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The African warbler genus *Hyliota* as a lost lineage in the Oscine songbird tree: Molecular support for an African origin of the Passerida

Jérôme Fuchs [a,b,*], Jon Fjeldså [c], Rauri C.K. Bowie [d], Gary Voelker [e], Eric Pasquet [a,b]

[a] *UMR5202, Origine, Structure et Evolution de la Biodiversité, Département Systématique et Evolution, Muséum National d'Histoire Naturelle, 55 Rue Buffon, 75005 Paris, France*
[b] *Service Commun de Systématique Moléculaire, IFR CNRS 101, Muséum National d'Histoire Naturelle, 43, rue Cuvier, 75005 Paris, France*
[c] *Zoological Museum, University of Copenhagen, DK-2100 Copenhagen, Denmark*
[d] *DST/NRF Centre of Excellence in Birds at the FitzPatrick Institute, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa*
[e] *Department of Biology, University of Memphis, 3700 Walker Avenue, Memphis, TN 38152, USA*

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Abstract

The African genus *Hyliota* includes three or four species of warbler-like birds of uncertain phylogenetic affinities, as it has historically been placed in different avian families that are now known to represent unrelated lineages: Malaconotidae (bush-shrikes), Platysteiridae (batises and wattle-eyes), Muscicapidae (Old World flycatchers) and Sylviidae (Old-World Warblers). To assess the affinities of *Hyliota* we sequenced a mitochondrial protein-coding gene (ND2, 1018 bp) and a nuclear intron (myoglobin intron-2, 685 bp). Our analyses suggest that all previous hypotheses concerning the affinities of *Hyliota* are erroneous. Instead, *Hyliota* represents a basal branch in the Passerida radiation with no close relatives. Our results, which also include analyses of relationships among other of other atypical songbird genera, lend support to an African origin of the Passerida songbird radiation.

Keywords: *Hyliota*; Biogeography; Passerida; Out of Africa

1. Introduction

The Oscine songbird genus *Hyliota* comprises three or four species of birds endemic to Africa (Dickinson, 2003). *Hyliota* species are small (10–13 cm), sexually dimorphic birds, which feed in the manner of warblers (e.g., *Eremomela* and *Parisoma*) within the canopies of savanna woodlands, gleaning insects from foliage (Erard, 1987). Their systematic affinities are uncertain, mainly due to the fact that only a few phylogenetically informative anatomical characters have been clearly described (e.g., lack of palatine process of the premaxilla, Bock, 1960). *Hyliota* has traditionally been included in the large Old World warbler family Sylviidae, due to its rather slender bill and foraging behavior (Dickinson, 2003; Erard et al., 1997; Traylor, 1970; Watson et al., 1986). However, its contrasting plumage with glossy black upperparts and white wing-stripe suggests affinities with the Platysteiridae (batises and wattle-eyes), Monarchidae (monarch flycatchers) and certain members of the Muscicapidae (Old World flycatchers) (Erard, 1987; Erard et al., 1997). *Hyliota* also resembles the Platysteiridae and Malaconotidae (bush-shrikes) in building small, neat nest-cups decorated with lichens (Erard, 1987; Erard et al., 1997; Wolters, 1975–1982).

* Corresponding author: Fax: +33 1 40 79 30 63.
E-mail address: fuchs@mnhn.fr (J. Fuchs).

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Hyliota species differ from Muscicapidae taxa by the absence of spotted juvenile plumage and from Platysteiridae in their pointed wings (Erard, 1987; Erard et al., 1997). Because warblers and flycatchers were considered to be closely associated in earlier avian classifications (Watson et al., 1986), the exact affinities of *Hyliota* were not considered of particular interest. Since the 1980s, molecular studies have produced compelling evidence (Sibley and Ahlquist, 1990) that warblers and flycatchers are polyphyletic, with certain flycatcher (Petroicidae, Platysteiridae, Monarchidae) and warbler (Maluridae, Acanthizinae) taxa included within Corvida (an assemblage now considered paraphyletic with respect to the Passerida) (Barker et al., 2004; Ericson et al., 2002b), and some atypical, enigmatic, African and Asian warblers and flycatchers (*Culicicapa*, *Elminia*, *Stenostira*) forming an independent deep branch in the Passerida (Barker et al., 2004; Beresford et al., 2005; Pasquet et al., 2002). However, the equally enigmatic *Hyliota* was never included in these studies, and the divergent opinions about its relationships are only briefly outlined by Erard et al. (1997). All the new findings concerning the oscine phylogeny (e.g., Barker et al., 2004) open a very broad range of potential sister-group relationships for *Hyliota*. To assess the phylogenetic relationships of *Hyliota*, we made use of 1703 bp of sequence data obtained from the nuclear myoglobin intron-2 and the mitochondrial ND2 gene.

2. Material and methods

2.1. Taxon sampling

We sampled representatives from all lineages with which *Hyliota* has been associated in the past, i.e., the Sylviidae, Muscicapidae, Monarchidae, Platysteiridae and the Malaconotidae (Appendix A), as well as eight species of uncertain affinities that were previously assigned either to the Monarchidae, Muscicapidae or Sylviidae (*Culicicapa ceylonensis*, *Elminia longicauda*, *Elminia albonotata*, *Erythrocercus mccallii*, *Hylia prasina*, *Melaenornis–Sigelus-silens*, *Sphenoeacus afer* and *Stenostira scita*) and are now thought to belong to other, although undefined, lineages (Barker et al., 2004; Beresford et al., 2005; Pasquet et al., 2002; Sefc et al., 2003). We also included several other African taxa of uncertain relationships (*Modulatrix*—including *Arcanator*-, *Nicator*, *Picathartes*, and *Promerops*) as well as the Asian Mountain Tailorbird (*Orthotomus cucullatus*), an enigmatic species that has been demonstrated to be outside a monophyletic Cisticolidae (N'Guembock et al., unpublished data). A total of 55 taxa were included in the data set, representing all major lineages from the Euoscines ('Corvoidea', 'Muscicapoidea', 'Passeroidea' and 'Sylvioidea'). Trees were rooted with the Superb Lyrebird (*Menura novaehollandiae*), a basal member of the Oscines (Barker et al., 2004; Ericson et al., 2002b). Sample origins and GenBank accession numbers are reported in Appendix A.

2.2. Laboratory procedures

We extracted DNA from frozen or alcohol preserved tissues (blood, feather, liver, muscle) using a CTAB-based protocol (Winnepenninckx et al., 1993) or a Puregene DNA isolation kit (Gentra Systems, Minneapolis, Minnesota) with an overnight Proteinase K (0.1 mg.ml-1) digestion. Myoglobin intron-2 was amplified with primers Myo2 (5′ GCCACCAAGCACAAGATCCC 3′) and Myo3F (5′ GCAAGGACCTTGATAATG ACTT 3′) (Heslewood et al., 1998; Slade et al., 1993). The ND2 gene was amplified with primers L5219Met (5′ CCCATACCCCGAAAATGATG 3′) and H6313Trp (5′ CTCTTATTTAAGGCTTTGAAGGC 3′) (Sorenson et al., 1999). The thermocycling conditions included a hotstart at 94 °C, an initial denaturation at 94 °C for 3 min followed by 35–40 cycles at 94 °C for 40 s, 52–56 °C for 30 s and 72 °C for 50 s and was completed by a final extension at 72 °C for 5 min. Three microliters of the amplification products were electrophoresed on a 1.5% agarose gel and visualized under UV light with ethidium bromide to check for the correct fragment size, and to control for the specificity of the amplifications. We purified the PCR products using the 'QiaQuick PCR Purification Kit' (Qiagen, Holden, Germany), or bands were cut and purified using GELase (Epicentre Technologies, Madison, Wisconsin). The purified products were cycle-sequenced using the 'CEQ Dye Terminator Cycle Sequencing' kit (Beckman Coulter, Inc, Fullerton, CA, USA) or with Big Dye terminator chemistry (Applied Biosystems) in both forward and reverse directions with the same primers used for PCR amplifications, as well as with internal primers (Myo2int: 5′ TRGACCCATAAA ACTAAGAT 3′; Myo3int: 5′ TGATCTGCTTCAT GACCTT 3′) (Fuchs et al., 2004). Sequences were obtained on an automated CEQ2000 DNA Analysis System sequencer (Beckman Coulter, Inc, Fullerton, CA, USA) or an ABI3100. We obtained sequences from both strands of DNA for all taxa.

No length variation between alleles were detected for myoglobin intron-2. The occurrence of single nucleotide polymorphisms (SNPs) in the myoglobin intron-2 sequences was suggested by the presence of double peaks. These double peaks were coded using the appropriate IUPAC codes. The absence of insertions, deletions and stop-codons in the reading frame of ND2 suggest that we had not amplified nuclear pseudogenes (Sorenson and Quinn, 1998).

2.3. Sequence alignment

Multiple alignment of intron sequences was accomplished by hand using Se-Al v1.0a1 (Sequence Alignment

Editor Version 1.0 alpha 1; Rambaut, 1996) after an initial alignment by Sequencher 4.1 (Gene Codes Corporation, Ann Arbor, MI, USA).

Final alignment indicated the presence of several insertion-deletions events in the nuclear intron. Gaps were treated as missing data. The myoglobin intron-2 alignment has been submitted to the EMBL database (accession number ALIGN_000913).

2.4. Phylogenetic analyses

Phylogenetic trees were estimated using parsimony (P) and probabilistic approaches, i.e., maximum likelihood (ML) and Bayesian inference (BI), as implemented in PAUP* 4.0b10 (Swofford, 2001) and MrBayes v.3.0 (Huelsenbeck and Ronquist, 2001). Likelihood models and parameters were estimated with Modeltest 3.6 (Posada and Crandall, 1998) and MrModeltest 2.0 (Nylander, 2004) using the AIC criterion (see Posada and Buckley, 2004 on the use of the hierarchical likelihood ratio test for model selection). P and ML analyses were performed using heuristic tree bisection and reconnection branch-swapping (TBR) with 1000 and 10 random addition replicates, respectively. Nodal support for P and ML was calculated using the non-parametric bootstrap (Felsenstein, 1985) (1000 and 100 replicates, respectively). ML bootstrap replicates were performed using PHYML (Guindon and Gascuel, 2003). We used the Approximate Unbiased Test (AU test) (Shimodaira, 2002) implemented within the CONSEL package (Shimodaira, 2001) for comparing different sets of phylogenetic hypotheses. The AU test is less conservative than the commonly used Shimodaira and Hasegawa test (SH test) (Shimodaira and Hasegawa, 1999). Simply, we manually built different competing sets of hypotheses (trees). Then, the site-wise log-likelihhood of each tree was calculated using PAML 3.14β (Yang, 2003) for the combined dataset using a GTR+G model assigned to each partition (ND2 first codon position, ND2 second codon position, ND2 third codon position, myoglobin intron-2) (the parameter proportion of invariable site is not implemented in PAML). PAML output was then prepared for the AU tests using the seqmt and makermt applications of CONSEL.

The two gene regions we sequenced differ considerably in their properties and substitution dynamics (see Table 1), we therefore did not perform combined ML and Bayesian analyses that assume a single model of evolution for the whole dataset. Four partitions were distinguished for the Bayesian analyses according to the functional properties of the markers (ND2 first codon position, ND2 second codon position, ND2 third codon position, myoglobin intron-2). Bayesian analyses for the combined data set were performed freeing different parameters (base frequencies, rate matrix, shape parameter, proportion of invariable sites) to vary between the partitions. Models selected were: GTR+G+I for ND2 first and second codon position, GTR+G for ND2 third codon position and GTR+G for myoglobin intron-2. Four incrementally heated Metropolis-coupled MCMC chains were run for three million generations with trees sampled every 100 generations (30,001 trees sampled). The first 200,000 generations (2000 trees) were discarded ('burn-in' period) and the posterior probabilities were estimated for the remaining sampled generations. Four independent Bayesian runs initiated from random starting trees were performed for each data set, and the log-likelihood values and posterior probabilities were checked to ascertain that the chains had reached stationarity.

Table 1
Data characteristics and estimated substitution parameters for myoglobin intron 2, ND2, and the combined data set

Gene	Myoglobin	ND2	Combined data set
Number of bases	685	1018	1703
Number variable /informative	439/223	659/573	1098/795
Model selected	TVM+G	GTR+G+I	NA
$R_{A–C}$	1.1104	0.1043	
$R_{A–G}$	4.6254	3.9161	
$R_{A–T}$	0.7989	0.3632	
$R_{C–G}$	1.3765	0.1463	
$R_{C–T}$	4.6254	3.2769	
$R_{G–T}$	1	1	
α	1.7709	0.4462	
I	0	0.2826	
−ln likelihood (ML)	6133.58	24962.22	NA
BI model	GTR+G	GTR+G+I	NA
BI score (SD)	6185.81 (2.20)	25015.45 (2.63)	NA
Partitioned BI score (SD)	NA	24372.82 (3.42)	30597.49 (1.70)
Tree length (P)	919	6567	7535
Number of trees (P)	>369200	16	30
CI/RI (P)	0.65/0.51	0.19/0.25	0.24/0.26

α corresponds to shape parameter, and I to the proportion of invariable sites. NA means 'Not Applicable'. Score of the Bayesian analyses represents the mean of the four independent runs with the associated standard deviations. CI/RI corresponds to Consistency Index and Retention Index.

We detected significant incongruences between the individual gene trees by comparing the topologies and nodal support obtained under different analytical methods (parsimony, maximum likelihood, Bayesian inferences). Criterions for incongruence were set at 70% for the bootstrap values (Hillis and Bull, 1993), and at 0.95 for posterior probabilities (Huelsenbeck and Ronquist, 2001).

3. Results

The two gene regions concatenated resulted in a final alignment of 1703 bp. Model parameters and tree statistics for all data sets are presented in Table 1.

For myoglobin intron-2, we obtained between 542 bp (*Copsychus saularis*) and 657 bp (*Zosterops palpebrosus*), resulting in an alignment of 685 bp. The number of parsimony informative sites was 223 (32.6%). The parsimony search was aborted after two days of TBR branch-swapping. Results indicated that at least 369,200 equally parsimonious trees of 919 steps were found (CI = 0.65, RI = 0.51). All the analyses performed with the myoglobin intron-2 yielded poorly resolved trees. Nevertheless, monophyly of the Corvoidea, Muscicapoidea and Passeroidea were recovered in all analyses albeit with varying support values (e.g., Fig. 1, Bayesian tree, mean of the four runs: −ln = 6185.81 SD = 2.20).

Final alignment for the ND2 gene was 1018 bp, corresponding to the positions 5246–6263 of the chicken mitochondrial sequence (Desjardins and Morais, 1990). We were unable to obtain a ND2 sequence for *Nicator chloris*. This species was thus excluded from all combined analyses. The total number of parsimony informative sites was 573 (56%), where 166 (16%) were at first

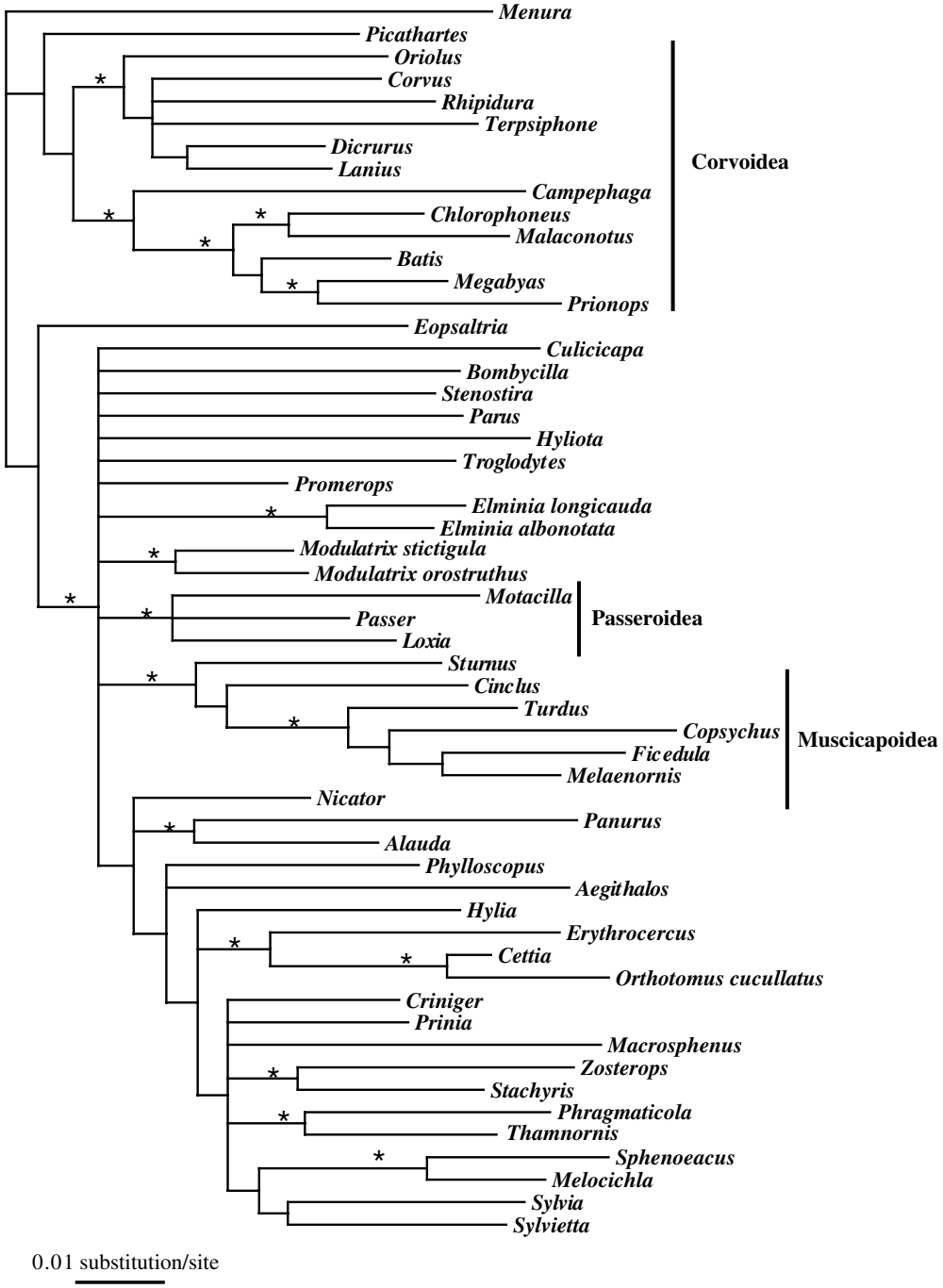

Fig. 1. Bayesian tree (mean of the four runs: −ln = 6185.81, SD = 2.20) obtained from the myoglobin intron-2 under a GTR+G model. Asterisks represent posterior probabilities greater than 0.95.

codon positions, 74 (7%) at second positions and 333 (33%) at third positions. Parsimony analyses recovered only five nodes supported by bootstrap values greater than 75%, a fact that may be explained by the large amount of homoplasy (CI = 0.19, RI = 0.25). The ML tree (score: −ln = 24962.22) supported recent revisions (e.g., Barker et al., 2004) of the passerine phylogeny. Nevertheless, even well supported groups such as the Malaconotidae (bush-shrikes, helmet-shrikes and platysteirids) clade, the Corvoidea clade or the Passeroidea clade only received bootstrap values of 69, 68 and 64%, respectively. Results, in terms of topology, were very similar between the ND2 partitioned by codon Bayesian analyses (Fig. 2) and the ND2 single partition Bayesian analyses, although likelihood scores were higher in the partitioned analyses (mean of the four runs −ln = 24372.82 SD = 3.42 versus −ln = 25015.45 SD = 2.63).

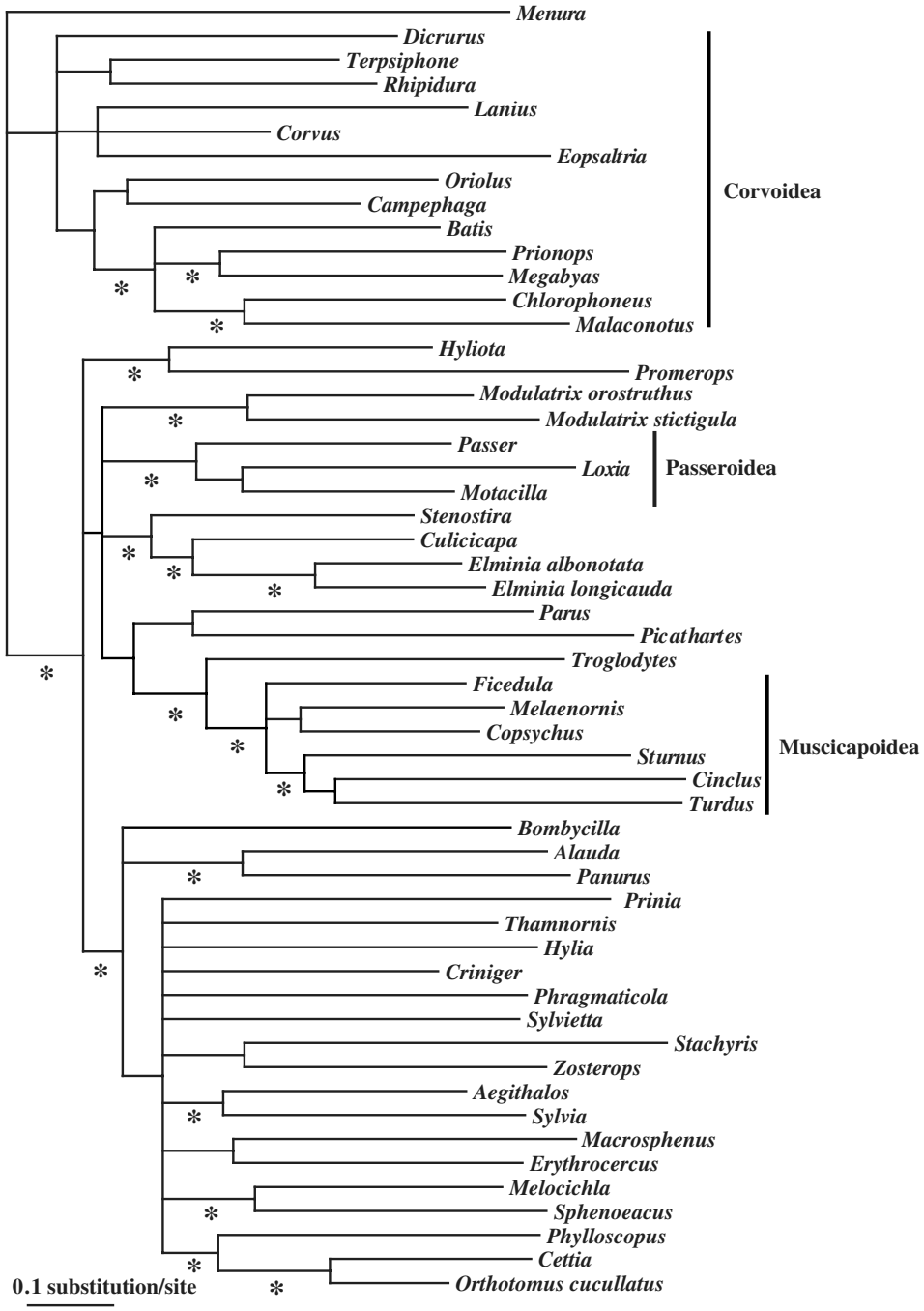

Fig. 2. Bayesian tree (mean of the four runs: −ln = 24372.82, SD = 3.42) obtained from the ND2 gene assuming different independent models for each codon position (GTR+G+I for ND2 first and second codon position, GTR+G for ND2 third codon position). Asterisks represent posterior probabilities greater than 0.95.

Hyliota clustered with *Promerops* in all ND2 analyses we performed, but support for this association was variable (ML < 50%, PP = 0.97), whereas the position of *Hyliota* was unresolved in all the myoglobin intron-2 analyses.

With one exception, the two gene trees were congruent. The single incongruent node (>70% bootstrap or >0.95 posterior probability) concerned the relative position of the starlings (Sturnidae) and dippers (Cinclidae) with respect to the thrushes and flycatchers (Turdidae and Muscicapidae) (see Figs. 1 and 2), which has generally proven difficult to resolve (Cibois and Cracraft, 2004; Klicka et al., 2005; Voelker and Spellman, 2004). Given that this incongruence concerns terminal taxa within a clade that is otherwise well supported, we combined the two genes to improve resolution.

3.1. Combined Bayesian analyses

The parsimony analysis yielded 30 equally parsimonious trees of 7535 steps (CI = 0.24, RI = 0.26). Only a few nodes were resolved and supported (e.g., Corvoidea, Muscicapoidea and Passeroidea). The topology obtained from the Bayesian combined analyses (mean of the four runs −ln = 30596.26 SD = 1.70 ; Fig. 3) shows increased resolution as evidenced by a higher number of supported nodes, as compared to single gene trees. Our likelihood-based analyses recovered well supported Corvoidea and Passerida assemblages (Fig. 3). Within the Passerida, monophyly of the following clades were also recovered with posterior probabilities of 1.0: Muscicapoidea with *Troglodytes*, Passeroidea, 'Stenostiridae' and a Sylvioidea assemblage containing most taxa traditionally assigned to this group; exceptions were the Paridae (*Parus*), *Hyliota* and *Modulatrix*. The positions of *Bombycilla* and *Hyliota* were unresolved at the base of the Passerida clade. The relationships of the African genera *Modulatrix* and *Promerops* were unresolved and thus our analyses failed to recover a monophyletic 'Promeropidae' (Beresford et al., 2005). The Asian Mountain Tailorbird (*Orthotomus cucullatus*) clustered strongly with the Asian genus *Cettia*. *Erythrocercus* and *Hylia* were in turn associated with the *Cettia*-*O. cucullatus* clade in the large Sylvioidea assemblage, although posterior probabilities were not significant.

4. Discussion

From this study, it is now clear that *Hyliota* falls outside all the main radiations of warbler- (Sylvioidea) and flycather-like birds (Muscicapoidea), and this results adds to the picture (Beresford et al., 2005) of a wide range of deep and relictual songbird lineages represented in Africa.

Previous discussions on the systematic position of *Hyliota* were based on rather superficial comparisons with other taxa represented in the same biogeographical region. Hyliotas have been associated with the Sylviidae warblers due to their slender bill and foliage-gleaning way of foraging, with the muscicapid genus *Ficedula* based on plumage pattern, and with the Platysteiridae and Maloconotidae based on plumage characters and nest building architecture. However, the pertinent plumage and morphological characters (very silky smooth plumage, dark glossy upperparts, long and loose rump feathers with whitish feather centres, exposed nostrils, rather long legs) are in fact widespread traits among crown corvoids, and to some extent shared by the Stenostiridae group. The white wing-stripe, involving greater coverts (interwing panel) and the outer edges of the inner secondaries, is also found in many crown corvoids, Petroicidae and *Stenostira* (and even in *Ficedula* and certain *Parus* spp., but never in stem corvoids), as is the round and neat, lichen-decorated nest. This would suggest that such traits are plesiomorphic within the crown corvoids and retained in some early branches of the Passerida. It is particularly interesting to note that *Hyliota* resembles members of the Australasian family Petroicidae (notably *Petroica* and *Melanodryas*), in many respects: socially monogamous or cooperative breeding, nest- and egg characteristics, plumage pattern and quality, wing-shape, and even behaviour (participation in mixed species flocks, wing-flicking, tail-bobbing; compare Erard et al., 1997 and Higgins and Peter, 2002). Petroicidae, represented by *Eopsaltria* in our study, is an assemblage of 13 closely related genera for which both DNA–DNA hybridization and sequence data support monophyly (Barker et al., 2004; Sibley and Ahlquist, 1990). Petroicidae was placed in the Corvida by Sibley and Ahlquist (1990), but basally in the Passerida by Barker et al. (2004) and Beresford et al. (2005). Our results are ambiguous in this respect (Figs. 1–3). However, an insertion of one codon in the c-myc gene, recently proposed as a synapomorphy for the entire Passerida clade (Ericson et al., 2000) is shared by *Hyliota* (GenBank Accession No. DQ125974, results not shown) but not by the Petroicidae (represented by *Eopsaltria australis*). It should also be noted that *Hyliota* did not possess the three-codon insertion that characterize a subset of the Passeroidea (*Loxia* and *Motacilla* in our sampling, *Passer* did not possess the insertion) (Ericson et al., 2000).

Obtaining clear support for relationships of enigmatic lineages could be very difficult, especially when these lineages are, like *Hyliota* relictual and species poor. Several comparable cases where affinities of relictual lineages have not been clearly ascertained, despite the use of large data sets, have already been described in birds, the most well known example being the Hoatzin (Sorenson et al., 2003). In addition to this problem, long-branch attraction could also be responsible for artificial groupings of relictual taxa. For example, long-branch attraction may be an explanation for the strong grouping between *Hyliota* and *Promerops* in the ND2 analyses (PP = 0.97). While it is clear that additional data are needed to fully

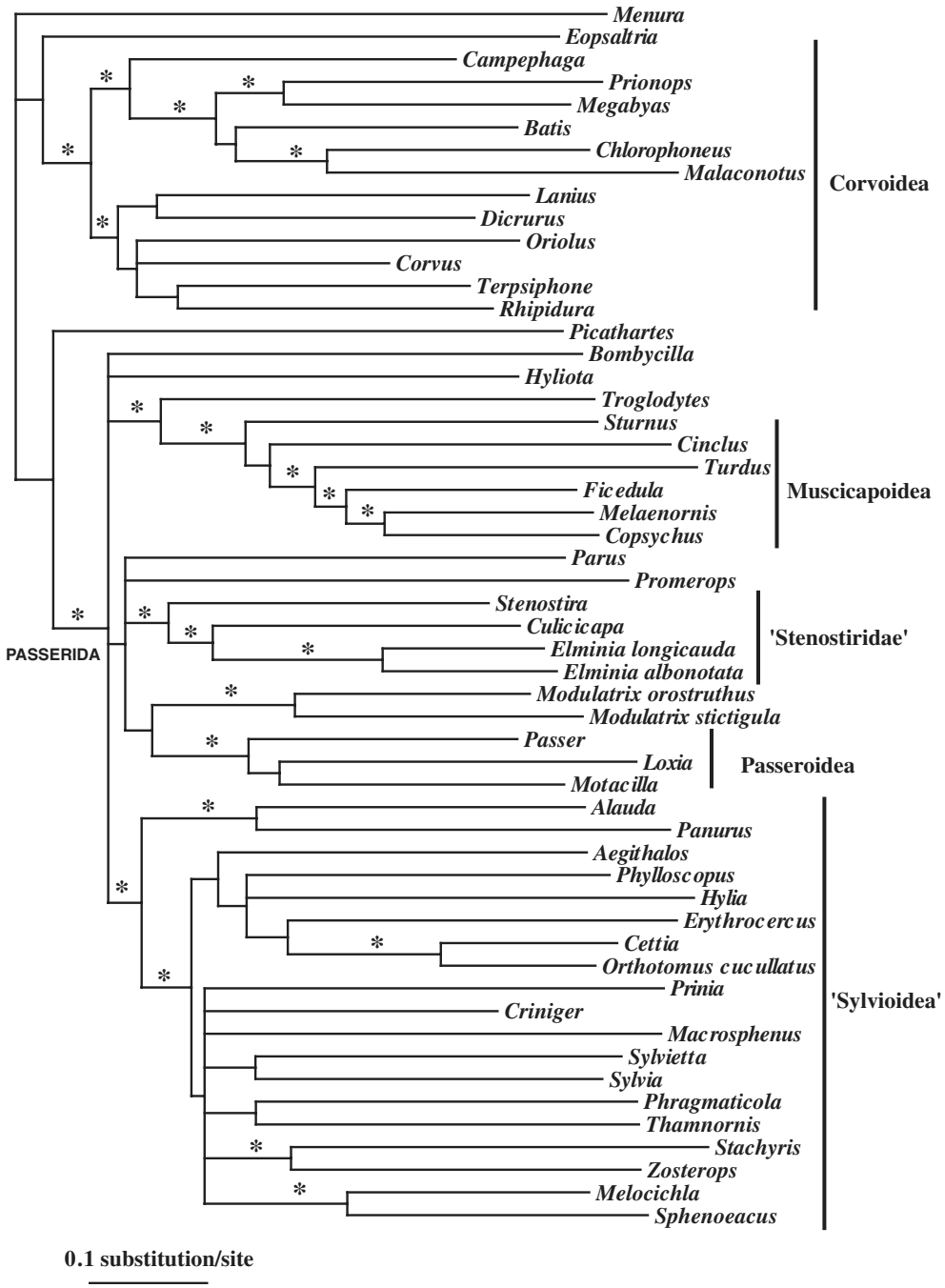

Fig. 3. Bayesian tree (mean of the four runs: −ln = 30597.49, SD = 1.70) obtained from the combined data set assuming different independent models for each partition (GTR+G+I for ND2 first and second codon position, GTR+G for ND2 third codon position, GTR+G model for myoglobin intron-2). Asterisks represent posterior probabilities greater than 0.95.

resolve the relationships of *Hyliota*, the lack of support for any relationships with named taxa support the recognition of *Hyliota* as a very distinctive entity per se.

4.1. Biogeographic implications

The position of *Hyliota* is particularly interesting in view of the accumulating evidence that Africa holds several other enigmatic ancient passerine genera that are morphologically distinct and have no close relatives, such as *Picathartes*, *Chaetops* and *Promerops*. The *Modulatrix* and *Stenostira–Culicicapa–Elminia* lineages could also be considered ancient African passerine lineages (Beresford et al., 2005, this study). Understanding why such taxa have no close extant relatives is of great concern (see Ricklefs, 2003). One likely explanation is that these taxa are relictual members of formerly widespread African clades that

declined in numbers of species as other African clades radiated, or as new clades colonized Africa from Asia. Such a hypothesis could only be tested when a complete phylogeny of all passerines clades with African and Asian representatives become available.

Currently accepted phylogenetic hypotheses for the Passerida suggest a dispersal event from Australasia via the Eurasian landmass to Africa (Barker et al., 2004;Barker et al., 2002; Ericson et al., 2002a). However, the presence of several very deep lineages in Africa (*Picathartes–Chaetops*, *Hyliota*, *Modulatrix*, *Promerops* and 'Stenostiridae' all basal in the Passerida tree, African *Nicator* and Alaudidae—primarily African in distribution—are basal to the whole Sylvioidea radiation—Barker et al., 2004; Beresford et al., 2005, this study) but not in Eurasia, could instead suggest a dispersal directly from Australasia to Africa, and then to Asia. Interestingly, among other deep Passerida branches, the Bombycillidae (as currently defined) are nomadic (*Bombycilla*, *Hypocolius*) or apparently relictual in the New World (*Dulus*, *Ptilogonys*, *Phainopepla*), and the Paridae lineage is widespread, but with a deep branch (*Anthoscopus*; see Gill et al., 2005) in Africa.

A successful direct dispersal of small passerine birds across the Indian Ocean (from Australasia to Africa) would seem unlikely. However, it is worth noting that ca 45 Mya BP (estimate of the split between *Picathartes* and the Passerida, see Beresford et al., 2005), and according to current plate tectonic models (e.g., Hall, 1998; Smith et al., 1994), the now (mostly) submerged Broken Ridge, Kerguelen, Crozet and South Madagascar plateaus in the southern Indian Ocean would have formed an almost unbroken chain between south-west Australasia and Africa (Fig. 4). At this time, the global climate was very warm (Kennett, 1995), so land masses in the southern Indian Ocean would have been expected to have had a seasonal temperate climate. Traditional models for plate tectonic reconstructions do not consider the possibility of vertical tectonic changes such as uplift along faults (see McCall, 1997) or subsidence of small terranes (plate fragments). Thus, it is unclear whether the said plateaus, or the chains of sea-mounds along the Ninety East, Maldive and Mascarene ridges (Fig. 4), may have formed land-masses, archipelagos or island chains at some point in time. The possibility for oceanic dispersal and radiations within archipelagos may have been strongly underestimated (de Queiroz, 2005), and a more detailed look at possibilities for dispersal across the Indian Ocean, using a combination of phylogenetic as well as geological evidence is sorely needed. It is worth

Fig. 4. The distribution of landmasses and submerged plateaus around the Indian Ocean ca. 45 Mya B.P., as redrawn from Smith et al. (1994), Hall (1998) and bathymetric maps. It is unknown to what extent the presently submerged plateaus may have been above sea level, or comprised archipelagos, at that time. Stippled lines mark strike-slip faults with rows of sea-mounts and volcanoes, which may also have had islands in the past.

noting that several studies already support such oceanic dispersal (Jansa et al., 1999 for rodents, Raxworthy et al., 2002 for chameleons). Traditional reconstructions of plate tectonics (along the lines provided by Hall, 1998 for the Australasian region) need to be supplemented with detailed studies of submerged ridges and plateaus in the oceans.

4.2. Additional findings on enigmatic passerines

The general branching pattern of our phylogeny is in accord with what is currently known of the passerine phylogeny (Barker et al., 2004; Beresford et al., 2005; Ericson et al., 2003), lending further credence to the radical taxonomic revisions suggested by molecular phylogenetic approaches.

Our broad sampling allows us to discuss additional significant findings concerning the relationships of some enigmatic taxa. The systematic placement of the genera *Nicator*, *Stenostira*, and *Sphenoeacus* are highly congruent with the findings of Barker et al. (2004) and Beresford et al. (2005), thus we will not discuss these results any further. However, we highlight the relationships of some other atypical genera or species for which traditionnal systematic placements are controversial (Beresford et al., 2005; Pasquet et al., 2002; Sefc et al., 2003; N'Guembock et al., unpublished data).

The African Chestnut-capped Flycatcher (*Erythrocercus mccallii*) is traditionally considered to be a monarchine flycatcher. Recently, Pasquet et al. (2002) demonstrated that *Erythrocercus* was instead nested in the Sylvioidea assemblage, although its exact affinities remain unresolved. In our study, *Erythrocercus* clustered with the Asian species *Cettia* and *Orthotomus cucullatus* in the myoglobin and combined analyses. Unlike in the myoglobin analyses (PP = 0.98), this relationship was nearly supported (PP = 0.94) in the combined Bayesian analysis

A new clade including *Promerops* and *Modulatrix* was erected under the family name Promeropidae based on molecular data (Beresford et al., 2005). Our analyses did not recover monophyly of the Promeropidae, although it was not statistically rejected (AU test: $P = 0.14$). Additional data from other genes and greater taxon sampling are clearly needed in order to evaluate the validity of this "clade" of very different-looking birds.

Hylia is a small insectivorous forest passerine, distributed in the Guinea-Congolian rain-forest. Its relationships have been disputed, with some authors considering it to be near the sunbirds (Nectariniidae) and other considering it to be near warblers (Sylviidae) (Dowsett and Dowsett-Lemaire, 1993; Sclater, 1930). In our analyses, *Hylia* clustered with *Aegithalos*, *Phylloscopus* and the *Erythrocercus–O. cucullatus–Cettia* clade (in agreement with Sefc et al., 2003), although with little to no support. Taxon sampling may prove crucial if the systematic placement of *Hylia* is to be unambiguously resolved.

Recent molecular studies have documented that at least one member of the genus *Orthotomus* (*O. sutorius*), traditionally considered a Sylviidae (Watson et al., 1986), is nested within the Old World cisticolid warbler assemblage (Beresford et al., 2005; Cibois et al., 2001; Sefc et al., 2003). An ongoing molecular study that addresses the molecular systematics of the cisticolid warblers suggests that *Orthotomus*, as currently defined, is polyphyletic, with *O. sutorius* and *O. atrogularis* being nested within the cisticolid warblers where *O. cucullatus* is found to be related to sylvioid outgroups (N'Guembock et al. unpub. data). In our analyses, *O. cucullatus* was never the sister-group of the 'typical' Cisticolidae we included (*Prinia bairdii*), but instead was sister to the Brownish-flanked Bush-Warbler (*Cettia fortipes*). This clade was also supported by a 15 bp deletion in the myoglobin intron-2. Due to insufficient taxonomic sampling within the genera *Orthotomus*, *Cettia* (and its closely related genus *Urosphena*), (Drovetski et al., 2004a), we prefer not to propose any taxonomic revision.

5. Conclusions

We highlighted throughout this paper that the African Warbler *Hyliota* represents a very old lineage in the Oscine tree with no close relative. This study has strong implications for the understanding of the evolution of passerine birds in Africa, and suggests that Africa has played a major role in the diversification of warbler-like birds in the Old World. Additional findings on problematic taxa (*Erythrocercus*, *Hylia*, *Promerops*, *Orthotomus cucullatus*) have also been highlighted. The African *Erythrocercus* seem to have affinities with the Asian Grass-Warblers *Cettia*, and the Mountain Tailorbird *Orthtomus cucullatus*. The monophyly of the Promeropidae, as defined by Beresford et al. (2005), was not recovered.

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Appendix A

List of taxa studied (following Dickinson, 2003), voucher number/specimens and GenBank accession numbers

Species	Family	Sample no.	Origin	Myoglobin	ND2
Ingroup taxa					
Aegithalos caudatus	Aegithalidae			AY228281[d]	AY136588[g]
Alauda arvensis	Alaudidae	MNHN CG 1995-19	France		DQ125975
Alauda arvensis	Alaudidae			AY228284[d]	
Batis poensis	Platysteiridae	MNHN CG 1998-783	Cameroon	AY529907[e]	AY529941[e]
Bombycilla garrulus	Bombycillidae			AY228286[d]	AY329412[i]
Campephaga flava	Campephagidae	RB613	Kenya	DQ125949	AY529944[e]
Cettia fortipes	Sylviidae	MNHN 15-34	China	DQ125948	DQ125976
Chlorophoneus sulfureopectus	Malaconotidae	MNHN CG 1998-823	Malawi	AY529912[e]	AY529947[e]
Cinclus cinclus	Cinclidae	NRM 20016138	Sweden	AY228291[d]	DQ146344
Copsychus saularis	Muscicapidae	MNHN 4-8H	Thailand	DQ125950	DQ125977
Corvus corone	Corvidae	MNHN CG 1995-41	France	AY529914[e]	AY529949[e]
Criniger calurus	Pycnonotidae	AMNH PB222	RCA	DQ125947	DQ125978
Culicicapa ceylonensis	Muscicapidae	MNHN 31-91	Lao RDP	DQ125951	DQ125979
Dicrurus paradiseus	Dicruridae	MNHN 5-57	Lao RDP	AY529916[e]	AY529951[e]
Elminia albonotata	*incertae sedis*	ZMUC 02939	Tanzania	DQ125952	DQ125980
Elminia longicauda	*incertae sedis*	MNHN 01-03	Cameroon	DQ125953	DQ125981
Eopsaltria australis	Petroicidae			AY064732[c]	AY064749[c]
Erythrocercus mccallii	*incertae sedis*	MNHN 03-25	Cameroon	DQ125954	DQ125982
Ficedula hypoleuca	Muscicapidae	NRM 976132	Sweden	AY228300[d]	DQ146345
Hylia prasina	Sylviidae	MNHN 01-39	Cameroon	DQ125955	AY136606[g]
Hyliota flavigaster	Sylviidae	MOM 2003.2.118	Malawi	DQ125956	DQ125983
Lanius collaris	Laniidae	MNHN 02-26	Cameroon	AY529925[e]	AY529960[e]
Loxia curvirostra	Fringillidae			AY228303[d]	AF447290[j]
Macrosphenus flavicans	Sylviidae	MNHN CG 1998-774	Cameroon	DQ125967[u]	DQ125997[u]
Malaconotus blanchoti	Malaconotidae	ZMUC 116824	Kenya	AY529926[e]	AY529961[e]
Megabyas flammulatus	Platysteiridae	MNHN CG 1968-1160	Kenya	AY529927[e]	AY529962[e]
Melaenornis silens	Muscicapidae	RB658	South Africa	DQ125957	DQ125984
Melocichla mentalis	Sylviidae	MNHN 01-51	Cameroon	DQ125958[u]	DQ125998[u]
Modulatrix stictigula	*incertae sedis*	FMNH 356751	Tanzania		DQ125985
Modulatrix stictigula	*incertae sedis*	ZMUC JF03-231102	Tanzania	DQ125963	
Modulatrix orostruthus	*incertae sedis*	FMNH 438269	Tanzania		DQ125986
Modulatrix orostruthus	*incertae sedis*	ZMUC 12351	Tanzania	DQ125962	
Motacilla alba	Motacillidae			AY228307[d]	AF407040[h]
Nicator chloris	*incertae sedis*	MNHN CG 1998-711	Cameroon	DQ125964	
Oriolus xanthornus	Oriolidae	MNHN 4-10D	Thailand	AY529929[e]	AY529964[e]
Orthotomus cucullatus	*incertae sedis*	FMNH 357483	Phillipines	DQ125961[u]	DQ125999[u]
Panurus biarmicus	Timaliidae			AY228308[d]	AY136604[g]
Parus major	Paridae			AY228310[d]	AY136587[g]
Passer montanus	Passeridae			AY228311[d]	AY030144[a]
Phragmaticola aedon	Sylviidae	MNHN 4-08D	Thailand	DQ125965	DQ125987
Phylloscopus collybita	Sylviidae	MNHN 28-37	France	DQ125966	DQ125988
Picathartes gymnocephalus	Picathartidae	AMNH AC350	Liberia	AY228314[c]	DQ125989
Prinia bairdii	Cisticolidae	MNHN 02-45	Cameroon	DQ125959[u]	DQ126000[u]
Prionops scopifrons	Malaconotidae	ZMUC 117528	Kenya	AY529932[e]	AY529967[e]
Promerops cafer	Promeropidae	RB659	South Africa	DQ125968	DQ125990
Rhipidura albicollis	Rhipiduridae	MNHN 5-48	Lao RDP	AY529934[e]	AY529969[e]
Sphenoeacus afer	Sylviidae	RB660	South Africa	DQ125969	DQ125991
Stachyris nigriceps	Timaliidae	MNHN 4-6H	Thailand		DQ125992
Stachyris nigriceps	Timaliidae			AY228321[d]	
Stenostira scita	Muscicapidae	RB661	South Africa	DQ125970	DQ125993
Sturnus vulgaris	Sturnidae	NRM 19966615	Sweden	AY228322[d]	DQ146346

(*continued on next page*)

Appendix A (*continued*)

Species	Family	Sample no.	Origin	Myoglobin	ND2
Sylvia atricapilla	Sylviidae	MNHN CG 1995-128	France		DQ125994
Sylvia atricapilla	Sylviidae			AY228323[d]	
Sylvietta brachyura	Sylviidae	MNHN 01-58	Cameroon	DQ125960[u]	DQ126001[u]
Thamnornis chloropetoides	Sylviidae	FMNH 356699	Madagascar	DQ125971	DQ125995
Terpsiphone viridis	Monarchidae	MNHN 2-20	Cameroon	AY529939[e]	DQ125996
Troglodytes troglodytes	Troglodytidae			AY228325[d]	AY460330[b]
Turdus merula	Turdidae	MNHN CG 1995-36	France	DQ125972	AY752348[f]
Zosterops palpebrosus	Zosteropidae	MNHN 16-3C	China	DQ125973	
Zosterops pallidus	Zosteropidae				AY329445[i]
Outgroup taxa					
Menura novaehollandiae	Menuridae			AY064744[c]	AY064754[c]

Abbreviations: AMNH, American Museum of Natural History, New York, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MOM, Museums of Malawi; NRM Swedish Museum of Natural History, Stockholm, Sweden; RB, Rauri Bowie; ZMUC, Zoological Museum, University of Copenhagen, Denmark. [u] refers to sequences provided by B. N'Guembock (unpublished).

[a] Cicero and Johnson (2001).
[b] Drovetski et al. (2004b).
[c] Ericson et al. (2002b).
[d] Ericson et al. (2003).
[e] Fuchs et al. (2004)
[f] Klicka et al. (2005).
[g] Sefc et al. (2003).
[h] Sorenson et al. (2001).
[i] Voelker and Spellman (2004).
[j] Yuri and Mindell (2002).

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