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# Convergent evolution of morphological and ecological traits in the open-habitat chat complex (Aves, Muscicapidae: Saxicolinae)

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ABSTRACT

Open-habitat chats (genera *Myrmecocichla*, *Cercomela*, *Oenanthe* and relative) are a morphologically and ecologically cohesive group of genera with unclear phylogenetic relationships. They are distributed mostly in open, arid and/or rocky habitats of Africa and Eurasia. Here, we present the most comprehensive molecular phylogenetic analysis of this group to date, with a complete taxon sampling at the species level. The analysis, based on a multilocus dataset including three mitochondrial and three nuclear loci, allows us to elucidate the phylogenetic relationships and test the traditional generic limits. All genera are non-monophyletic, suggesting extensive convergence on similar plumage patterns in unrelated species. While the colour pattern appear to be a poor predictor of the phylogenetic relationships, some of the ecological and behavioural traits agree relatively well with the major clades. Following our results, we also propose a revised generic classification for the whole group.



## 1. Introduction

The open-habitat chats occur mostly in open, arid and/or rocky habitats of Africa and Eurasia. The members of this group of birds share many elements of their ecology, behaviour and morphology (Tye, 1989a; Lynes, 1924–1926; Panov, 2005; Kaboli et al., 2007). Most species display a predominantly black-and-white, brown or grey plumage pattern. They are currently included in five genera, *Campicoloides*, *Cercomela*, *Myrmecocichla*, *Oenanthe* and *Thamnolaea* (Dickinson, 2003), with 39 or so species-level taxa. Despite extensive work on open-habitat chats' ecology, biogeography, ethology, and morphology (Vaurie, 1955; Cornwallis, 1975; Potapova and Panov, 1977; Ivanitzky, 1980; Loskot, 1983; Grabovsky and Panov, 1992; Panov, 2005; Kaboli et al., 2007) their alpha-taxonomy is not fully understood. In the wheatears of the genus *Oenanthe*, the species delimitation is complicated by the presence of distinct subspecies and/or the occurrence of light and dark morphs in certain populations. Recent molecular analyses have detected a considerable genetic distance within some species (*Oenanthe lugens*: Förschler et al., 2010; *Myrmecocichla arnotti*: Glen et al., 2011; *Oenanthe hispanica*: Randler et al., 2012), suggesting that some well differentiated populations should be treated as distinct species.

The group as a whole is clearly monophyletic, but the internal relationships recovered from three published datasets are conflicting with respect to the branching pattern of the major lineages (Zuccon and Ericson, 2010a; Sangster et al., 2010; Outlaw et al., 2010), possibly because of the incomplete taxon sampling. While the phylogenic relationships in *Oenanthe* and *Cercomela* have been elucidated in greater detail (Aliabadian et al., 2007; Outlaw et al., 2010), the relationships of *Myrmeococichla* and *Thamnolaea* with the other chats remain to be investigated.

The genus *Myrmecocichla* consists of seven open-habitat chats endemic to the Sub-Saharan Africa (Sibley and Monroe, 1990; Borrow and Demey, 2001; Dickinson, 2003; Clements, 2007). These small to medium-sized ground-dwelling chats have a predominant black plumage, a very upright stance, a short but often cocked tail,

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a curious low buzzing flight, and highly simplified songs (Collar, 2005). The limits of *Myrmecocichla* have sometimes been enlarged to include also *Thamnolaea*, two African, relatively large, rufous-bellied species that inhabit rocky hillsides and often nest in old swallows' nest (Keith et al., 1992). However, while *Thamnolaea semirufa* was recently shown to be part of the *Monticola* radiation (Zuccon and Ericson, 2010b), *T. cinnamomeiventris* is effectively closely related to *Myrmecocichla* (Zuccon and Ericson, 2010a; Sangster et al., 2010). Alternatively *Myrmecocichla arnotti* and *M. albifrons* were removed from *Myrmecocichla* and transferred to the genus *Pentholaea* for the lack of white wing panels, more elaborated songs and the tendency to nest in tree holes (Collar, 2005). The resemblance of *Myrmecocichla* to certain species of *Oenanthe* (most notably the close similarity of *M. arnotti* to *O. monticola*) has been considered an indication of a close relationship between *Oenanthe* and *Myrmecocichla* (Collar, 2005).

Hitherto the main difficulty with open-habitat chats classification is the heavy reliance on highly variable plumage characters that can be susceptible to selective pressure obscuring true phylogenetic relationships. Indeed a reassessment of the relationships of *Cercomela* revealed extensive polyphyly, with four distinct lineages variously interspersed in the open-habitat chat clade, with repeated convergence in plumage pattern in *Cercomela* and *Oenanthe* (Outlaw et al., 2010).

Here, we present the most comprehensive molecular phylogenetic analysis of the open-habitat chats to date with a complete taxon sampling at the species level. The analysis, based on a multilocus dataset including both fast-evolving mitochondrial DNA genes and more moderate-to-slow evolving nuclear DNA loci, allows us to elucidate the phylogenetic relationships, test the traditional generic limits and propose a revised classification of the whole group.

## 2. Materials and methods

### 2.1. Taxon sampling and gene choice

We sampled all species in the genera *Campicoloides*, *Cercomela*, *Myrmecocichla* and *Oenanthe*, plus *Thamnolaea cinnamomeiventris*. *Thamnolaea semirufa*, which belongs to the *Monticola* clade (Zuccon and Ericson, 2010b), was excluded from the analysis. Following the redefinition of certain species limits, we treated *Myrmecocichla* (*arnotti*) *collaris*, *O.* (*lugens*) *persica*, *O.* (*lugens*) *lugubris*, and *O.* (*hispanica*) *melanoleuca* as valid species (Förschler et al., 2010; Glen et al., 2011; Randler et al., 2012).

We used five species belonging to the genera *Saxicola*, *Monticola* and *Phoenicurus* as outgroups, since these are the sister lineages to our ingroup (Zuccon and Ericson, 2010a; Sangster et al., 2010).

Samples were obtained from freshly collected specimens as well as from museum skins. Table 1 provides a list of the taxa included in this study, together with museum accession numbers, collection localities and Genbank accession numbers.

The sequences used in this study were obtained in different laboratories for independent projects and merged only at a later stage. The original projects chose different markers and used samples deriving from different individuals, although the species sequenced were almost the same. In the Stockholm lab, we sequenced the NADH dehydrogenase subunits II and III (ND2 and ND3) and three nuclear loci, intron 11 of the glyceraldehyde-3-phosphodehydrogenase (GAPDH), intron 2 of the myoglobin gene (MYO), and introns 6 and 7 of the ornithine decarboxylase (ODC), while in Paris and Amsterdam, we sequenced ND2, the cytochrome oxidase subunit 1 (COX1) and 16S ribosomal RNA gene (16S). For each species sequences in both labs, we used the ND2 sequences to compare the genetic distance between the two individuals, supplemented with other sequences obtained from Genbank. The degree of divergence was inspected using a neighbour-joining (NJ) tree with uncorrected *p*-distances calculated in PAUP v.4.0b10 (Swofford, 2003). In almost all comparisons, the genetic divergence between our two samples was minimal and we concatenated the sequences in a single dataset (see also in Section 3).

### 2.2. Laboratory protocols

The total genomic DNA from fresh tissues samples (blood, muscle, feathers) was extracted using DNEasy Tissue Extraction Kits (Qiagen, Inc.) following the manufacturer protocol. We used the Qiagen DNA Micro Kit for the museum skin samples with a modified protocol as described by Irestedt et al. (2006). The mitochondrial and nuclear genes were amplified and sequenced using standard primers and amplification procedures as described in Fjeldså et al. (2003) for GAPDH, Irestedt et al. (2002) for myoglobin, Allen and Omland (2003) for ODC, Zuccon et al. (2006) for ND2, Chesser (1999) for ND3, Hebert et al. (2004) for COI and Palumbi et al. (1991) for 16S. The museum study skins were amplified in a series of 200–300 bp overlapping fragments, using a large number of internal primers, whose sequences are available from the authors. The PCR products were purified using QIAquick PCR Purification Kit (Qiagen) following manufacturer instructions and sequenced using dye-labelled dideoxy terminator cycle sequencing with BigDye v3.1 (Applied Biosystems, Inc.).

### 2.3. Phylogenetic analyses

The seven loci were concatenated in a partitioned dataset analysed under the Bayesian inference and the maximum likelihood criteria.

The Bayesian inference was carried out using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003), implemented on the freely available Bioportal (www.bioportal.uio.no). A mixed model approach was implemented to account for the potential differences in evolutionary model parameters between the data partitions corresponding to the five genes. The models best fitting the data were obtained with MrModelTest (Nylander, 2004), using the AIC criterion (Akaike, 1973), in conjunction with PAUP* (Swofford, 2003). MrModelTest output suggested as the best fit the HKY + $\Gamma$ model for GAPDH and myoglobin introns and the HKY + I + $\Gamma$ model for the COI gene, while the GTR + $\Gamma$ + I model was used for remaining loci. We assumed uniform interval priors for the parameters, except for base frequencies, which were assigned a Dirichlet prior (Huelsenbeck and Ronquist, 2001). We run two independent runs of four incrementally heated Metropolis-coupled MCMC chains for 20 million generations, with sampling every 1000 generations, yielding 20,000 trees. We used the online version of AWTY (Nylander et al., 2008) to assess the convergence of the MCMC chains and to estimate the number of generations to discard as "burn-in" (2000 trees).

Maximum likelihood searches of the partitioned dataset were conducted with RAxML v. 7.0.3 (Stamatakis, 2006) using a GTR + $\Gamma$ + I model and random starting tree, with $\alpha$-shape parameters, GTR-rates, and empirical base frequencies estimated and optimised for each partition. Nodal support was estimated using 100 bootstrap replicates.

Additionally, we compared the phylogenetic signal in the nuclear and mitochondrial genomes analysing two combined datasets, concatenating the three nuclear and the four mitochondrial loci, respectively, applying the same conditions indicated above for the Bayesian inference.

We compared alternative phylogenetic hypotheses using the Shimodaira–Hasegawa test (SH-test, Shimodaira and Hasegawa, 1999), as implemented in RAxML v. 7.0.3 (Stamatakis, 2006). The tested

**Table 1**
Samples and sequences included in the phylogenetic analysis, with museum accession numbers and collection localities. The taxonomy follows Dickinson (2003). GenBank accession numbers of sequences published previously are followed by their references. Museum acronyms: BMNH, The Natural History Museum, Tring; IAR, Institute of Avian Research Wilhelmshaven, Vogelwarte Helgoland; MIUT, Museum of Ispahan University of Technology; MNHN, Muséum National d'Histoire Naturelle, Paris; NHMO, Natural History Museum, University of Oslo; NMBV, National Museum, Bloemfontein; NRM, Swedish Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum, and ZMUC, Zoological Museum of the University of Copenhagen. References: [1] Zuccon and Ericson (2010a); [2] Zuccon and Ericson (2010b); [3] Outlaw et al. (2010); [4] Aliabadian et al. (2007); [5] Glen et al. (2011); [6] Förschler et al. (2010).

| Taxon | Sample | GADPH | Myoglobin | ODC | ND2 | ND3 | COI | 16S | ND2* | Locality |
|---|---|---|---|---|---|---|---|---|---|---|
| *Campicoloides bifasciatus* | NMBV 06249 | GU358973 [1] | GU358710 [1] | GU358838 [1] | GU358779 [1] | xxx | | | | South Africa, Free State |
| | MNHN RSA073 | | | | | | xxx | xxx | xxx | South Africa |
| *Cercomela dubia* | BMNH 1902.1.20.89 | xxx | xxx | xxx | xxx | xxx | – | – | | Ethiopia |
| *Cercomela familiaris* | NRM 680265 | GU358974 [1] | GU358711 [1] | GU358839 [1] | GU237102 [2] | xxx | | | | Botswana, Francistown |
| | MNHN GA59064 | | | | | | xxx | xxx | xxx | South Africa, Berfontein |
| *Cercomela fusca* | UMMZ 181352 | xxx | xxx | xxx | xxx | xxx | – | – | | India |
| *Cercomela melanura* | NRM 89950 | xxx | xxx | xxx | xxx | xxx | | | | Israel, Sinai, Wadi Hebran |
| | IAR JA12106 | | | | | | xxx | xxx | xxx | Jordan |
| *Cercomela schlegelii* | NRM 89947 | xxx | xxx | xxx | xxx | xxx | – | – | | Angola, Benguella |
| *Cercomela scotocerca* | NRM 89960 | xxx | xxx | xxx | xxx | xxx | – | – | | Eritrea, Cheren |
| *Cercomela sinuata* | NRM RA.02 | xxx | xxx | xxx | xxx | xxx | – | – | | South Africa, Basutoland |
| *Cercomela sordida* | NRM 558924 | GU359040 [1] | GU358774 [1] | GU358905 [1] | GU358832 [1] | xxx | – | – | | Ethiopia, Addis-Abeba |
| *Cercomela tractrac* | BMNH 1950.50.434 | xxx | xxx | xxx | xxx | xxx | – | – | | Namibia, Witputs |
| *Myrmecocichla aethiops* | NRM 89928 | xxx | xxx | xxx | xxx | xxx | – | – | | Kenya, Eldoret |
| *Myrmecocichla albifrons* | NRM 558941 | xxx | xxx | xxx | xxx | xxx | – | – | | Sudan, Zande District |
| *Myrmecocichla arnotti* | NRM 558901 | GU359016 [1] | GU358751 [1] | GU358881 [1] | GU358815 [1] | xxx | – | – | | South Africa, Transvaal |
| *Myrmecocichla collaris* | FMNH 438821 | – | – | – | HM595025 [5] | – | – | – | | Tanzania |
| *Myrmecocichla formicivora* | NMBV 06296 | xxx | xxx | xxx | xxx | xxx | | | | South Africa |
| | MNHN B038907 | | | | | | xxx | xxx | xxx | South Africa, Kimberley |
| *Myrmecocichla melaena* | BMNH 1952.25.13 | xxx | xxx | xxx | xxx | xxx | – | – | | Eritrea, Senafe |
| *Myrmecocichla nigra* | NRM 570041 | GU359017 [1] | GU358752 [1] | GU358882 [1] | GU237119 [2] | xxx | – | – | | Angola, Dembos |
| *Myrmecocichla tholloni* | BMNH 1957.35.276 | xxx | xxx | xxx | xxx | xxx | – | – | | Angola, Vouga |
| *Oenanthe alboniger* | MIUT 2003-95(18) | xxx | xxx | xxx | xxx | xxx | DQ683480 [4] | DQ683446 [4] | | Iran, Firouz Abad |
| *Oenanthe bottae* | NRM 558916 | xxx | xxx | xxx | | xxx | | | | Saudi Arabia, Taik |
| | IAR A1147 | | | | xxx | | xxx | xxx | | Ethiopia |
| *Oenanthe chrysopygia* | NRM 896463 | xxx | xxx | xxx | xxx | xxx | | | | Russia, Ordubad |
| | MIUT 2003-96(19) | | | | | | DQ683481 [4] | DQ683447 [4] | xxx | Iran, Kashan |
| *Oenanthe cypriaca* | NRM 553236 | xxx | xxx | xxx | xxx | xxx | – | – | | Cyprus, Ayia Phyla |
| *Oenanthe deserti* | NRM 20046660 | GU359019 [1] | GU358754 [1] | GU358884 [1] | GU237121 [2] | xxx | | | | Iran, Mashhad |
| | MIUT 2003-99(22) | | | | | | DQ683485 [4] | DQ683451 [4] | xxx | Morocco, Eastern high plateaus |
| *Oenanthe finschii* | NRM 896462 | xxx | xxx | xxx | xxx | xxx | | | | Russia, Dzhulfa, |
| | BMNH A/2005.2.11 | | | | | | DQ683487 [4] | DQ683453 [4] | xxx | Iran, Firouz Abad |
| *Oenanthe heuglini* | MNHN 1966.549 | xxx | xxx | xxx | xxx | xxx | – | – | | Ethiopia |
| *Oenanthe hispanica hispanica* | NRM 551781 | xxx | xxx | xxx | xxx | xxx | | | | Spain, Zafra |
| | MNHN 1995-104 | | | | | | xxx | xxx | xxx | France |
| *Oenanthe hispanica melanoleuca* | DZC 20010729.02 | xxx | xxx | xxx | xxx | xxx | | | | Greece, Rhodos |
| | IAR 81418926 | | | | | | xxx | xxx | xxx | Mali |
| *Oenanthe isabellina* | NRM 90181 | xxx | xxx | xxx | xxx | xxx | | | | Eritrea, Gheleb |
| | BMNH A/2005.2.1 | | | | | | DQ683492 [4] | DQ683458 [4] | xxx | Iran, Ispahan |

(*continued on next page*)

**Table 1** (*continued*)

| Taxon | Sample | GADPH | Myoglobin | ODC | ND2 | ND3 | COI | 16S | ND2* | Locality |
|---|---|---|---|---|---|---|---|---|---|---|
| *Oenanthe leucopyga leucopyga* | NRM 90334 | xxx | xxx | xxx | xxx | xxx | | | | Algeria, Ouad Itlou |
| | IAR HA01112 | | | | | | DQ683508 [4] | DQ683474 [4] | xxx | Morocco, Tazenakht |
| *Oenanthe leucopyga ernesti* | NHMO 22655 | xxx | xxx | xxx | xxx | xxx | – | – | | Israel |
| *Oenanthe leucura* | NRM 90197 | xxx | xxx | xxx | xxx | xxx | | | | Algeria, Tilatou |
| | IAR 82004655 | | | | | | xxx | xxx | xxx | Morocco |
| *Oenanthe lugens halophila* | IAR 503 | xxx | xxx | xxx | xxx | xxx | HM046858 [6] | HM046838 [6] | | Morocco, Boumalne |
| *Oenanthe lugens lugens* | IAR 396 | xxx | xxx | xxx | xxx | xxx | HM046860 [6] | HM046840 [6] | | Jordan, Wadi Raman |
| *Oenanthe lugens persica* | NRM 20046701 | xxx | xxx | xxx | xxx | xxx | | | | Iran |
| | BMNH A/ 2005.2.7 | | | | | | DQ683497 [4] | DQ683463 [4] | xxx | Iran, Ispahan |
| *Oenanthe lugubris* | IAR 447 | xxx | xxx | xxx | xxx | xxx | HM046871 [6] | HM046871 [6] | | Ethiopia, Jemmu |
| *Oenanthe moesta* | NRM 90315 | xxx | xxx | xxx | xxx | xxx | | | | Algeria, Bordj Saada |
| | MIUT 2003-103(26) | | | | | | DQ683500 [4] | DQ683466 [4] | xxx | Morocco, Eastern high plateaus |
| *Oenanthe monacha* | NRM 90320 | xxx | xxx | xxx | xxx | xxx | | | | Egypt, Suez |
| | IAR BG22386 | | | | | | xxx | xxx | xxx | Israel |
| *Oenanthe monticola* | NRM 90042 | xxx | xxx | xxx | xxx | xxx | | | | South Africa, Great Namaqualand |
| | MNHN RSA037 | | | | | | xxx | xxx | xxx | South Africa |
| *Oenanthe oenanthe* | NRM 966643 | GU359020 [1] | GU358755 [1] | GU358885 [1] | GU358816 [1] | xxx | | | | Sweden, Stockholm |
| | BMNH A/ 2005.2.4 | | | | | | DQ683502 [4] | DQ683468 [4] | xxx | Iran, Ispahan |
| *Oenanthe phillipsi* | MNHN 1974-1550 | xxx | xxx | xxx | xxx | xxx | xxx | | | Ethiopia |
| *Oenanthe picata* | NRM 20046664 | xxx | xxx | xxx | xxx | xxx | | | | Iran |
| | MIUT 2003-7.1(27) | | | | | | DQ683509 [4] | DQ683475 [4] | | Iran, Touran |
| *Oenanthe pileata* | NRM 90366 | xxx | xxx | xxx | xxx | xxx | | | | Tanzania, Tanga |
| | MNHN 36-E05 | | | | | | xxx | xxx | xxx | South Africa, Berfontein |
| *Oenanthe pleschanka* | NRM 20046694 | xxx | xxx | xxx | xxx | xxx | | | | Sweden (vagrant) |
| | MIUT 2003-26(30) | | | | | | DQ683507 [4] | DQ683473 [4] | xxx | Iran, Dar Gaz |
| *Oenanthe xanthoprymna* | NHMO 23723 | xxx | xxx | xxx | xxx | xxx | xxx | xxx | | Israel |
| *Thamnolaea cinnamomeiventris* | NRM 20086147 | GU359034 [1] | GU358769 [1] | GU358899 [1] | GU358828 [1] | xxx | xxx | xxx | | Nigeria, Jos |
| Outgroup | | | | | | | | | | |
| *Phoenicurus phoenicurus* | NRM 20016219 | GU359022 [1] | GU358757 [1] | GU358887 [1] | GU237122 [2] | xxx | | | | Sweden, Stockholm |
| | MNHN 22-43 | | | | | | xxx | xxx | xxx | France, Ahetze |
| *Saxicola rubetra* | NRM 20016186 | GU359028 [1] | GU358763 [1] | GU358893 [1] | GU237123 [2] | xxx | | | | Sweden, Stockholm |
| | ZMUC 131941 | | | | | | xxx | xxx | xxx | Denmark, Kongelunden |
| *Saxicola* (*torquata*) *stejnegeri* | NRM 947295 | xxx | xxx | xxx | xxx | xxx | xxx | xxx | | Vietnam |
| *Monticola gularis* | NRM 20036789 | GU359006 [1] | GU358741 [1] | GU358871 [1] | GU237106 [2] | xxx | | | | Vietnam, Kon Tum |
| | MNHN JF031 | | | | | | xxx | xxx | xxx | Cambodia |
| *Monticola solitarius* | NRM 20016756 | GU359007 [1] | GU358742 [1] | GU358872 [1] | GU358808 [1] | xxx | | | | Captivity, unknown |
| | MNHN 22-33 | | | | | | xxx | xxx | xxx | France, Corsica |

* These ND2 sequences were used only to evaluate the intraspecific divergence in the neighbour-joining tree, but they were not included in the phylogenetic analyses.

topologies were obtained enforcing the monophyly of selected taxa (see Table 3) in the maximum likelihood searches in RAxML.

We investigated the congruence of some plumage characters as well as ecological and behavioural traits with the phylogeny by mapping them onto the Bayesian topology and calculating the homoplasy and retention indices in PAUP*. The characters scores were retrieved from the literature (Cramp, 1988; Urban et al., 1997; Ali and Ripley and Ali, 1998; Panov, 2005; Collar, 2005).

**Table 2**
Sequence characteristics of the seven loci analysed. The numbers of variable and parsimony informative bases are calculated for the ingroup only.

| Gene region | GAPDH | Myoglobin | ODC | ND2 | ND3 | COI | 16S |
|---|---|---|---|---|---|---|---|
| Alignment length | 278 | 730 | 673 | 1041 | 351 | 648 | 544 |
| Number of variable bases (%) | 66 (23.7%) | 100 (13.7%) | 124 (18.4%) | 516 (49.6%) | 156 (44.4%) | 213 (32.9%) | 64 (11.8%) |
| Number of parsimony informative bases (%) | 24 (8.6%) | 26 (3.6%) | 58 (8.6%) | 419 (40.2%) | 132 (37.6%) | 168 (25.9%) | 41 (7.5%) |
| % A nucleotides (range) | 21.1 (19.6–22.6) | 28.9 (28.2–32.3) | 28.4 (27.6–29.4) | 30.3 (28.8–32.0) | 27.3 (25.1–29.6) | 23.9 (23.0–25.0) | 31.0 (29.9–31.7) |
| % C (range) | 20.5 (19.3–21.3) | 22.8 (20.5–23.2) | 16.3 (15.3–16.9) | 35.4 (33.9–36.9) | 34.8 (31.3–38.2) | 35.0 (33.8–36.6) | 26.3 (25.3–27.4) |
| % G (range) | 33.0 (31.3–34.2) | 22.7 (22.1–24.4) | 20.4 (18.8–21.2) | 11.3 (9.8–12.9) | 13.1 (11.4–15.4) | 17.2 (16.6–17.9) | 21.3 (20.6–22.1) |
| % T (range) | 25.3 (24.3–26.6) | 25.6 (22.8–26.4) | 35.0 (34.0–36.2) | 23.0 (21.7–24.6) | 24.8 (21.8–27.6) | 23.9 (22.8–24.8) | 21.4 (20.2–22.5) |
| Selected substitution model | HKY + Γ | HKY + Γ | GTR + Γ + I | GTR + Γ + I | GTR + Γ + I | HKY + Γ + I | GTR + Γ + I |

**Table 3**
Comparison of alternative phylogenetic hypotheses using the Shimodaira–Hasegawa test performed with RAxML. Δ-ln *L*: difference in tree likelihood compared to the best tree. Significant: significantly worse than the best topology, $p < 0.05$.

| Topology tested | Tree likelihood | Δ-ln *L* | SH-test |
|---|---|---|---|
| Best tree | −26133.237484 | | Best |
| Monophyly of *Cercomela* | −26370.053486 | −236.816001 | Yes |
| Monophyly of *Myrmecocichla* | −26224.734982 | −91.497498 | Yes |
| Monophyly of *Oenanthe* | −26441.402422 | −308.164938 | Yes |
| Monophyly of *Pentholaea sensu* Collar (2005) | −26283.823520 | −150.586036 | Yes |

## 3. Results

### 3.1. Gene properties

We obtained full sequences for most taxa (Table 1). The nuclear introns, ND2 and ND3genes were sequenced for all taxa, while for *Oenanthe cypriaca*, *O. heuglini*, *O. leucopyga ernesti* and for most *Cercomela* and *Myrmecocichla* species we miss COI and 16S. We checked the possible amplification of pseudogenes translating the protein coding genes into amino acids sequences, but we did not observe any unexpected stop codons or unusual amino acidic substitutions.

The sequence alignment was straightforward, thanks to the limited number of indels in the three introns and in the 16S gene. The seven genes were concatenated in a single dataset of 4265 bp. Of these 1239 sites were variable (29.1%) and 868 parsimony informative (20.4%). Table 2 presents a summary of the molecular properties of each partition.

### 3.2. Intraspecific variability

The NJ tree includes all our ND2 sequences plus the *Oenanthe* and *Cercomela* dataset of Outlaw et al. (2010) and a selection of other Muscicapidae (Suppl. material Fig. S1). In all cases the genetic distance between our sequences for the same taxon was modest (0–0.9%, uncorrected *p*-distance) and we are confident that concatenating the sequences obtained from the two individuals in a single dataset does not affect the results in a species-level analysis as the one presented here.

Comparing our sequences with other ND2 sequences retrieved from Genbank, we generally observed a very low intraspecific divergence in most species. Only *Oenanthe finschi*, *O. hispanica*, *O. leucopyga*, *O. lugens*, *Cercomela melanura* and *C. sordida* showed higher intraspecific genetic distances (2.0–4.3% *p*-distance). These results are not surprising since these species are polytypic, with large and fragmented ranges, and thus it is not surprising that they might be genetically structured.

However, we noted that three ND2 sequences (*Cercomela dubia* GU055396–GU066397 and *C. scotocerca* GU055410) included in Outlaw et al.'s analysis (2010) were deeply different from ours for the same species and were misplaced in the NJ tree in comparison to the remaining open-habitat chats. Also one sequence of *Cercomela fusca* (GU055403) and one of *C. sordida* (GU055414) are quite different from the others from the same species (5.5% and 6.9% *p*-distance, respectively). An in depth analysis of the sequences used by Outlaw et al. (2010) revealed that some of them are likely chimaeras containing fragments belonging to other species of Muscicapidae (see Suppl. materials for details).

### 3.3. Phylogenetic analysis

The Bayesian tree (Fig. 1) results in a well resolved topology with four major clades, where none of the polytypic genera (*Cercomela*, *Myrmecocichla* and *Oenanthe*) are monophyletic. Our results support a clade including *Campicoloides bifasciatus* and the three southern African sickle-winged chats (*Cercomela schlegelii, C. tractrac,* and *C. sinuata*) (Clade 1 in Fig. 1). In this clade, *C. tractrac* and *C. sinuata* are sister taxa with 100% bootstrap support.

In the clade 2, *Cercomela sordida* is the basal lineage, followed by *Thamnolaea cinnamomeiventris* and the group of most *Myrmecocichla* plus *Oenanthe monticola*. Here *Myrmecocichla formicivora*, *M. aethiops* and *M. tholloni* form a well defined lineage as well the group *M. melaena, M. arnotti* and *M. collaris*, whereas the positions of *M. nigra* and *Oenanthe monticola* are not supported.

The clade 3 comprises exclusively of *Oenanthe* species. *Oenanthe oenanthe*, *O. pileata*, *O. bottae*, *O. heuglini* and *O. isabellina* form a well defined lineage as well the group composed by *O. deserti*, *O. monacha*, *O. hispanica hispanica*, *O. hispanica melanoleuca*, *O cypriaca* and *O. pleschanka*. *Oenanthe hispanica melanoleuca*, *O cypriaca* and *O. pleschanka* appear to be closely related, with minimal genetic divergence.

The last clade (clade 4) is the most heretogeneous taxonomically, including about half *Oenanthe* species, *Myrmecocichla albifrons* and five *Cercomela*. *Myrmecocichla albifrons* together with *Oenanthe phillipsi* form the sister lineage to the remaining species. Four North-African *Cercomela* form a separate lineage, whereas the Indian *C. fusca* is sister to *Oenanthe picata* within a group of mostly Palearctic species.

The maximum likelihood analysis recovered a topology congruent with the Bayesian tree. The few observed differences involve the resolution of two polytomies. However, in the ML tree, the nodes involved receive poor support values.

The analysis of the mitochondrial and nuclear datasets recovers less well-resolved trees, in both the Bayesian and maximum likelihood analyses (Suppl. material Figs. S2 and S3). This is especially true in the nuclear topology, where most nodes have very low support values.

The Shimodaira–Hasegawa test rejected as significantly less likely the traditionally defined genera *Cercomela*, *Myrmecocichla*

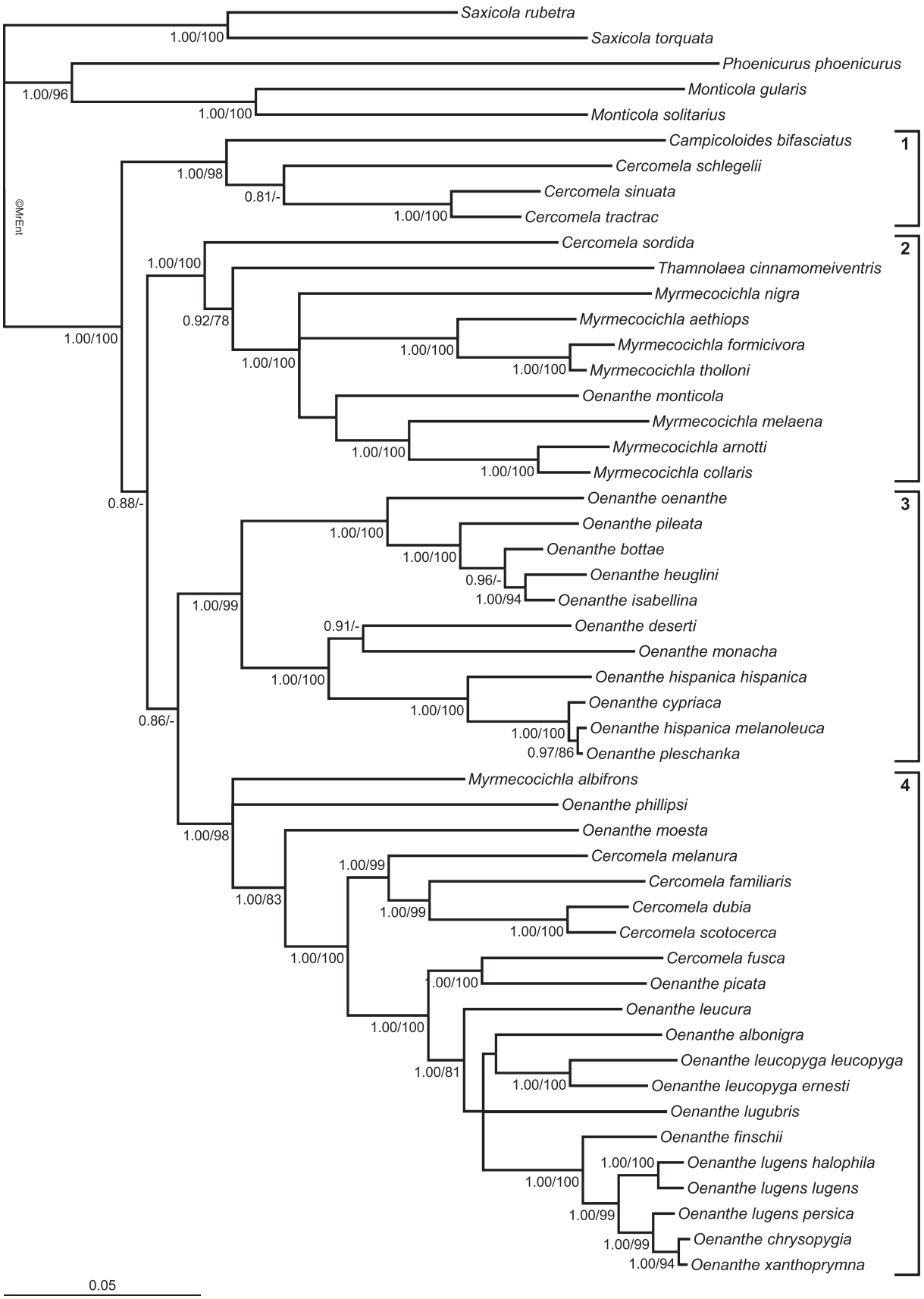


**Fig. 1.** The majority rule consensus tree obtained from the mixed-model Bayesian analysis of the concatenated dataset. The support values indicated at the node are the posterior probability (threshold 0.70) and the bootstrap support (threshold 70%) obtained from the maximum likelihood analysis, respectively. Brackets and numbers on the right refer to the clades discussed in the text. The tree was edited in MrEnt v.2.2 (Zuccon and Zuccon, 2010).

and *Oenanthe*, as well the genus *Pentholaea* sensu Collar (2005) (Table 3).

The character mapping onto the Bayesian topology reveals that most analysed traits are highly homoplastic (high homoplasy indices and low retention indices, Fig. 2). Only the choice of nest meterial agrees rather well with the tree topology (homoplasy index 0.60 and retention index 0.86).

## 4. Discussion

### 4.1. Relationship among the open-habitat chats

Open-habitat chats are a morphologically and ecologically cohesive group of genera with unclear phylogenetic relationships (Zuccon and Ericson, 2010a; Sangster et al., 2010). Some molecular

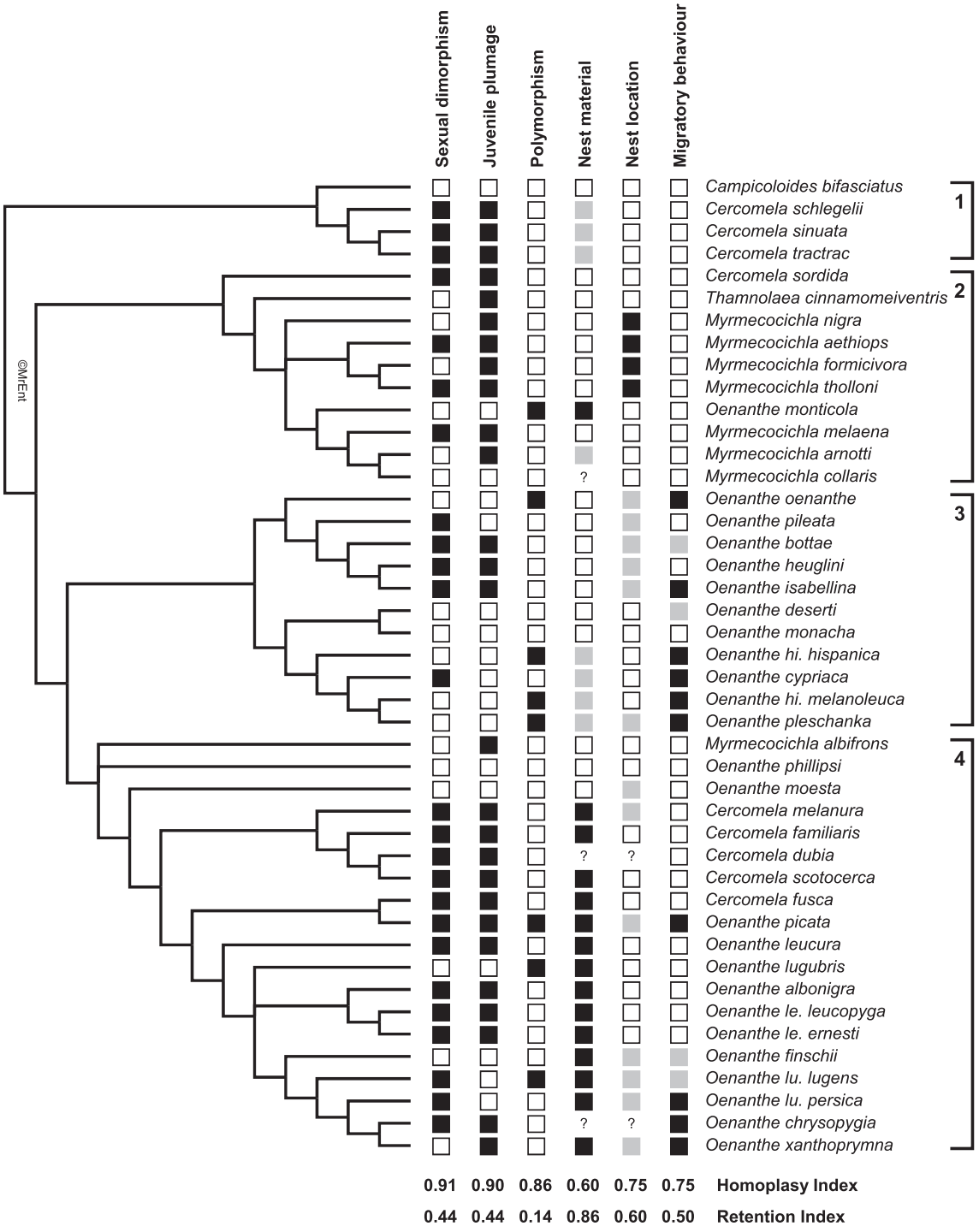


**Fig. 2.** The character states of selected morphological, ecological and behavioural characters have been mapped onto the Bayesian topology (see Fig. 1, outgroup not shown). Brackets and numbers on the right refer to the clades discussed in the text. The homoplasy and retention indices of each character have been estimated using PAUP*. ? Denotes unknown character states. Sexual dimorphism: sex alike (black) or dichromatic (white). Juvenile plumage: like adult (black) or markedly different from adult (white). Polymorphism: non-polymorphic (white) or polymorphic (black). Nest material: classical (white), nest with twigs (grey) or nest with small pebbles (black). Nest location: on ground, under stone or bush, in hole, but not in burrow (white), nest more or less regularly in (rodent) burrows (grey), or in burrows dug by the birds themselves (black). Migratory behaviour: sedentary (white), partial migrant (grey) or long-distance migrant (black).

studies investigated the relationship among selected taxa (*Oenanthe*: Aliabadian et al., 2007, *Cercomela* and *Oenanthe*: Outlaw et al., 2010), but a detailed phylogeny for the entire group was still missing. With a complete dataset, we are able to provide the first well resolved phylogenetic hypothesis for all species in the clade. The congruence between the mitochondrial and nuclear topologies with the full dataset analysis further supports our results. We are able to generally confirm the outcomes of previous analyses, but the more comprehensive taxon sampling suggests also novel relationships.

The composition of the genera *Myrmecocichla*, *Cercomela* and *Oenanthe* remained relatively stable overall since Ripley's revision of the Turdidae (1964). *Myrmecocichla* included only African species, with black, black-and-white, or dark plumage, *Cercomela* was used for mostly greyish or pale brown African and Indian birds, while *Oenanthe* included more strongly patterned species occurring in both Africa and Eurasia. But none of these currently admitted genera is monophyletic, as already shown by Sangster et al. (2010) and Outlaw et al. (2010), suggesting extensive convergence on similar plumage patterns in less closely related species.

All the analyses identify four major clades as defined in Fig. 1, with the same branching order. The same lineages and topology were recovered by Zuccon and Ericson (2010a). Outlaw et al.'s analysis (2010) recovers our clades 3 and 4 as sister lineages, but the clades 1 and 2 are intermixed. The topological differences with our results might be due to a low resolution power of the mitochondrial markers in Outlaw et al.'s analysis, suggested also by the lack of support in all basal nodes.

The placement of *Campicoloides bifasciatus* has long been disputed. This species has been included either in *Myrmecocichla* (Seebohm, 1881), *Oenanthe* (e.g. Ripley, 1964) or *Saxicola* (e.g. Tye, 1989b; Keith et al., 1992), or segregated in its own monotypic genus *Campicoloides* (e.g. Wolters, 1980; Dickinson, 2003). Illera et al. (2008), Zuccon and Ericson (2010a) and Sangster et al. (2010) confirmed that *Campicoloides bifasciatus* is not part of *Saxicola*, but they could not resolve its taxonomic position due to the limited taxonomic sampling. With a more inclusive dataset, Outlaw et al. (2010) showed that it is the sister lineage of the three sickle-winged chats (*Cercomela schlegelii, C. sinuata* and *C. tractrac*) (Clade 1). Our results support the findings of Outlaw et al. (2010).

The genus *Myrmecocichla* comprises only African species (e.g. Ripley, 1964; Dickinson, 2003), but opinions on its limits have varied. On one side, *Myrmecocichla* was enlarged to encompass also *Thamnolaea cinnamomeiventris* and *T. semirufa* (Keith et al., 1992; Sibley and Monroe, 1990), on the other Wolters, 1980 resurrected the genus *Pentholaea* for three species, *Myrmecocichla melaena*, *M. albifrons* and *M. arnotti*, restricting *Myrmecocichla* to the remaining species. Collar (2005) also used *Pentholaea*, but applied it to *Myrmecocichla albifrons* and *M. arnotti* only. When compared with the other *Myrmecocichla* species, Collar noted that *Pentholaea* taxa are more arboreal, often nest in tree holes, have more elaborate songs and lack a white wing patch.

Neither of these taxonomic treatments reflects the real phylogenetic relationships. Our results confirm a close relationship between *Thamnolaea cinnamomeiventris* and *Myrmecocichla* (clade 2). However, only seven species of *Myrmecocichla* are part of this clade, together with one species of *Oenanthe*, *O. monticola* (clade 2). Two lineages are well supported: a group with strongly patterned species (*Myrmecocichla arnotti*, *M. collaris* and *M. melaena*) and a group characterised by a more mottled plumage (*M. formicivora*, *M. aethiops* and *M. tholloni*). The *Oenanthe monticola* subspecies vary in the relative amount of black, grey and white in the plumage, and the nominotypical subspecies shows a black and white plumage quite similar to *Myrmecocichla arnotti*. Indeed in our topology, *O. monticola* is sister to the lineages containing also *M. arnotti*. A close relationship of *O. monticola* with *Myrmecocichla* is not totally unexpected, as it was already advanced by Tye (1989a), based on similar pattern of white wing-covers, and Wolters, 1980 proposed to place it in the monotypic genus *Dromolaea*.

We confirm the extensive polyphyly in the genera *Cercomela* and *Oenanthe* already observed by Outlaw et al. (2010). Although ours and Outlaw et al.'s topologies generally agree, they differ in a number of points. With a larger dataset in term of species and number of characters, we obtained a better resolved topology with higher nodal support.

Collar (2005) advocated the separation of *Cercomela sordida* in the monotypic genus *Pinarochroa* for its longer tarsi and shorter tail. Outlaw et al. (2010) findings and our results are congruent in placing the species in a distinct lineage, removed from the other *Cercomela*. But Outlaw et al. (2010) were unable to resolve its position with respect to the other taxa in the clades 1 and 2. Our analyses suggest that *Cercomela sordida* is placed with strong support as the sister taxon to the *Thamnolaea cinamomeiventris-Myrmecocichla* group.

Tye (1989b) suggested that *Oenanthe* as currently defined may not be monophyletic, and he noted similarities with some species of *Cercomela*. We confirm Tye's hypothesis: all *Oenanthe* species, with the exclusion of *O. monticola*, form a large clade that includes also *Myrmecocichla albifrons* and five *Cercomela* species.

Our topology in clade 3 is virtually identical to Outlaw et al.'s, differing only in the relative placement of *Oenanthe deserti*, either sister to *O. monacha* or to the *O. hispanica-pleschanka-cypriaca* complex. However, neither arrangement received a significant support values.

Several *Oenanthe* species are polytypic and/or polymorphic (Collar, 2005). The *O. hispanica* complex represents a challenging group of forms whose relationships have been recently investigated by Randler et al. (2012). In our tree, the genetic distance among *O. hispanica melanoleuca*, *O. pleschanka* and *O. cypriaca* is minimal. Nonetheless playback experiments and the presentation of different dummy models showed that *O. cypriaca* responds stronger to conspecific stimuli, suggesting that it is already behaviourally distinct (Randler et al., 2012) and it should be treated as a valid species. *O. hispanica melanoleuca* and *O. pleschanka* are morphologically well distinct, with limited overlap in both breeding and wintering ranges (Cramp, 1988). However, they are known to hybridize in the overlap zones (Panov and Ivanitzky, 1975) and further studies are needed to clarify the relationships and the taxonomic status of the two forms. Instead the west Mediterranean subspecies *O. hispanica hispanica* is deeply divergent from the rest of the complex and probably it deserves to be raised to full species.

The composition of clade 4, allowing for the differences in taxon sampling, is congruent with Outlaw et al.'s results. Both studies indicate that *Oenanthe phillipsi* belong to the basal lineages in this clade. At the base of the clade falls also two species that have not been sampled before, *O. moesta* and *Myrmecocichla albifrons*.

The incongruences between the two studies lie in two main areas, the *Cercomela* lineages on the one hand, and the position of *Oenanthe leucura*, *O. leucopyga* and *O. alboniger* on the other. According to our results four *Cercomela* species form a well supported lineage, with the same topology supported also by the nuclear and mitochondrial data alone. In Outlaw et al.'s tree *Cercomela scotocerca* and *C. dubia* branch off first, followed by the *C. familiaris–C. melanura* lineage and the remaining taxa. We suspect that the differences are probably due to the inclusion in Outlaw et al.'s dataset of some chimaeric sequences containing regions belonging to other Muscicapidae species (see Suppl. material S1). Also the large genetic intraspecific divergences observed by Outlaw et al. in *C. dubia* and *C. fusca* should be treated with caution since these too were estimated on the suspected chimaeric sequences.

The different relationships among some *Oenanthe* species more likely reflect conflicting signals in the loci analysed, as shown by the contrasting topologies supported by the nuclear and mitochondrial trees.

Preliminary analyses of the *Oenanthe lugens* complex disclosed high genetic distances among the various subspecies (Förschler et al., 2010), but failed to include other congeneric taxa for a throughout comparison. Here we show that the different lineages identified by Förschler et al. (2010) are not the each other closest taxon. The Iranian form *O. lugens persica* is sister to the species pair *O. chrysopygia–O. xanthoprymna*, while the nominate *O. lugens lugens* and *O. lugens halophila*, distributed from Egypt to Iraq, are more basal. Although often considered part of the *O. lugens* complex, the Ethiopian *O. lugubris* appers to be sister to *O. leucopyga*. In the latter taxon the two subspecies, the North African *leucopyga* and the Middle Eastern *ernesti*, are surprising highly divergent (4.8% *p*-distance in ND2), possibly an indication that they should be raised to full species.

### 4.2. Ecological preferences in the open-habitat chats

The habitats of the different species of the whole group are not very diversified, consisting in most cases in arid landscapes with or without a low vegetation cover. Few species tolerate a substantial tree cover (*Cercomela faminiaris*, *Thamnolea cinnamomeiventris*, *Myrmecocichla arnotti*; although some of them occasionally breed in tree holes: *Oenanthe cypriaca*, *Myrmecocichla albifrons*), and this character is scattered all over the phylogeny. Several species belonging to different clades can be found at high altitudes (*Myrmecocichla melanea*, *Oenanthe oenanthe*, *O. deserti*, *O. chrysopygia*, *Cercomela sordida*), and about half of the species of clades 3 and 4 are long distance or partial migrants. Subtle differences in morphometry between species correspond more to behavioural differences than to ecological factors (Kaboli et al., 2007), and niche conservatism seems to be a common trait of the group (Aliabadian et al., 2007). Each of the main clades of our phylogeny can be related to a dominant habitat-type (Fig. 2):

- the species of clade 1, resident, are typical of South-African semi-deserts with scant scrubland or heath land (karoo, fynbos), on flat or broken grounds;
- the species of clade 2, resident and ground dwelling, are mainly found in flat and short-grass terrains of Africa with or without scattered bushes or trees and/or termite mounds, on sandy or marshy, sometimes rocky (*Oenanthe monticola, Myrmecocichla melanea*) substrates. Typically, the *Myrmecocichla* breed on burrow which they can dig themselves, or in old nests;
- the species of clade 3 are good fliers and most of them are migratory. They are distributed in three contrasted habitats of Africa and Eurasia: deserts (*Oenanthe deserti*, *O. monacha*), steppes (*O. bottae*, *O. isabellina*, *O. pileata*, to some extent *O. oenanthe;* these species often use rodent burrows as nest sites), or habitats with a certain degree of woody cover (*O. hispanica*, *O. pleschanka*, *O. cypriaca*; these species often perch on bushes or even on trees; they use to bring twigs at the nest);
- the species of clade 4 inhabit as well Arica and Eurasia; except the three most basal ones, they are typical of broken substrates, and usually perch on rocks and breed in rock crevices. They share the common habit to carry stones at the nest, a trait that is only and occasionally found in *Oenanthe monticola* among the other chats.

Despite their rather high Homoplasy Indices, particular traits seem to prevail in certain clades (stone-carrying in clade 4, long-distance migration in clades 3 and 4, burrow-digging in clade 2) (Fig. 2). But further syntheses of behavioural traits within the whole group are needed.

### 4.3. Notes on plumages

In the open-habitat chats, the sexes are mostly alike in clades 1 and 4; the situation is mixed in clades 2 and 3 (Fig. 2). The females tend to be dull-coloured in species breeding on the ground (e.g. in clade 3), while male-like females (often black or dark brown) are more frequent in species breeding in holes or in burrows (Panov, 2005), but there are exceptions. When the sexes are similar, juveniles tend to fledge with a plumage that is more or less similar to the adult plumage. This mainly concerns sedentary species where families keep close together for some time (clade 4), in particular when there are cases of helpers and cooperative breeding (clade 2). This seems to give some credit to Moreno and Soler, 2011 hypothesis that juveniles are more likely to have adult-like plumage when they participate to more extended interactions with adults and other youngs.

A well known, but still largely unexplained, characteristic of the group is the di- or poly-chromatism of the males (Mayr and Stresemann, 1950): the males of eighth species, seven of them belonging to the clades 3 and 4, are dimorphic or polymorphic. But this characteristic is also met in an isolated species of clade 2 (*Oenanthe monticola*). The Homoplasy Indices of the three plumage traits considered here are very high, clearly indicating that plumage and colour patterns seem to be highly labile between the species of the group, and convergences and reversals are frequent, so that it is impossible to rely on plumage characters for constructing phylogenies.

An example of convergence, among others, is the black-and-white pattern (throat, upper back, and wings black; crown, rump, and belly white) that can be met with in non-closely related species belonging to clades 3 and 4 (*Oenanthe picata*, *O. lugens*, *O. pleschanka*, *O. monacha*). In the open-habitat chats, morphological features appear more correlated to phylogeny that plumage patterns do (Kaboli et al., 2007). For example, the split of the former *Cercomela* genus in two independent lineages, hardly justified by any striking difference in colour pattern, correspond to marked difference in wing morphology. The close relatedness of *Oenanthe lugens* and *O. chrysopygia*, which has never been suspected from the comparison of their plumage pattern in former systematic syntheses, is supported by their close morphological similarity (Kaboli et al., 2007). Inversely, the resemblance between the plumages of *Oenanthe oenanthe* and *O. phillipsi*, that has led certain authors to lump them in a same superspecies (e.g., Hall and Moreau, 1970; Keith et al., 1992), is a homoplasy that had been suspected from well marked differences in morphometry (Kaboli et al., 2007). But a thorough study of the relationships between plumage evolution, adaptation and speciation in the open-habitat chats remain to be made.

### 4.4. Taxonomic recommendations

On the basis of the results presented here, we recommend to redefine the generic limits in the open-habitat chats as the following:

1. the three sickel-winged chats (*Cercomela schlegelii*, *C. sinuata* and *C. tractrac*) form a well supported clade for which can be resurrected the genus name *Emarginata* Shelley, 1896 (type species *Luscinia sinuata* Sundevall, 1858), as suggested by Outlaw et al. (2010);
2. *Cercomela sordida* should be transferred to the monotypic genus *Pinarochroa* Sundevall, 1872, as suggested by Outlaw et al. (2010);
3. the genus *Thamnolaea* Cabanis, 1850 should be retained for the species *cinnamomeiventris* only while *T. semirufa* should be

included in the genus *Monticola* following Zuccon and Ericson (2010b);

4. *Myrmecocichla arnotti*, *M. collaris*, *M. melaena*, *M. nigra*, *M. formicivora*, *M. aethiops*, *M. tholloni* and *Oenanthe monticola* should be included in the same genus. Two generic names available for this taxon were established simultaneously: *Myrmecocichla* Cabanis, 1850 (type species *Oenanthe formicivora* Vieillot, 1818) and *Dromolaea* Cabanis, 1850 (type species *Oenanthe monticola* Vieillot, 1818). To our knowledge no precedence have ever been established between *Myrmecocichla* and *Dromolaea*, nor *Myrmecocichla formicivora* and *Oenanthe monticola* have ever been treated as congeneric under either generic names. In agreement with the provisions of the International Code of Zoological Nomenclature for simultaneously published names (Art. 24, ICZN 1999) and acting as First Reviser, we select the genus name *Myrmecocichla* Cabanis, 1850 to take precedence over *Dromolaea* Cabanis, 1850. This choice assures nomenclatural stability since *Myrmecocichla* has been consistently applied to the majority of species in this clade while *Dromolaea* has only rarely been considered valid and it has been applied only to some *Oenanthe* taxa;
5. we recommend, for the sake of nomenclatural stability, to apply the genus name *Oenanthe* Vieillot, 1816 to all the species of the clades 3 and 4, including the former *Myrmecocichla albifrons*, *Cercomela melanura*, *C. familiari*, *C. scotocerca*, *C. dubia* and *C. fusca*. Alternatively should the clades 3 and 4 in Fig. 1 be found to deserve separate generic or subgeneric status, the valid names would be *Campicola* Swainson, 1827 (type species *Motacilla pileata* Gmelin, 1789) and *Oenanthe* Vieillot, 1816 (type species *Turdus leucurus* Gmelin, 1789), respectively.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2012.05.011.

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