A Large Evaluation of Passerine Cisticolids (Aves: Passeriformes): More About Their Phylogeny and Diversification

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Abstract: African warblers (or Cisticolidae family) are small perching song birds with a large number of genera distributed throughout the World. The phylogeny of Cisticolidae is well-supported but their diversification is currently poorly known. To deepen their understanding of phylogeny and investigate their diversification, we sequenced four loci (mitochondrial ATPase 6, ND2 and ND3, and nuclear myoglobin intron 2) for several new cisticolid taxa and added several other sequences. Our analyses retrieve the monophyly of the African warblers and confirm Neomixis as their deepest branch. A group of taxa appear as their potential sister-taxa with our ND2 analyses but not with our combined analyses. New relationships are well-supported. Thus Scotocerca iniqua nests in the cettid clade whereas Camaroptera superciliaris, Cisticola chubbi, Cisticola tinemens, Prinia flavicans and Poliolais lopezi belong to the cisticolid clade. Our results support a splitting of the African warblers in two main clades. The first clade consists of genera Orthotomus, Prinia, Cisticola, Scopomycter, Incana, Bathmocercus, Eminia, Hypergerus and Heliolais while the second includes genera Poliolais, Camaroptera, Urolais, Artisornis, Oreolais, Apalis, Schistolais, Calamonastes and Spiloptila. Our results confirm the polyphyly of Orthotomus which generates a muddle between some Cettia species and other Asian tailorbirds. Waiting a study with Orthotomus sepium Horsf., 1821, to clarify their taxonomy, we suggest temporarily that the name Phyllergates cucullatus Temminck, 1836, refers to Orthotomus cucullatus of the present study. Our dating analysis reveals that cisticolid clades began their diversification during the transition Early-Middle Miocene epoch and at the beginning of the Pliocene epoch. The diversification of the “open cisticolid” clade would have occurred during the Middle Miocene but that of the “forest cisticolid” lineage would have taken place during the Upper Miocene.

Keywords: African warblers, maximum-likelihood, Bayesian inference, polyphyly, taxonomy, molecular dating, diversification, Miocene, Pliocene.

INTRODUCTION

African warblers represent an Old World passerine clade of tropical birds which has been established [1]. Several cisticolid genera are endemic to Africa or of obvious African origin. These warblers are small (around 9 cm) but some are medium size (19–20 cm). Cisticolid taxa often have underparts and head more distinctively patterned than their upperparts. On average, males are larger than females and the length of their tail is often more dimorphic [2]. The cisticolid bill is rather short, slender or long. Their wings are short and rounded but the number of tail feathers varies among the genera. Some cisticolid genera like Orthotomus, Heliolais, Cisticola, Incana, Camaroptera, Calamonastes, Euryptila and Spiloptila have twelve rectrices and others only ten or eight [2-4]. The cisticolid plumage colour varies from drab and cryptic to brightly coloured.

For many years, the cisticolid clade was included in the Old World Warblers (Sylviidae) but after the work of Sibley and Ahlquist [1], it has been erected to the family level. Afterwards, several molecular studies have strongly confirmed this clade [5-8]. Interestingly, considerable taxonomic advances have been achieved in keeping with the cisticolid clade. Several studies showed that Rhopophilus pekinensis did not belong to cisticolid clade but genera Bathmocercus and Orthotomus belonged to it [8, 3]. Concerning tailorbirds, Nguembock et al. [3] showed that African tailorbirds (Artisornis) were distantly related to Asian tailorbirds (Orthotomus). Otherwise, Nguembock et al. [3] found that the Moreau Warbler, which was always included in the genus Bathmocercus, was rather distantly related to it; they used this result to resurrect the genus Scopomycter [3].

In another study, Nguembock et al. [4] proposed a new generic name, Oreolais, for odd putative apalis pulchra and ruwenzorii. Johansson et al. [9] found that the ancient sylvid genus Eremomela nested within the cisticolid clade. Equally, Nguembock et al. [10] also found that Scotocerca
inquieta nested within the cettid clade. Other subjects have been developed concerning this clade, for instance, the adaptation of the main basic nest type to their environment, the evolution of the stitching technique in “tailorbirds” but in return these studies did not shyly tackle subjects in keeping with their sister group, origin or diversification [3, 6].

According to diverse authors [3, 4, 8-11], the cisticolid clade constitutes a well diversified family which includes approximately 29 genera. These genera are distributed throughout the World and their origin is currently unknown. Our first results [3] suggested that some genera should have colonized the African mainland but we do not know how or when. In this study [3], we found that the insular genus Neomixis was their basal branch. Their closest relatives are currently poorly known. Beresford et al. [7] found that the cisticolid clade was close to some Pycnonotidae or Timaliidae taxa but this relationship was unresolved. Often regarded as a sister-taxon but only with the ND2 gene.

Aims of this study which includes several new cisticolid taxa were to enlarge a thorough knowledge of this group, to investigate their relationships and to obtain support for their sister-taxa. Otherwise leaning on our molecular dating, we aimed to discuss preliminary elements of their origin and diversification. We used 2716 bp of aligned sequenced data obtained from three mitochondrial protein-coding genes (ATPase 6, ND2 and ND3) and one intron (myoglobin intron 2).

MATERIALS AND METHODS

Taxon Sampling

Samples used comprised tissues from fresh specimens as well as Genbank and Embl-bank sequences. Fresh tissues came from banks of tissues (ZMUC, MNHN and FMNH) and others directly collected in Cameroonian highlands forests. We included 20 some 28 potential genera listed under Cisticolidae [12] and updated by recent molecular works [3, 4, 8, 9]. We added several taxa which are closely related to the cisticolid clade [3, 4, 7, 8] and other insular genera which could be closest relatives of this clade [5, 13]. To discuss the origin and the diversification of the cisticolid taxa within the Passerida, we additionally sampled 11 oscine passerine families recognized in Dickinson [12] and two recent suggested families (Stenostiridae and Picathartidae) [7, 14, 15] (Annexe). We selected one Monarchid, Tersiphone rufiventris, as an outgroup which was demonstrated outside the cisticolid clade [16]. Our molecular dataset was also increased by including ND2 and myoglobin intron 2 sequences taken in Genbank and Embl-bank (Annexe). A total of 123 Operational Taxonomic Units are included in our analyses (Annexe).

Laboratory Procedure

Genomic DNA was isolated from fresh tissues (blood or muscle) using a CTAB-based protocol [17]. We amplified and sequenced four gene regions which are known to have different evolutionary rates in birds, one evolving slowly (myoglobin intron 2) and others more rapidly (ATPase 6, ND2 and ND3). The mitochondrial ATPase 6 (684 bp) and ND3 (351 bp) were amplified as a single fragment [18, 19] whereas ND2 (1041 bp) as a single fragment [20] or as several smaller fragments. The nuclear myoglobin intron 2 (~624 bp) was amplified as a single fragment and conditions described by Heslewood et al. [21] and Slade et al. [22] or as several smaller fragments. All these primers are detailed in Table 1.

For amplifications, cycling conditions were standard for these four markers [3, 4, 10]. Three microcolits of the PCR-amplification product was electrophoresed on a 1.5% agarose gel and visualized under UV light with ethidium bromide to check the size of the fragment and hence ensure that the correct fragment had been amplified. We purified the PCR-amplification product using the ‘QiQuick PCR Purification Kit’ (Qiagen, Holden, Germany). The purified products were cycle-sequenced using a ‘Big Dye’ (Applied Biosystems Inc, Forster City, CA, USA). Sequences were obtained on an ABI3100 sequencer. All sequences of ND2, ND3 and ATPase 6 were aligned using the algorithm in Sequencher 3.1. No insertions, deletions and stop-codons were detected in the reading frame of these three protein-coding genes suggesting that our sequences are of mitochondrial origin and not nuclear pseudogenes [23]. For the nuclear intron, sequences were aligned using Sequencher 3.1 and then exported to BioEdit v6.0.5 [24] where they were aligned more precisely by eye; these alignments indicated the presence of several insertion/deletion events. The occurrence of Single Nucleotide Polymorphisms (SNPs) in this locus was suggested by the presence of double peaks; these double peaks were coded using the appropriate IUPAC codes.

Phylogenetic Analyses

Two methods were used to infer phylogenetic relationships. Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were conducted for each dataset separately (ND2-96 taxa; ATPase 6-79 taxa; ND3-80 taxa; myoglobin intron 2-103 taxa) and for the combined dataset (67 taxa). Gaps were treated as missing data. The topologies and parameters estimated were obtained for the ML and BI with MrMODELTEST 2.0, running in conjunction with PAUP* 4.0b [27-29]. The selected models were then used for the separate ML analyses; these models and parameters estimated (base frequencies, rate matrix, shape parameter, proportion of invariable sites) are detailed in legends of the figures (Figs. 1-4). Nodal supports in ML were estimated with 1000 bootstrap pseudo-replicates [30].

Bayesian inference was conducted for each dataset, and models as determined by MrMODELTEST 2.0 were applied to estimate optimal parameters. Four incrementally heated Metropolis-coupled Monte Carlo Markov chains were run for three million generations with trees sampled every 100 generations (30 001 trees sampled). With our sample, the stationarity was rapidly reached; the first 300 000 genera-
Fig. (1). Bayesian inference tree (mean log-likelihood value = 31103.21 SD = ± 2.89) obtained from the mitochondrial ND2 sequences under a GTR + I + G model of sequence evolution. Asterisks above the nodes indicate posterior probabilities (≥ 0.95) and those below, PhyML bootstrap values (≥0.70). Base frequencies: A = 0.40040, C = 0.36703, G = 0.06865, T = 0.16389, α = 0.688, 1 = 0.26 (estimated from PhyML) and Maximum likelihood tree (-ln = 24286.39) obtained from the mitochondrial ND2 gene is not shown.

Tensions (3000 trees) were discarded (‘burn-in’ period) and posterior probabilities (PP) were estimated from the remaining sampled generations. Four independent Bayesian runs initiated from random starting trees were performed for each dataset. Log-likelihood values and posterior probabilities across the four runs were also checked to warrant that chains had reached stationarity. For the combined Bayesian analysis, we used the selected models in a partitioned analysis (genes and codon positions) with the “unlink” command.

The topologies and nodal support obtained from different models were compared to detect incongruences. A node was considered to be supported if recovered with greater than 70% for bootstrap support [31] or with a posterior probability greater than 0.95 [32].

**Analysis of Time of Divergence**

For the diversification, we used the same method and calibration point already published in Zoologica Scripta [14] and in Journal of Avian Biology [33].

Thus, we used a Bayesian approach for estimates of divergence time using the MULTIDISTRIBUTE Software package [34, 35]. Our aim was to establish firstly the time of separation between other passerine taxa and the cisticolid clade; secondly, we aimed to find time periods within the cisticolid clade in order to discuss the origin and the diversification of the cisticolid taxa in keeping with geological events which took place during the corresponding time periods. We performed dating analyses in a relative time frame...
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**RESULTS**

**Individual and Concatenated Datasets**

We obtained between 617 (Scotocerca inquieta MNHN) and 1041 bp (majority of samples) for the ND2. Out of the full alignment of 1041 characters, 628 (60.33%) were parsimony informative and 718 (68.97%) variable. MrMODELTEST selected the GTR + G + I as the best-fit model. For Bayesian inference, the average of the four runs resulted in −ln = 31103.21 with a SD = ± 2.89. Both BI and ML recovered the same topology which received high bootstrap and posterior probabilities (Fig. 1).

With the myoglobin intron 2, we obtained between 634 (Prinia flavicans bihe MNHN) and 640 bp (majority of samples). Indels were observed of which the most noteworthy

![Bayesian inference tree](image-url)
are indicated in the Table 2. The aligned myoglobin sequences comprised 640 characters, of which 220 (34.37%) and 406 (63.44%) were parsimony informative and variable, respectively. MrMODELTEST designated the GTR + G + I as the best-fit model. Parameters were estimated by PhyML and are given in detail in the legend of the Fig. (2). For Bayesian inference, the average of the four runs resulted in –ln = 5552.09 (sd = ± 0.78). Both ML and BI recovered the same topology which received moderate bootstrap and posterior probability support (Fig. 2).

We obtained between 485 (Bathmocercus rufus vulpinus ZMUC/CDI) and 684 bp (majority of samples) for the ATPase 6. Out of the full alignment of 684 characters, 350 (51.17%) and 381 (55.7%) were parsimony informative and variable, respectively. MrMODELTEST selected the GTR + G + I as the best-fit model. For Bayesian inference, the average of the four runs resulted in –ln = 15183.45 with a SD = ± 5.8. Both BI and ML recovered the same topology which received moderate bootstrap and posterior probability support (Fig. 3).

For the ND3, sequences length ranged from 226 bp (Platysteira cyanea MNHN) to 351 bp (majority of samples). Out of the full alignment of 351 characters, 192 (54.7%) were parsimony informative and 218 (62.11%) variable. MrMODELTEST designated the GTR + G + I as the best-fit model. For Bayesian inference, the average of the four runs resulted in –ln = 7909.51 (sd = ± 5.14). Both BI and ML

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### Table 1. Primers Sequences Used for Amplification and Sequencing

<table>
<thead>
<tr>
<th>Primers</th>
<th>Sequence</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>L5219Met (ND2)</td>
<td>5’ CCC ATA CCC CGA AAA TGA TG 3’</td>
<td>Sorenson et al. (1999)</td>
</tr>
<tr>
<td>INTL (ND2)</td>
<td>5’ TGR ATR GGV CTN AAY CAR AC 3’</td>
<td>Nguembock et al. (2007)</td>
</tr>
<tr>
<td>INTH (ND2)</td>
<td>5’ GNG MGM GAT RAK GAG AAG GTC A 3’</td>
<td>Nguembock et al. (2007)</td>
</tr>
<tr>
<td>H6313Trp (ND2)</td>
<td>5’ CTC TTA TTT AAG GCT TTG AAG GC 3’</td>
<td>Sorenson et al. (1999)</td>
</tr>
<tr>
<td>ATPase 6 (A8PWL)</td>
<td>5’ CCTGAACCTGACCATGAAC 3’</td>
<td>Eberhard and Bermingham (2004)</td>
</tr>
<tr>
<td>ATPase 6 (CO3HMH)</td>
<td>5’ CACATAGTRGACCCCGACCGCATG 3’</td>
<td>Eberhard and Bermingham (2004)</td>
</tr>
<tr>
<td>L10755 (ND3)</td>
<td>5’ GACTTCAATCTTAAAATCTGG 3’</td>
<td>Chesser (1999)</td>
</tr>
<tr>
<td>H11151 (ND3)</td>
<td>5’ GATTGTTGAGCCGAAATCCAAC 3’</td>
<td>Chesser (1999)</td>
</tr>
<tr>
<td>MYO2 (Myoglobin)</td>
<td>5’ GCCACCAGGCAACAGAAGATCCC 3’</td>
<td>Slade et al. (1993)</td>
</tr>
<tr>
<td>MYO2IntF</td>
<td>5’ TRA GAC CCA TAA AAC TAA GTG 3’</td>
<td>Nguembock et al. (2007)</td>
</tr>
<tr>
<td>MYO3IntR</td>
<td>5’ TGA TCT GCT TCA TGA CCT C 3’</td>
<td>Nguembock et al. (2007)</td>
</tr>
<tr>
<td>MYO3F (Myoglobin)</td>
<td>5’ GCAAGGACCTTGATAATGACTT 3’</td>
<td>Heslewood et al. (1998), modified</td>
</tr>
</tbody>
</table>

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### Table 2. The Most Noteworthy Indels Observed in the Myoglobin Intron 2

<table>
<thead>
<tr>
<th>Types of indel identified</th>
<th>Total length of the indels</th>
<th>Taxa sharing each of the different indel</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 – autapomorphic deletion</td>
<td>seven bases</td>
<td>representatives of Orthotomus</td>
</tr>
<tr>
<td>2 – autapomorphic insertion</td>
<td>one base</td>
<td>representatives of Orthotomus sutorius</td>
</tr>
<tr>
<td>3 – synapomorphic deletion</td>
<td>seven bases</td>
<td>Prinia bairdi, Prinia subflava and Heliolais erythropterus</td>
</tr>
<tr>
<td>4 – autapomorphic deletion</td>
<td>seven bases</td>
<td>representatives of Prinia flavicans</td>
</tr>
<tr>
<td>5 – autapomorphic insertion</td>
<td>one base</td>
<td>representatives of Prinia flavicans</td>
</tr>
<tr>
<td>6 – synapomorphic deletion</td>
<td>four bases</td>
<td>members of the Asiatic prinias</td>
</tr>
<tr>
<td>7 – autapomorphic deletion</td>
<td>two bases</td>
<td>samples of Eminia lepida</td>
</tr>
<tr>
<td>8 – autapomorphic deletion</td>
<td>one base</td>
<td>samples of Hypergerus atriceps</td>
</tr>
<tr>
<td>9 – synapomorphic insertion</td>
<td>three bases</td>
<td>Oreolais and Artisornis</td>
</tr>
<tr>
<td>10 – synapomorphic deletion</td>
<td>two bases</td>
<td>Oreolais and Artisornis</td>
</tr>
<tr>
<td>11 – synapomorphic deletion</td>
<td>four bases</td>
<td>Urolais, Schistolais, Oreolais and Artisornis</td>
</tr>
<tr>
<td>12 – autapomorphic insertion</td>
<td>one base</td>
<td>members of Artisornis metopias</td>
</tr>
</tbody>
</table>
recovered the same topology which received low bootstrap and posterior probability (tree not shown).

The concatenated dataset included 67 OTUs and 2723 bp. In Bayesian analyses, the concatenated dataset was partitioned by gene and codon position (ten partitions). The four independent runs with the concatenated dataset partitioned yielded a 50% majority consensus rule tree (-ln = 49395.72 ± 1.64, Fig. 4) where 36 out of 43 nodes of the ingroup taxa were supported by posterior probabilities of greater than 0.95. Not surprisingly our results suggest that the tree based on mitochondrial protein-coding data (ATPase 6, ND2 and ND3) are more resolved than the tree based on nuclear intron sequences (myoglobin intron 2) but the topology based on the combined dataset is the best resolved. As a consequence, we focus the interpretation of our results almost mainly on the combined analysis.

Phylogenetic Results

No major conflict was observed between four individual genes used, or when compared to the concatenated dataset. The only incongruence involves the position of the basal insular Neomixis; ND2 and concatenated dataset suggest that Neomixis is basal within the cisticolid clade (Figs. 1 and 4) whereas myoglobin intron 2 also recovers a basal position of this genus but only for the “forest cisticolid” clade (Fig. 2).
According to our analyses, African warblers can be divided into two main clades, very well delimited with the most informative character partitions, ND2 (Fig. 1) as well as the combined analysis (Fig. 4) but differently recovered with other markers (Figs. 2 and 3). The DNA data give high support for the monophyly of the African warblers (Figs. 1-4). Of the eight multi-specific genera studied, only Orthotomus appears polyphyletic (Figs. 1-4). We will lean on the combined tree for the presentation of the two main clades except for some particular cases where we will use individual trees.

The “open cisticolid” clade, which includes nine currently recognized genera, is moderately supported with the ND2 but not with the concatenated dataset (Figs. 1 and 4). Apalis is monophyletic in this study and A. thoracica appears in a basal position (Fig. 4).

<table>
<thead>
<tr>
<th>Node</th>
<th>Description</th>
<th>Minimum</th>
<th>Mean</th>
<th>Maximum</th>
<th>Confidence Interval (95%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Other passeridan taxa/Cisticolidae</td>
<td>14.06</td>
<td>15.14</td>
<td>16.22</td>
<td>13.14 – 17.38</td>
</tr>
<tr>
<td>3</td>
<td>Open warblers clade/other cisticolid taxa</td>
<td>11.9</td>
<td>12.92</td>
<td>13.94</td>
<td>11.02 – 15.01</td>
</tr>
<tr>
<td>4</td>
<td>Orthotomus and Prinia/other taxa of the open warblers clade</td>
<td>10.45</td>
<td>11.43</td>
<td>12.4</td>
<td>9.58 – 13.41</td>
</tr>
<tr>
<td>5</td>
<td>Forest warblers clade/other cisticolid taxa</td>
<td>10.03</td>
<td>10.99</td>
<td>11.95</td>
<td>9.2 – 12.98</td>
</tr>
<tr>
<td>6</td>
<td>Orthotomus/Prinia</td>
<td>8.42</td>
<td>9.34</td>
<td>10.26</td>
<td>7.65 – 11.24</td>
</tr>
<tr>
<td>7</td>
<td>Poliolais, Calamonastes and Camaroptera/Urolais, Oreolais, Artisornis and Schistolais</td>
<td>7.92</td>
<td>8.84</td>
<td>9.76</td>
<td>7.16 – 10.74</td>
</tr>
<tr>
<td>8</td>
<td>Incana, Scepmomycter and Bathmocercus/Cisticola</td>
<td>7.2</td>
<td>8.01</td>
<td>8.82</td>
<td>6.52 – 9.71</td>
</tr>
<tr>
<td>9</td>
<td>Schistolais/Urolais, Oreolais and Artisornis</td>
<td>7.06</td>
<td>7.95</td>
<td>8.84</td>
<td>6.31 – 9.83</td>
</tr>
<tr>
<td>10</td>
<td>Prinia (Asia)/Prinia (Africa)</td>
<td>6.39</td>
<td>7.21</td>
<td>8.03</td>
<td>5.72 – 8.93</td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Phylogeny of the African Warblers**

The phylogram obtained represents the best estimate of the relationships within the cisticolid clade and two main clades appear to be strongly supported.

In their phylogeny, Neomixis appears to be in a basal position and this result agrees with Nguembock et al. [3]. With regard to their sister-group neither Yellow Longbill nor Pycnonotidae nor Timaliidae taxa were found close to Afri-
can warblers. In return two insular genera, Oxylabes and Cryptosylvicola, and two other taxa, Hylia prasina and Pholidornis rufiastra, are well-supported as their sister-taxon in our ND2 tree but these two last taxa were lacking in our combined tree. Otherwise, some sylviid taxa, such as the genus Sylvia, were lacking. Thus, their sister-group can be best considered as unresolved and we prefer to wait a further study to confidentially define them.

According to our main results, two clades of the African warblers are well-supported (Figs. 1-4). These two clades have been suggested by some authors [2, 11] but only this splitting was not based on molecular results. With regard to these authors, the cisticolid clade should be divided into two lineages and our results virtually retrieve their suggestion. The first includes the largest genus, Cisticola, a combination of African genera, Scopomycter, Bathmocercus, Incana, Heliolais, Eminia and Hypergerus, an Asian-African genus, Prinia, and an Asian genus, Orthotomus. The second includes mainly African genera, Apalis, Schistolais, Urolais, Poliolais, Camaroptera, Calamastes, Artisornis and Oreola.

In reflection to our results, the splitting of the African warblers is almost in agreement with their living environment. Thus, African warblers included in the “open cisticolid” clade are almost all or less birds living in an open environment. These taxa often present brightly plumage color [2, 11, 36]. Many of their members also show some common characteristics such as the nest structure which is usually enclosed, typically a ball with a side entrance at the top [2, 11, 36].

Also, for taxa in the “forest cisticolid” clade, practically all these birds live in forest, in dense woodland or in more dense areas [2, 11, 36]. This “forest cisticolid” clade was already obtained by Sefc et al. [6], Alström et al. [8], Nguembock et al. [3] and Nguembock et al. [4]. This “forest
The Streaked Scrub-warbler, Scotocerca inquieta, is a Palearctic monotypic species. Molecularly, it would have been studied by Sokolov [38] and has been formally studied by Nguembock et al. [10]. Preliminary results obtained by these authors have been confirmed by Alström et al. [37]. This species was previously placed in the cisticolid clade but according to our combined results (with 2716 bp), the Streaked Scrub-warbler is a cettid taxon (Fig. 4). Its isolated position was surprising at first glance but it is consistent with several morphological and ecological traits particularly in their juveniles.

Furthermore, the White-tailed Warbler, Poliolais lopezi, is a cisticolid taxon (Figs. 1, 2 and 4). This taxon is a monospecific genus endemic to the south-east of Nigeria, Cameroon highlands and the Bioko Island. It is a tiny forest warbler with a noteworthy fine and longish bill (B. Nguembock personal observation) and it inhabits mountain forest. According to [2], its affinities are uncertain and our study fails to find its sister-taxon.

Otherwise, for cisticolid taxa newly included in a molecular study (for instance Camaroptera superciliaris, Cisticola tinniens, Prinia flavicans, etc.), several new sub-specific, inter-specific and inter-generic relationships appeared strongly supported (Figs. 1, 2, 3 and 4). Our study also confirms a strong relationship between the new cisticolid genus Oreolais sensu Nguembock et al. [4] and the genus Artisornis.

Suggestion of the Taxonomic Change

Our study included two tailorbirds (Artisornis metopias and Orthotomus sutorius) which belong to the Cisticolidae family (Figs. 1-4). But it also includes an Asian species, Orthotomus cucullatus, which belongs to the Cettidae family. In the past, this species was included in the cisticolid clade but Alström et al. [8] had shown that it was close to Cettia. Nguembock et al. [3] had confirmed that this taxon was outgroup to a cisticloid clade. To avoid a muddle between this Cettia species and other Asian tailorbirds and waiting a large study including the type species of Orthotomus, O. septum Horsf., 1821, we propose temporarily that the name Phyllergates cucullatus Temminck, 1836, be used for samples hitherto referred to Orthotomus cucullatus of the present study.

Diversification of the Cisticolid Taxa

Within the Passerida, Barker et al. [16] suggested that the diversification of most groups took place during the Miocene epoch. Like Barker et al. [16] concerning the two clades of the African warblers, our data suggest that they began their diversification during the transition Early-Middle Miocene epoch (Table 3). As a result, we think that it is not careful to suggest a hypothesis on the origin of the cisticolid clade because we did not confidentially resolve their sister-taxa.

Currently, cisticolid taxa are throughout the World but mainly in the African mainland. Their phylogram gives high support for their basal branch (the insular Neonixis). We estimated the time period of the insular basal divergence from other remaining continental cisticolid taxa at 13.55 Ma and this date virtually corresponds to that estimated for the arrival of Carnivora to Madagascar [39]. These authors noted that these mammals probably emigrated from Africa. In accordance, the diversification of insular African warblers from continental Africa seems to be likely due to the fact that interchanges between some mammals ranging from Madagascar and Africa have equally been proved during this time frame [39]. The diversification of other cisticolid taxa would have involved dispersal and vicariance processes inside the African mainland.

The diversification of the “open cisticolid” clade would have occurred during the Middle Miocene. As for the diversification of the “forest cisticolid” lineage, it would have taken place during the Upper Miocene (Table 3). Within this “open cisticolid” clade, at least two intercontinental dispersal events, involving African and Asian mainlands, took place during the Upper Miocene epoch (Fig. 5). We note that these two intercontinental events coincide with our estimation of the divergence between the Asian Orthotomus and the African-Asian Prinia. Similarly, the diversification of other endemic African taxa took place during the same Neogene period (Fig. 5). According to [40], the mammalian faunal interchange between Afro-arabia and Eurasia took place less than 27 Myrs during the Neogene period. We think that the dispersal of some African taxa from Asia would have likely taken place during the same period.

For the diversification of endemic African taxa of the cisticolid clade during the Neogene period, it is well documented that a few geological changes have affected African biota. Particularly, there is a spread of grasslands corresponding to a contraction of the forest cover in the early Miocene, and an uplift of rift shoulders [41, 42]. Moreover, during the Neogene age, the uplift caused the isolation of eastern lowland forests from the main Guinea-Congolian rainforest block [43-46]. Furthermore, some palynological evidence suggests high rainforest biodiversity during the Miocene epoch in Africa [47, 48]. Due to the geological and climatic deterioration, the dispersal of cisticolid clades in Africa was very likely by the break-up of tropical forests during the Neogene period. Within the “forest cisticolid” lineage, our data suggest an early dispersal of genera Camaroperta, Calamonastes and Poliolais during the Late Miocene but the diversification of the genus Schistolais took place during the Upper Miocene (Fig. 5).
**CONCLUSION**

The phylogeny of the African warblers appears more structured with our study. Firstly their monophyly as well as their basal branch are strongly supported. Secondly this group, which was included during long time in the paraphyletic Old World Warblers, comprises henceforth two main clades (the “open cisticolid” and the “forest cisticolid”) with the “forest cisticolid” clade which appears to be a natural lineage. Within these clades, several new relationships are strongly supported.

The diversification of the African warblers in time and in space aligns oneself with previous results [16, 39, 40]. Thus, the diversification of their two clades would have taken place during the Neogene period. Otherwise in our study, we observe that dispersal and vicariance processes inside the African mainland would have influenced the diversification within the two cisticolid clades.

**ACKNOWLEDGEMENTS**

We are grateful to many people who contributed to the knowledge of the Cisticolidae family throughout the World. We thank Jon E. Ahlquist for their study which permitted to identify the cisticolid clade. We thank all researchers who took part in a study in keeping with this cisticolid clade: Burt L. Monroe, Jr., Alice Cibois, Thomas S. Schulenberg, Kris-
The author(s) confirm that this article content has no conflicts of interest.

**ABBREVIATIONS**

- **Bp** = base pairs
- **ATPase 6** = ATP synthase subunit 6
- **ND2** = NADH dehydrogenase subunit 2
- **ND3** = NADH dehydrogenase subunit 3
- **BI** = Bayesian Inference
- **ML** = Maximum Likelihood
- **Myrs/Ma** = Millions years
- **SD** = Standard Deviation
- **OUT** = Operational Taxonomic Unit

### Annexe

**Annexe. Names of Taxa (Following Dickinson [12] and Several Recent Molecular Works), Family and Country for Individual Specimens, Museum Voucher or Tissue Numbers and the Length of DNA Sequences Used in This Study. Acronyms are: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; NRM, Swedish Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; MNHN, Museum National d’Histoire Naturelle; ZMUC, Zoological Museum of the University (Copenhagen)**

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**CONFLICT OF INTEREST**

We are also grateful to various researchers, particularly Jon Fjeldsä and Eric Pasquet, and institutions that caught and provided several samples or those whose sequences have been used in our study: FMNH, UMMZ, MNHN, ZMUC and all staff of WWF-Nyassosso (Cameroon). We wish to thank J. Lambourdière and C. Bonillo for their help during laboratory work (France). In additional, we thank several anonymous referees for their comments on an earlier version of this manuscript, particularly a few Anglophone researchers and students of the University of Yaounde I (Cameroon). We also thank the “Service de Systématique Moléculaire” of the “Muséum National d’Histoire Naturelle”, the Génoscope “Consortium National de Recherche en Génomique” (France) and the Zoological research Laboratory of the University of Yaounde I (Cameroon) for their technical support.
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**Cisticolidae** (Genbank and Eml-bank sequences)

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*Cisticola cantans swanzii*  
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UMMZ 235.853  
AY136593

*Cisticola fulvicapilla hallae*  
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*Cisticola juniceps juniceps*  
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MNHN  
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*Cisticola juniceps juniceps*  
Italia  
Cisticolidae  
NRM  
DQ008544

*Eminia lepida*  
Kenya  
Cisticolidae  
UMMZ 211635  
AY136598

*Heliolais erythropterus erythropterus*  
Niger  
Cisticolidae  
NRM  
DQ008550

*Hypergerus atriceps*  
Gambia  
Cisticolidae  
UMMZ A345  
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*Orthotomus atrogularis nitidus*  
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NRM  
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*Orthotomus satorius inexpectatus*  
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Cisticolidae  
NRM  
DQ008542

*Prinia criniger catharia*  
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NRM  
DQ008540

*Prinia familiaris*  
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AY136595

*Schistolais leucopogon leucopogon*  
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*Other groups included in this study*

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UMMZ A571  
AY136588

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*Cettia fortipes*  
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Cettidae  
-  
DQ125976  
DQ125948

*Cettia fortipes*  
-  
Cettidae  
KIZ05353  
DQ837490

*Copsychus saularis*  
Thailand  
Musciapidae  
MNHN  
JX259121  
DQ125977  
JX259228  
DQ871424

*Criniger chloronotus*  
Cameroon  
Pycnonotidae  
MNHN  
JX259157  
JX259250  
JX259184

*Cryptospiza reichenovii*  
Cameroon  
Estrildidae  
MNHN  
JX259158  
JX259206  
JX259251  
JX259185

*Dyaphorophia concreta*  
Cameroon  
Platyaeidae  
MNHN  
JX259160  
JX259208  
JX259253  
JX259187

*Elminia albiventris*  
Cameroon  
Stenostiridae  
MNHN  
40-63  
JX259151  
EU652712  
JX259246  
JX259179

*Hylia prasina*  
-  
Cettidae  
LSUMZ 163337  
AY136606  
DQ125955

*Illadopsis albiceps*  
Cameroon  
Timaliidae  
MNHN  
JX259153  
JX259205  
EU866336  
JX259181

*Kakamega politothorax*  
Cameroon  
Timaliidae  
MNHN  
40-4  
JX259131  
EU686330  
EU686374  
EU686289

*Linurgus olivaceus*  
Cameroon  
Fringillidae  
MNHN  
40-8  
EU880940  
EU652706  
EU881006  
EU669964

*Orthotomus cucullatus cucullatus*  
Indonesia  
Cettidae  
NRM  
DQ008566

*Orthotomus cucullatus heteroalaeus*  
Philippines  
Cettidae  
FMNH 357483  
JX259116  
DQ125999  
JX259225  
DQ871419

*Picathartes gymnocephalus*  
Liberia  
Picatharidae  
AMNH AC350  
DQ125989  
AY228314

*Pholidornis rushiae*  
-  
Paridae  
ZFMK 61.1422  
AY136586

*Platysteira cyanea*  
Cameroon  
Platysteiridae  
MNHN  
JX259161  
JX259209  
JX259254  
JX259188
### Pseudocippe abyssinica monachus
- Cameroon
- Timaliidae
- MNHN 40-75
- JX259154
- EU652717
- EU686376
- EU669975

### Pycnonotus barbatus inornatus
- Cameroon
- Pycnonotidae
- MNHN
- JX259156
- -
- JX259249
- JX259183

### Rhopophilus pekinensis
- China
- Timaliidae
- NRM
- DQ008538

### Scotocerca inquieta
- Cettidae
- MNHN
- JX259145
- JX259203
- JX259244
- JX259177

### Sylvia atricapilla
- Israel
- Timaliidae
- NC_010228

### Sylvia atricapilla
- Sweden
- Timaliidae
- NRM 976380
- AY887727

### Zosterops japonicus
- -
- Zosteropidae
- GLGS2247
- DQ837491

### Zosterops palpebrosus
- -
- Zosteropidae
- MNHN
- DQ125973

### Zosterops poliogaster
- -
- Zosteropidae
- GLGS1833
- DQ837502

### Acrocephalus bistrigiceps
- Japan
- Sylviidae
- UMMZ 234.837
- AY136601

### Cryptosylvicola randrianasoloi
- -
- Sylviidae
- MNHN
- JX259128
- JX259233
- JX259166

### Garrulax chinensis
- -
- Sylviidae
- NRM 20046790
- DQ008536

### Garrulax erythrocephalus
- -
- Sylviidae
- MNHN
- DQ861987

### Macrosphenus flavicans
- Cameroon
- Sylviidae
- MNHN
- JX259094
- DQ125997
- JX259213
- DQ871393

### Nesilla typica
- -
- Sylviidae
- MNHN
- JX259130
- JX259193
- JX259234
- JX259167

### Oxylabes madagascariensis
- -
- Sylviidae
- MNHN
- JX259089
- JX259210
- JX259162

### Sylvietta brachyura
- -
- Sylviidae
- MNHN
- JX259095
- DQ871386
- -

### Sylvietta virens
- Gambia
- Sylviidae
- UMMZ 235.840
- AY136602

### Sylvietta whytii
- Kenya
- Sylviidae
- ZMUC
- DQ871423

### Yuhina brunneiceps
- -
- Sylviidae
- MNHN
- JX259127
- DQ871386
- -

### Yuhina gularis
- -
- Sylviidae
- MNHN
- DQ861973

### Outgroup

### Tersiphone rufiventer
- Cameroon
- Monarchidae
- MNHN 40-64
- JX259152
- JX259204
- JX259247
- JX259180

### Hylia (Hylia prasina), and Tit-hylia (Pholidornis rashiae). Ostrich 2003; 74: 8-17.


