were conducted in PAUP* 4.0b10 (Swofford 2002), using a heuristic search, 10 random stepwise addition starting tree replicates, TBR branch swapping and 1000 bootstrap replicates (100 for ML). We conducted Bayesian analyses in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003), using default parameters and two simultaneous runs of 50 million generations of Markov chain Monte Carlo simulations, sampled every 1000 generations. The first 25% of the generations (12,500 trees) were discarded as burn-in, and posterior probabilities were estimated from the remaining topologies. To determine if stationarity was reached during the burn-in generations, we examined likelihood graphs of the runs in Tracer 1.5 (Rambaut & Drummond 2009). Uncorrected *p*-distances were calculated in MEGA 4 (Kumar *et al.* 2008).

Type specimens. *Mentocrex kioloides kioloides*.—We have examined the type specimen of the nominate form (MNHN type # 83, catalog number 13719), which was collected by M. Sganzin at an undisclosed locality on Madagascar. As much of Sganzin's collections from Madagascar were obtained on Ile Sainte Marie or the mainland region of the modern central Toamasina Province (Sganzin 1840), we restrict the type locality of this species to the central portion of Toamasina Province.

Mentocrex kioloides berliozi.—During a visit to the BMNH, the holotype collection was closed due to construction. However, we were able to examine a number of specimens from the type locality of Bezona in the AMNH, BMNH and MNHN, which show little variation in coloration and presumably show the same characters used in the description by Salomonsen (1934).

Sexual dimorphism. In order to render comparisons more meaningful for the external measurement data, it was necessary to determine if *Mentocrex kioloides* shows mensural differences between the sexes. Whether grouped by local populations (birds from the Maroantsetra area) or subspecies, no difference was found between males and females in wing and tail measurements, but they showed statistically significant differences in tarsus length and, in most cases, all three bill measurements (Table 1).

Results

After morphological comparisons of a recent adult specimen collected in the lowland central west to specimens of both *M. k. kioloides* and *M. k. berliozi*, as well as the results of the molecular genetic analysis, we conclude that the birds from the central west region are sufficiently different in numerous characters to merit naming as a species new to science.

Mentocrex beankaensis, **sp. nov.**
Tsingy Wood Rail (English)
Râle des Tsingy (French)
Tsikozanalan'i Tsingy (Malagasy)

Holotype. Département de Biologie Animale, Université d'Antananarivo (UADBA 48179). Adult male collected by S. M. Goodman and M. J. Raherilalao at Madagascar: Province de Mahajanga, District de Maintirano, Forêt de Beanka, 4.9 km S. Ambinda, 18°3.7'S, 44°31.5'E, 320 m, on 31 October 2009. The specimen bears the field number MJR 866 and was used in both the morphological and molecular analyses.

   Paratype. The Field Museum of Natural History (FMNH 431145). Female downy young collected by S. M. Goodman and D. W. Willard at Madagascar: Province de Mahajanga, Parc National de Bemaraha, S bank Manambolo River, 3.5 km NE Bekopaka, 19°08.4'S, 44°49.7'E, 100 m, on 4 December 2001. The specimen bears the field number DW 5363 and was used in both the morphological and molecular analyses.

   Etymology. The specific name is derived from the holotypical locality, Forêt de Beanka. The roots of this compound word are from the Malagasy "hanka", which is the vernacular name of the Madagascar Long-eared Owl (*Asio madagascariensis*), and "be", which refers to many. Hence, the word means the place where this owl is common.

   Diagnosis. *Mentocrex beankaensis*, occurring in the central west of Madagascar, is distinctly larger than the two subspecies of *M. kioloides*, found in the east and northwest, in wing, tail and tarsus measurements. There are also distinct plumage coloration differences, most notably that in *M. beankaensis* the Cinnamon-Rufous (40) throat and moustachial stripe abut the lower portion of the eye, and the lores and forehead are mixed Smoke Gray (45) and Dark Grayish Brown (20).

   Description of holotype. Lores, forehead, crown and upper nape a mixture of Smoke Gray (45) and Dark Grayish Brown (20) feathers, giving a mottled appearance (Figs. 2, 3a). Ear-coverts and moustachial region dark Cinnamon-Rufous (40). Chin and throat off-white and bordered proximally by narrow Blackish Neutral Gray (82) line demarcating the division of the proximal limit of the throat, which terminates in a pointed shape. Breast and upper flanks dark Cinnamon-Rufous (40). Central portion of belly dark Clay Color (26) merging to tri-colored lower flanks composed of individual feathers barred with Dusky Brown (19), Raw Umber (23) and light Buff (24). Undertail coverts barred Raw Umber (23) and mixed with Tawny (38) and Cinnamon-Rufous (40). Thighs and tarsal feathering a mixture of feathers barred with Dusky Brown (19) and off-white. Axillaries, underwing coverts and flight feathers broadly barred back and white. Lower nape dark Clay Color (26), grading into a color approaching a light Raw Umber (23) on the mantle. Lower back, scapulars and wing coverts Amber (36) of slightly different intensities. Rump, uppertail coverts, uppertail and undertail Ferruginous (41).

   Measurements of holotype. Wing (flattened) 142 mm, tail length 65 mm, tarsus length 46.1 mm, exposed culmen 27.1 mm, bill from anterior nostril 17.0 mm, bill width at anterior nostril 4.6 mm, weight 180 g (Table 1).

   Other details associated with the holotype. The following details are as noted on the specimen label of the holotype (UADBA 48179), which is an adult male (our translation from the French): iris—reddish-chestnut; man-

dible—distal half black, proximal half whitish-gray; maxilla—whitish-gray; tarsus—black; stomach—empty; habitat—obtained in slightly disturbed dry deciduous valley forest with trees reaching 20 m in height; skull—fully ossified; gonads (testes)—left 4 x 3 mm, right 3 x 2 mm.

FIGURE 2. Color illustration of *Mentocrex beankaensis*, **sp. nov.**, based on color photos of the holotype and the specimen in hand (UADBA 41879). (Illustration by Velizar A. Simeonovski.)

FIGURE 3. Color illustrations of the heads, upper backs, and breasts (from left to right) of *Mentocrex beankaensis*, **sp. nov.**, based on the holotype specimen and photos (UADBA 41879), *M. k. kioloides* (AMNH 410358) collected 40 km NW Maroantsetra, and *M. k. berliozi* (AMNH 410371) obtained 1 day south of Anaborano. (Illustration by Velizar A. Simeonovski.)

Description of paratype. The following details were noted on the soft part coloration of the paratype (FMNH 431145), which is a downy young female: iris—dark brown, mandible and maxilla—black with pale tip, tarsus—brownish black. The plumage coloration of this animal is seemingly identical to *M. kioloides* based on the illustration in Olson (1973, frontispiece).

Comparisons. There are notable differences in the head coloration between *Mentocrex beankaensis* and the two forms of *M. kioloides* (Fig. 3a–c). In *M. k. kioloides* and *M. k. berliozi* the dark Cinnamon-Rufous (40) associated with the outer portion of the throat and moustachial stripe ends below the eye, while in the holotype of *M. beankaensis* this coloration abuts the lower portion of the eye. There are a few exceptions amongst the specimens

of *M. k. berliozi* we have examined, with the dark Cinnamon-Rufous (40) nearly reaching the lower limit of the eye, but a small lores is clearly visible (e.g., AMNH 410370, 410376). In *M. k. kioloides* and *M. k. berliozi*, the lores and forehead are distinct, tending towards Olive-Gray (42) in the former and Smoke Gray (44) in the latter, as compared to the mixture of Smoke Gray (45) and Dark Grayish Brown (20) in *M. beankaensis*. In some individuals of *M. k. kioloides*, the forehead is slightly mottled with darker gray feathers (e.g., UADBA 48178, AMNH 410358) and the crown and upper nape are a dark Olive-Brown (28) as compared to a Fawn Color (25) or Clay Color (26) in *M. k. berliozi* or the mixture of Smoke Gray (45) and Dark Grayish Brown (20) in *M. beankaensis*. The ear coverts in *M. k. kioloides* and *M. k. berliozi* form a continuation of the same gray color passing posteriorly from the lores and below the eye, while in *M. beankaensis* this area is a continuation of the dark Cinnamon-Rufous (40) of the throat. The white portion of the throat in *M. k. kioloides* and *M. k. berliozi* is notably more extensive than in *M. beankaensis*, and in all three forms the proximal portion is delimited with a variable dark border that may be associated with how a given specimen was prepared.

In all three forms breast and upper body flanks are Cinnamon-Rufous (40), but based on the material available to us this is darker and more saturated in *M. beankaensis*, moderate in *M. k. kioloides* and lighter in *M. k. berliozi*. In this latter form the central portion of the belly is distinctly lighter than *M. beankaensis*, approaching a light Clay Color (26) with Buff Yellow (53) feather tips, and in the nominate form numerous individuals show light Buff (24) or whitish-cream feather tips. Undertail coverts in *M. k. kioloides* and *M. k. berliozi* are similar to *M. beankaensis*, but in the nominate form the Cinnamon-Rufous (40) tends to be more saturated.

The thigh and tarsal feathers in *M. k. kioloides* and *M. k. berliozi* are as in *M. beankaensis*, being dominated by Dusky Brown (19), but with a greater percentage of white barring. Axillaries, underwing coverts and flight feathers in *M. k. kioloides* and *M. k. berliozi* are similar to *M. beankaensis*, being broadly barred back and white. The lower nape in *M. k. kioloides* is a lighter Clay Color (26) than in *M. beankaensis*, while in *M. k. berliozi* it is dark Buff-Yellow (53) to light pinkish Clay Color (26). The mantle in *M. k. berliozi* is distinctly lighter, approaching dark Buff (24) or Clay Color (26), as compared to the other two forms in which it is light Raw Umber (23). Lower back, scapulars and upperwing coverts of *M. k. berliozi* approximate light Clay Color (26), as compared to the Amber (36) of the other two subspecies. Rump, uppertail coverts and rectrices of *M. k. berliozi* are light Ferruginous (41), as compared to a more saturated coloration in *M. k. kioloides* and *M. beankaensis*. On the basis of plumage coloration, no noticeable differences were found between a downy young of *M. k. kioloides* (AMNH 410365) and that of *M. beankaensis* (FMNH 431145).

Certain external measurements of the holotype of *M. beankaensis* (UADBA 48179) indicate that it is notably larger than *M. kioloides* (Table 1). For the wing, tail and tarsus measurements, there is no overlap between these two species. In the case of the three different bill measurements, *M. beankaensis* falls within the range of *M. kioloides*. Given that only a single adult specimen is available of *M. beankaensis*, and that it is notably large, no statistical analyses have been conducted, as these would not be more meaningful than simple examination of the different measurement values.

Very few of the museum specimens available have detailed information on soft part coloration. The holotype of *M. beankaensis* (UADBA 48179) has a bicolored mandible, with the proximal half being blackish, the distal grayish-white and the leading edge grayish-white; the maxilla is grayish-white; and the tarsi black. In contrast, a specimen (FMNH 345622) referable to *M. k. kioloides* has the mandible and maxilla bluish-gray proximally, merging to a dull yellow tip, and the tarsi are black. Notes on labels of other specimens referred to the nominate form include: bill—blackish above, whitish below, legs—brownish-black (female, MNHN 1932.497); bill—black upper and bluish-white lower (female, MNHN 1932.496); bill—grayish base upper, blackish lower, legs—black (female, BMNH 1931.1008); bill—blue (male, BMNH 91.8.1.81); bill—pearl grey, legs—pearl grey (male, BMNH 1969.45.22). Whether these morphological differences are seasonal, sexual or individual will require further data from the field.

Although we examined a large percentage of the specimens of *Mentocrex* available in the world's museums, the sample sizes are insufficient from most localities or too widely dispersed to properly assess patterns of geographical variation in size and coloration. Some conclusions can be presented here. Within specimens of *M. kioloides* from eastern Madagascar little morphological variation was found and these animals are referable to the nominate subspecies (Table 1). The exceptions are three small adult specimens from extreme southeastern Madagascar, specifically the localities of Bemangidy (FMNH 215460, 215461) and Eminininy (AMNH 703565). These birds have notably small bills, short wings, and more richly saturated Cinnamon-Rufous undersides. In contrast, those specimens from the northwestern portion of the island, generally considered the form *M. k. berliozi*, have dif-

ferent plumage patterns, particularly the head, upper back and breast and tend to be slightly larger than *M. k. kioloides* (Figure 3, Table 1). The molecular analysis presented herein supports the separation of these two forms (Figure 4), but the level of differentiation is small enough to retain them as subspecies.

Molecular genetics. Phylogenetic tree constructions from MP, ML and BI analyses of the full dataset yield the same topology (Fig. 4). The ND3-only dataset has an identical topology but with slightly lower nodal support values (not shown). The two samples of *M. beankaensis* form a well-supported clade sister to a clade comprising *M. k. kioloides* and *M. k. berliozi*. Those two subspecies are also reciprocally monophyletic, although the support for the two clades is not very strong. Additional sequence data may strengthen these nodes, but the lack of any samples from the far northern range of *M. k. kioloides* leaves the exact genetic relationship between these subspecies unclear. Combined with the morphological data, the molecular genetic results support the treatment of *M. k. kioloides* and *M. k. berliozi* as subspecies.
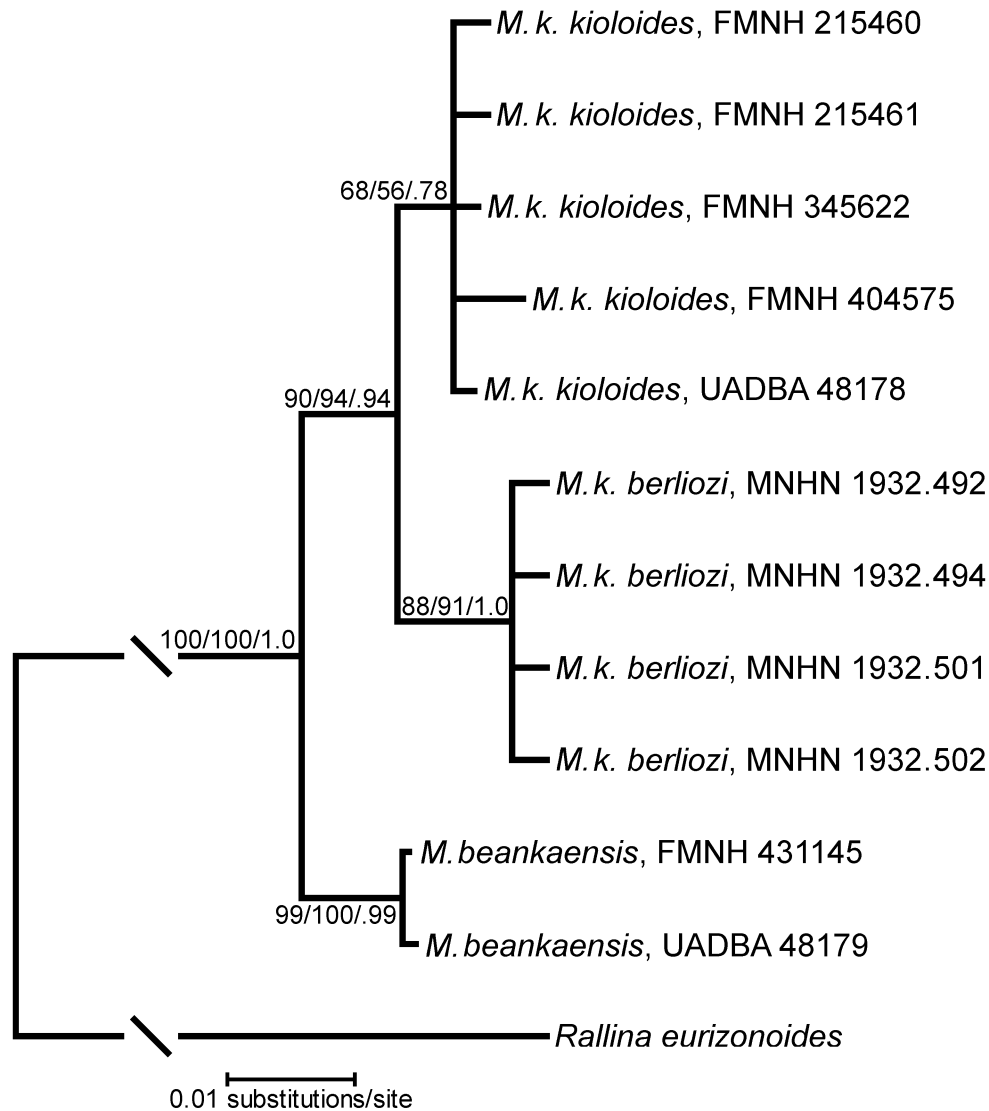

FIGURE 4. Phylogram of the *Mentocrex kioloides* complex and outgroup. Tree shown is the BI consensus tree, although MP and ML topologies are the same. Node labels show percent support from MP bootstrap (1000 reps), ML bootstrap (100 reps) and posterior probabilities from BI analysis. *Rallina* sequence from GenBank AP010822.

For the ND3-only dataset, the average uncorrected *p*-distance between *M. beankaensis* and the *kioloides/berliozi* clade is 0.015 ± 0.005 SE (0.013–0.016), while it is 0.019 ± 0.003 (0.019–0.020) for the full dataset. Assessed separately, cytB's *p*-distance between the clades ranges from 0.020–0.022, while ATP6's ranges from 0.018–0.021. These full-dataset levels would likely increase with the addition of *M. k. berliozi* samples, as they were the most

distant at ND3. Although species-level molecular data for Rallidae are scarce, the limited available data show that these *p*-distances are similar to those between other sister species in the family (J.M. Maley, pers. comm.; Trewick 1997; Hebert *et al*. 2004; Tavares *et al*. 2010).

Eight sites vary among the 372 bp of ND3, with four of the sites exhibiting fixed differences that diagnose *M. beankaensis* (Table 2). Three of the eight mutations resulted in amino acid substitutions as well, and all three are among the four that diagnose *M. beankaensis*. Of the 15 variable sites among the 654 bp of ATP6, 11 are fixed differences (Table 2). Four of the mutations caused amino acid substitutions, with three among the fixed differences. Finally, with cytB's 917 bp, 17 of 21 variable sites are fixed. Only three changes were nonsynonymous, with two being fixed.

Distribution. Currently, *Mentocrex beankaensis* is known from a limited area of lowland central-western Madagascar, specifically portions of the Bemaraha and Beanka Massifs. This species was found at elevations from 100 to 320 m in areas of limestone karst characterized by rock pinnacles known in Malagasy as *tsingy*, often in canyons or valleys closed or bordered by exposed rock, and with dry deciduous forest that is more mesic than nearby more open formations.

The nominate form of *kioloides* has a broad distribution across the eastern length of the island, being known from lowland forest habitats near sea level to montane forest up to around 2000 m (Morris & Hawkins 1998). We are unaware of any verified reports from the central portion of the Central Highlands, although it is known from numerous sites along the eastern edge of the Central Highlands (e.g., Raherilalao *et al*. 2007). We were unable to locate the specimen collected and reported by Salvan (1970) 30 km north of Ankazobe at 1450 m, which would be in the general vicinity of the Réserve Spéciale d'Ambohitantely, but as suggested by Benson *et al*. (1976), based on measurements, it might be referable to *Dryolimnas cuvieri*.

Mentocrex k. berliozi is known from the Sambirano area of the northwest. All examined specimens referable to this form were obtained in late 1930 and early 1931 during the Mission Zoologique Franco-Anglo-Américaine (Rand 1936). In 1988, an expedition to this region working the western slopes of the Manongarivo Massif, between 120 and 400 m, did not find *Mentocrex* (Thompson & Buisson 1988). In 1999, a biological inventory of the northern slopes of the massif found this species in the zone between 785 and 1240 m (Raherilalao *et al*. 2002), and those birds were tentatively assigned to *M. k. berliozi*.

Nomenclatural considerations. The name *griseofrons* Gray 1846 is a junior synonym of *kioloides* (Sharpe 1894). The illustration associated with the description of *griseofrons* (Gray 1846, pl. 161) clearly shows the reduced amount of Cinnamon-Rufous on the outer portion of the throat and moustachial stripe, diagnostic of the nominate form. Hence, the name *griseofrons* is not applicable to the central western population described herein as *M. beankaensis*.

Conservation status. Few details are available on the distribution of *Mentocrex beankaensis*. It has been observed in different portions of the Bemaraha Massif. The direct line distance between the southernmost known record in the Bemaraha and the site at Beanka is 125 km and the width of appropriate habitat across this zone does not exceed 5 km in most areas. Hence, based on current information this species has a very limited distribution. Further research is needed to define its known geographical range more clearly and to derive estimates of population density. Most of the Bemaraha Massif falls within the protected areas system of Madagascar and the *terra typica* of this new species is under the conservation management by the organization Biodiversity Conservation Madagascar (BCM).

TABLE 2. Variable sites (numbered) within three mtDNA loci for the *Mentocrex* taxa.

Taxon	Specimen	ND3								ATP6														
		4	36	79	153	214	258	285	301	28	29	72	103	177	182	240	249	405	429	447	498	505	561	636
M. k. berliozi	MNHN 1932-492	G	C	T	T	C	T	C	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. k. berliozi	MNHN 1932-494	G	C	T	T	C	T	C	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. k. berliozi	MNHN 1932-501	G	C	T	T	C	T	C	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. k. berliozi	MNHN 1932-502	G	C	T	T	C	T	C	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. k. kioloides	FMNH 215460	G	T	T	C	C	T	T	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. k. kioloides	FMNH 215461	G	T	T	C	C	T	T	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. k. kioloides	FMNH 345622	G	T	T	C	C	T	T	A	A	T	C	G	G	C	C	C	C	C	C	C	G	T	T
M. k. kioloides	UADBA 48178	G	T	T	C	C	T	T	A	A	T	A	A	G	C	C	C	C	C	T	T	G	A	T
M. k. kioloides	FMNH 404575	G	T	T	C	T	T	T	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. beankaensis	FMNH 431145	A	T	C	C	C	C	C	G	G	C	A	A	A	A	A	T	T	T	T	C	A	A	C
M. beankaensis	UADBA 48179	A	T	C	C	C	C	C	G	G	C	A	A	A	A	A	T	T	T	T	C	A	A	C

		cytB																				
		29	125	152	170	272	317	354	368	434	440	491	618	623	634	686	701	713	738	764	770	797
M. k. kioloides	FMNH 345622	G	T	T	C	T	T	A	G	T	G	T	G	A	T	C	T	A	T	C	A	A
M. k. kioloides	UADBA 48178	G	C	T	C	C	T	A	A	T	G	T	G	A	T	C	T	A	T	C	A	A
M. beankaensis	FMNH 431145	A	T	C	T	C	C	A	G	C	A	C	A	G	C	T	C	G	C	T	G	C
M. beankaensis	UADBA 48179	A	T	C	T	C	C	C	G	C	A	C	A	G	C	T	C	G	C	T	G	C

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APPENDIX 1. Museum specimens of *Mentocrex kioloides berliozi* and *M. k. kioloides* examined for this study. See Materials and methods for definitions of museum acronyms. Specimens used in the molecular analysis are highlighted in **bold.**

Mentocrex kioloides berliozi
Province d'Antsiranana: 1 day S Anaborano (BMNH 1931.8.18.1018, **MNHN 1932.502**); Bezona, east of Ambanja (BMNH 1931.8.18.1020-1931.8.18.1024, AMNH 410366, 410370-410378, **MNHN 1932.492, 1932.494, 1932.501**).
Province de Mahajanga: 1 day east Maromandia (BMNH 1931.8.18.1025-1931.8.18.1027).

Mentocrex k. kioloides
Province d'Antananarivo: Bords de l'Ikopa (MNHN 1909.317); E. Imerina (AMNH 545712, 545713).
Province d'Antsiranana: 40 km NW Maroantsetra (AMNH 410357-410359, BMNH 1931.8.18.1005, 1931.8.18.1008, 1931.8.18.1009); Andapa (MNHN 1932.500).
Province de Fianarantsoa: 20 km W. Vondrozo (MNHN 1932.496); Manombo (MNHN 1932.495, 1932.497).
Province de Toamasina: 2 days N.E. Maroantsetra (AMNH 410365, 410365A, 410369, BMNH 1931.8.18.1010, 1931.8.18.1013, 1931.8.18.1016, FMNH 411048); 20 km S.W. Maroantsetra (AMNH 410360-410364, 410367, 410368, BMNH 1931.8.18.1006, 1931.8.18.1007, 1931.8.18.1011, 1931.8.18.1012, 1931.8.18.1014, 1931.8.18.1015, 1969.45.21, MNHN 1932.489-1932.491, 1932.493, 1932.498,1932.499,1932.503); Forêt d'Analamay, 9 km NE du village Ambohimanarivo, 18°47'55"S, 48°19'23.6"E, 1106 m (**UADBA 48178**); Environs de Tamatave (MNHN 1913.387); Forêt de Lakato (**FMNH 404575**); Forêt Sianaka (Forêt des Antsianaka, Forêt Sihanaka) (AMNH 410356, BMNH 1931.8.18.1017, 1939.12.9.585, MNHN 1974.73); Rogez (BMNH 1969.45.22); Périnet (MNHN 1994.311).
Province de Toliara: Forêt d'Analalava, 7 km N Manantenina, 24°13'S, 47°19'E, 40 m (**FMNH 345622**); Bemangidy (**FMNH 215460, 215461**); Emininiminy (AMNH 703565).
Undetermined localities: "Forêt de Senbendro" or "Forêt de Senbendra" (Sharpe, 1894) (BMNH 89.9.5.8-89.9.5.10); S.E. Madagascar (BMNH 91.8.1.81); Int. de Madagascar, C-Est (MNHN 1882.2108).