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# Phylogeny of Palaearctic wheatears (genus *Oenanthe*)—Congruence between morphometric and molecular data

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**Abstract**

Wheatears of the genus *Oenanthe* are birds specialized to desert ecosystems in the Palaearctic region from Morocco to China. Although they have been the subject of many morphological and ecological studies, no molecular data have been used to elucidate their phylogenetic relationships, and, their relationships are still debated. Here we use DNA sequences of 1180 bp of two mitochondrial genes, 16S rRNA and cytochrome oxidase subunit I, from 32 individuals from Middle East and North Africa, and Bayesian methods to derive a phylogeny for 11 species of *Oenanthe*. The resulting tree supported three major clades: (A) *O. alboniger*, *O. chrysopygia*, *O. lugens*, *O. finschii*, *O. leucopyga*, *O. picata*, *O. moesta*, (B) *O. deserti* and *O. pleschanka*; and (C) *O. isabellina* and *O. oenanthe*. These results largely differ from previous hypotheses based on analysis of morphological and chromatic characters. However, the two clades (B) and (C) were also supported by a phenetic analysis of new morphometric data presented here, indicating that characters related to colouration and ecology in *Oenanthe* are more strongly influenced by homoplasy than those of body shape.


*Keywords:* Aves: Passeriformes; *Oenanthe*; Wheatears; Palaearctic; cox1; 16S rRNA

## 1. Introduction

The wheatears of the genus *Oenanthe* constitute an important part of the avifauna of the arid and desert ecosystems of the Palaearctic, where they are often the most conspicuous passerines. Although this genus has been the subject of numerous ecological or behavioural studies (Cornwallis, 1975; Grabovsky and Panov, 1992; Ivanitzky, 1980; Loskot, 1983; Potapova and Panov, 1977; Panov, 2005; Kaboli et al., unpublished manuscript), their taxonomy have been only rarely investigated (Haffer, 1977; Loskot, 1976; Panov, 2005; Panov and Ivanitzky, 1975; Tye, 1987, 1989). In fact, many species of this genus are poorly known (for example, see Cramp, 1988; Keith et al., 1992; Panov, 1992, 2005). Moreover, species are sometimes treated as junior synonyms by some authors but re-validated as clear-cut species by others, and some taxa are treated as mere colour morphs (e.g., Dickinson, 2003; Panov, 2005). As a consequence, the actual number of taxa in the genus remains uncertain (Panov, 2005). Hybridization between several species, such as *O. hispanica* and *O. pleschanka* and *O. xanthoprymna* and *O. chrysopygia*, add to taxonomical ambiguity (Aliabadian et al., 2005; Haffer, 1977; Panov and Ivanitzky, 1975; Panov, 2005). Altogether, 18–22 species of wheatears (including 45–47 subspecies)

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(Cramp, 1988; Dickinson, 2003; Keith et al., 1992; Monk, 1992; Sibley and Monroe, 1990) are recognised, 15–16 species of which have mainly a Palaearctic distribution.

Beyond the problem of species definition, the phylogenetic relationships between species remain even more disputed. The complexity of the colour patterns, in particular the frequency of polymorphism, together with an apparent homogeneity of the group in body shape, behaviour, and regime, obscured many attempts to clarify their systematics. From similarities in plumage, Hall and Moreau (1970) grouped the African species of *Oenanthe* into several superspecies whose members are strictly allopatric. Tye (1989) generalized this system to all wheatears, and defined three broad assemblages: (i) a broad group of mostly black and white coloured species from northern China to southern Africa including the *picata* superspecies (*O. picata*, *O. lugens*, and *O. finschii*), *pileata* superspecies (*O. pileata*, *O. bottae*, and *O. isabellina*). *Oenanthe moesta*, *O. chrysopygia* (as subspecies of *O. xanthoprymna*), and *O. deserti*, of uncertain relationships, remain isolated but cluster with the *picata* group, (ii) a group of small-sized species from southern Siberia and Europe to North-west Africa with *pleschanka* superspecies (*O. pleschanka*, *O. hispanica*), (iii) a black–white–grey species-group, from the Holarctic and North Africa, including the *alboniger* superspecies (*O. alboniger*, *O. leucopyga*) and *O. oenanthe* (Fig. 1A). This system relies on the two main assumptions that overall colouration bears a phylogenetic signal, and that related species must necessarily be allopatric. Even if hybridization zones between sister-species are of limited extent (e.g., *O. hispanica* × *O. pleschanka*, *O. xanthoprymna* × *O. chrysopygia*), allopatry only concerns the species of very recent origin. Due to the large and numerous vegetational changes since the differentiation of most species of *Oenanthe*, current distribution ranges are unlikely to coincide with the original ones, and range overlap could occur between species, even related, since the time they have initially achieved genetic isolation.

Another recent attempt to infer the phylogeny of *Oenanthe* is that of Panov (2005). From a set of morphological characters (mainly plumage colouration), but also ecological and behavioural characters, and using a non-explicit methodology, he presented a putative scheme of the phylogeny of wheatears with three main groups: (i) three steppe species, including *O. isabellina* and two African species (*O. bottae* and *O. pileata*), (ii) the *O. pleschanka* and *O. hispanica* group, including *O. monacha*, (iii) the remaining species, among which *O. oenanthe* and *O. phillipsi* form a subgroup (Fig. 1B). In this classification, *O. deserti* remains isolated. However, colour patterns are frequently misleading to assess bird relationships (e.g., Cibois et al., 2004; Crochet et al., 2000; Olsson et al., 2005); morphological and behavioural characters are suspected to be subject of selective pressures and to be largely uncorrelated with phylogeny (e.g., Böhning-Gaese et al., 2003), and the interpretation of current distribution patterns to infer between-species relationships is delicate.

In this paper, we look for phylogenetic relationships among 11 species of *Oenanthe* of the Palaearctic arid zone from the sequencing of two mtDNA genes. Using the partitioned Bayesian approach, we tried to infer a species-level phylogeny, testing in particular the previously hypothesized close relationships between certain species. We compared our molecular phylogeny with a phenetic tree based on morphometric similarities to assess the value of morphology for wheatear systematics.

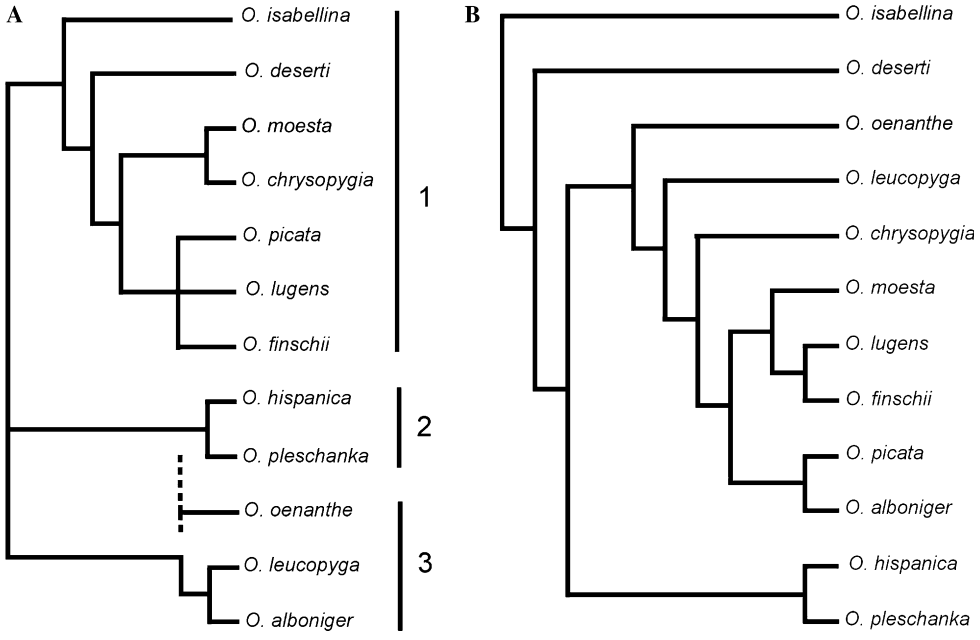


Fig. 1. Phylogenetic relationships of species in the genus *Oenanthe* derived from (A) ecological, geographical, and morphological characters (Tye, 1989) (B) plumage colouration (Panov, 2005). Both trees were modified by excluding taxa not available for molecular analysis. The dashed line indicates an alternative placement.

## 2. Materials and methods

### 2.1. Samples and measurements

A sample of 32 individuals supposed to represent 12 species of Palaearctic wheatears was collected in the field for the molecular analysis (for taxonomic treatment we followed Dickinson, 2003). One of the individuals, first identified as *O. hispanica*, may in fact be a hybrid of *O. pleschanka* × *O. hispanica* (this cannot be proven since a pure *hispanica* was not included in our analysis and theoretically *hispanica* and *pleschanka* could have identical haplotypes). The specimens and samples of muscle tissues were collected on the breeding grounds of the birds in Iran and Morocco. Voucher specimens were deposited in The Natural History Museum, Tring, UK, and Museum of Ispahan University of Technology. Sample identification and GenBank accession numbers are given in Table 1. The phylogenetic trees were rooted on two species of the genus *Luscinia* (*L. luscinia*, *L. megarhynchos*).

Moreover, 21 biometrical variables ('primary variables') were measured on 237 male skins, including 14 of the outgroup, in the collections of the Natural History Museum Tring, Museum d'Histoire Naturelle de Paris and the Zoological Museum Amsterdam, to the nearest 0.1 mm following Gaston (1974), Leisler (1980) and Svensson (1992). These variables were assigned to three functional groups: (i) flight apparatus (wing and tail; 12 variables), (ii) feeding apparatus (4 variables), (iii) foot-leg complex (5 variables) (Appendix A). Six ratios were calculated from the primary variables (see Appendix B for details).

### 2.2. DNA extraction and sequencing

Total genome DNA from 96% ethanol-preserved tissue samples was extracted by over-night incubation at 55 °C in extraction buffer (2% sodium dodecyl sulphate (SDS), 0.5 mg/ml proteinase K, using a standard salt extraction protocol (Bruford et al., 1992). We amplified fragments of two mitochondrial genes, the 16S rRNA gene (16S) and the cytochrome oxidase subunit I gene (cox1), using primers

Table 1
Tissue samples and GenBank accession number (cox1/16S)

| Specimen | Sample no. | GenBank accession 16S | GenBank accession COX1 | Locality |
|---|---|---|---|---|
| *Luscinia_luscinia* | NRM20026317 | DQ683442 | DQ683476 | Malmön_SW |
| *Luscinia_megarhynchos* | MIUT200359 | DQ683443 | DQ683477 | Bazangan_IR |
| *O. alboniger* | MIUT2003-7.2(28) | DQ683444 | DQ683478 | Touran_IR |
| *O. alboniger* | MIUT2003-104(29) | DQ683445 | DQ683479 | Touran IR |
| *O. alboniger* | MIUT2003-95(18) | DQ683446 | DQ683480 | Firouz Abad_IR |
| *O. chrysopygia* | MIUT2003-96(19) | DQ683447 | DQ683481 | Kashan IR |
| *O. d. deserti* | MIUT2003-3(33) | DQ683448 | DQ683482 | Touran_IR |
| *O. d. deserti* | BMNH A/2005.2.5 | DQ683449 | DQ683483 | Ispahan_IR |
| *O. d. deserti* | MIUT2003-98(21) | DQ683450 | DQ683484 | Ispahan_IR |
| *O. deserti homochroa* | MIUT2003-99(22) | DQ683451 | DQ683485 | Eastern high plateaus_MO |
| *O. finschii barnesi* | MIUT2003-91(14) | DQ683452 | DQ683486 | Ispahan_IR |
| *O. finschii barnesi* | BMNH A/2005.2.11 | DQ683453 | DQ683487 | Firouz Abad_IR |
| *O. finschii barnesi* | MIUT2003-100(23) | DQ683454 | DQ683488 | Firouz Abad_IR |
| *O. isabellina* | MIUT2003-84(7) | DQ683456 | DQ683490 | Ispahan_IR |
| *O. isabellina* | BMNH A/2005.2.12 | DQ683457 | DQ683491 | Ispahan_IR |
| *O. isabellina* | BMNH A/2005.2.1) | DQ683458 | DQ683492 | Ispahan_IR |
| *O. isabellina* | BMNH A/2005.2.2 | DQ683459 | DQ683493 | Borazjan_IR |
| *O. isabellina* | BMNH A/2005.2.3 | DQ683460 | DQ683494 | Ispahan_IR |
| *O. isabellina* | MIUT2003-90(13) | DQ683461 | DQ683495 | Ispahan_IR |
| *O. lugens persica* | BMNH A/2005.2.6 | DQ683462 | DQ683496 | Ispahan_IR |
| *O. lugens persica* | BMNH A/2005.2.7 | DQ683463 | DQ683497 | Ispahan_IR |
| *O. lugens persica* | BMNH A/2005.2.8 | DQ683464 | DQ683498 | Ispahan_IR |
| *O. lugens persica* | MIUT2003-94(17) | DQ683465 | DQ683499 | Ispahan_IR |
| *O. moesta moesta* | MIUT2003-103(26) | DQ683466 | DQ683500 | Eastern high plateaus_MO |
| *O.o. libanotica* | BMNH A/2005.2.9 | DQ683467 | DQ683501 | Ispahan_IR |
| *O.o. libanotica* | BMNH A/2005.2.4 | DQ683468 | DQ683502 | Ispahan_IR |
| *O.o. libanotica* | MIUT2003-81 | DQ683469 | DQ683503 | Ispahan_IR |
| *O.o. libanotica* | BMNH A/2005.2.10 | DQ683470 | DQ683504 | Borazjan_IR |
| *O. o. seebohmi* | MIUT2003-83 | DQ683471 | DQ683505 | Middle Atlas_MO |
| *O. pleschanka* | MIUT2003-102(25) | DQ683472 | DQ683506 | Kashan_IR |
| *O. pleschanka* | MIUT2003-26(30) | DQ683473 | DQ683507 | Dar Gaz_IR |
| *O. pleschanka* × *O. hispanica* | MIUT2003-37(32) | DQ683455 | DQ683489 | Bazangan_IR |
| *O. leucopyga aegra* | MIUT2003-137(X) | DQ683474 | DQ683508 | Tazenakht_MO |
| *O. picata picata* | MIUT2003-7.1(27) | DQ683475 | DQ683509 | Touran_IR |

*Abbreviations:* IR (Iran), MO (Morocco), SW (Sweden), BMNH (British Museum of Natural History), MIUT (Museum of Ispahan University of Technology).

16SA-L (light chain; 5′-CGC CTG TTT ATC AAA AAC AT-3′) and 16SB-H (heavy chain; 5′-CCG GTC TGA ACT CAG ATC ACG T-3′) of Palumbi et al. (1991), and BirdF1 (5′-TTC TCC AAC CAC AAA GAC ATT GGC AC-3′) and BirdR1 (5′-ACG TGG GAG ATA ATT CCA EET CCT G-3′) of Hebert et al. (2004). PCR conditions for 16S and CO1 followed Vences et al. (2000) and Hebert et al. (2004), respectively.

PCR products were purified using the Qia-quick PCR Purification Kit (Qiagen). Sequencing reactions included 0.5 μl reaction mix, 1.75 μl of 5× sequencing buffer, 1 μl of pmol/μl primer, 1.8 μl of ABI sequence mix (BigDye Terminator V3.1 sequencing standard, Applied Biosystems), and 5.75 μl water. The sequence reaction was 23 cycles of 10 s at 96 °C, 10 s at 50 °C and 4 min at 60 °C. Products were resolved on automated DNA sequencers (ABI 3100 and ABI 3730). Sequences have been submitted to Genbank (see Table 1 for accession numbers).

The cox1 protein-coding sequences were edited and aligned by eye. The 16S sequences were aligned with reference to published secondary structure maps (Gutell and Fox, 1988), using Sequence Navigator software version 1.0.1 (Applied Biosystems). The final aligned data set included 1181 bp for each taxon: 514 bp for 16S, 667 bp for cox1.

### 2.3. Sequence analysis

We carried out maximum likelihood (ML), maximum parsimony (MP), and partitioned Bayesian phylogenetic analysis. ML and MP phylogenetic analyses for the entire data set were performed using PAUP* 4.0b10 (Swofford, 2002). ML models and parameters were determined by a hierarchical likelihood ratio test (HLRT) as implemented in Modeltest (Posada and Crandall, 1998). The estimated models were used in a subsequent ML heuristic tree search with 10 random addition sequence replicates, and TBR branch swapping. MP analysis was performed using heuristic searches with TBR branch swapping, stepwise addition starting tree, and random addition sequence with 10 replicates. To test the robustness of nodes, we ran 500 and 2000 bootstrap replicates under ML and MP, respectively, with a single random addition sequence replicate per bootstrap replicate.

Bayesian analyses, using the Markov Chain Monte Carlo method, were performed with MrBayes 3.1.1 (Huelsenbeck and Ronquist, 2001). Previous studies have shown that genes and gene regions can evolve under different models of evolution, and that this fact is best addressed by using a partitioned analysis (e.g., Brandley et al., 2005; Irestedt et al., 2004; Nylander et al., 2004; Ronquist and Huelsenbeck, 2003; Schmitz et al., 2005). We here selected four partitioning strategies hereafter designed as $P_1$, $P_2$, $P_3$, $P_4$ (Table 2). Partitions were a priori based on gene identity (i.e., 16S, and cox1), taking into account biochemical or evolutionary constraints (i.e., codon positions, stems and loops). Appropriate models of sequence evolution (Table 3) were chosen for each partition using HLRT as implemented in Modeltest (Posada and Crandall, 1998).

Table 2
Partitioning strategies used in the partitioned Bayesian analyses

| Strategy | Partition strategy |
|---|---|
| $P_1$ | All data combined (16s + cox1) in one single partition |
| $P_2$ | One partition for the combined stems 16S, one for the loops of 16S, and one for the unpartitioned cox1 |
| $P_3$ | One partition for unpartitioned 16s, and three partitions for cox1 (one for each codon position) |
| $P_4$ | Full partition: one partition each for the combined stems and loops of the 16s, and one for each codon position of cox1 |

Table 3
Data partitions, their estimated models of sequence evolution, and total number of characters of each partition used in phylogenetic analysis

| Partition | Model | Number of characters in partition |
|---|---|---|
| All data | GTR + I + G | 1181 |
| cox1 | TUM + G | 667 |
| cox1 1st, 2nd codon | HKY + G | 445 |
| cox1 3rd codon | TrN + G | 223 |
| 16S | TrNef + I + G | 415 |
| 16S stems | GTR + I + G | 235 |
| 16s loops | GTR + I + G | 170 |

See text for details.

To search for partitioning strategies that explain the data set with the least random error, we followed the method of Brandley et al. (2005), and used the Bayes factor. A strategy using fewer partitions that was not strongly different from the more partitioned one regarding its Bayes factor would be chosen as the best strategy. Bayes factors were estimated by subtracting the log-transformed harmonic means of the posterior likelihoods between the two analyses tested, and multiplying the resulting value by 2 (Brandley, M., personal communication; Newton and Raftery, 1994). Harmonic means were calculated using the *sump* command in MrBayes. The Bayes factors were evaluated using the criterion of 2ln Bayes factor $\geqslant 10$ as a strong support (Brandley et al., 2005; Huelsenbeck and Imennov, 2002; Kass and Raftery, 1995; Schmitz et al., 2005).

In the Markov chain Monte Carlo process, we ran four chains simultaneously for 1,000,000 generations, with trees sampled every 100th generations (resulting in 10,000 trees), using default priors. The analyses began on a random starting tree. We discarded the first 5000 trees as a conservative "burn–in", and the posterior probability values were calculated from the remaining trees. Stationarity was assumed when the cumulative posterior probabilities of all clades stabilized.

Non-parametric bootstrap values are assumed to be conservative estimates of clade confidence (Brandley et al., 2005; Hillis and Bull, 1993) whereas Bayesian posterior probabilities ($P_p$) are thought to represent closer estimates of clade probabilities (e.g., Alfaro et al., 2003; Erixon et al., 2003; Wilcox et al., 2002). We therefore, in the Bayesian approach, considered clades with $P_p \geqslant 0.95$ to be strongly (significantly) supported.

### 2.4. Morphometric analyses

Morphometric distances, i.e., overall morphological dissimilarities, between the 12 species were inferred by average linking (UPGMA) in two ways using ADE-4 software (Thioulouse et al., 1997): (i) by computing Mahalanobis distances from the mean values of the 21 primary variables plus the six ratios, (ii) by computing mean Euclidian distances between species from their scores on the 2nd to the 9th axes of a Principal Component Analysis performed on the primary variables only (correlation matrix). This second method aimed at removing most of the size effects. In both cases the resulting distance matrices were used to perform an upward hierarchical classification with average links, and illustrated by the corresponding trees. Dissimilarity matrices were regressed on the genetic distance matrix (Kimura 2-parameter distance; Kimura, 1980) and the significance of the regression tested by Monte Carlo randomizations through Mantel's test, using 'R 2.0.1' (Ihaka and Gentleman, 1996), and the 'ape' library (http://lib.stat.cmu.edu/R/CRAN). We also regressed individually in the same way certain morphological variables on the genetic distance matrix.

Topological congruence as measure of similarity between molecular and morphological trees was compared between pairs of trees using the program Component, version 2.0 (Page, 1993). In the analysis we omitted the hybrid specimen (*O. pleschanka* × *O. hispanica*) and *O. hispanica* from our molecular and morphological trees, respectively. Probabilities of obtaining the observed distance between two compared trees by chance (null distribution generated by sampling all possible binary trees at random) were calculated by partition metric and quartets measures (Sheldon and Bledsoe, 1993). Furthermore, using PAUP*, we compared trees by Shimodaira–Hasegawa's tests (Shimodaira and Hasegawa, 1999) under full optimization (one-tailed test) and 1000 replicates.

## 3. Results

### 3.1. MP and ML analysis

We obtained sequence data totalling 1181 base pairs for two genes (16S and cox1) and 32 individuals. Of these 1181 characters, 957 were constant and 185 were parsimony-informative. MP searches recovered 20 equally most likelihood trees (426 steps) with a consistency index of 0.63 and a retention index of 0.87. A strict consensus of these trees (not shown) supported three major clades: (A) *O. moesta*, *O. picata*, *O. leucopyga*, *O. alboniger*, *O. chrysopygia*, *O. lugens*, *O. finschii*, (B) *O. deserti* and *O. pleschanka*; and (C) *O. isabellina* and *O. oenanthe*, with clades A and B being placed sister to each other.

Results of the model selection regime are provided in Table 3. Maximum likelihood analysis yielded a single tree ($-\ln L = 3751.11$) which agreed largely with the MP consensus tree, except details of positioning individuals within species, and in supporting a sister-group relationship between clade B and C.

Table 4
Mean $-\ln L$ and 95% confidence interval results of each partitioning strategy

| Partition strategy | Mean $-\ln L$ | Upper 95% CI | Lower 95% CI |
|---|---|---|---|
| $P_1$ | 3842.03 | 4034.13 | 3649.93 |
| $P_2$ | 3771.87 | 3960.46 | 3583.28 |
| $P_3$ | 3443.10 | 3615.25 | 3270.94 |
| $P_4$ | 3405.98 | 3576.280 | 3235.68 |

### 3.2. Effect of partitioning on mean $-\ln L$, tree topology, and Bayes factors

Our data show that increased data partitioning does greatly improve the harmonic mean of the posterior likelihoods $-\ln L$ (Table 4). Simply adding partitions does not necessarily further improve the mean $-\ln L$. Rather, the identity of each partition is important. For example, partitioning the cox1 data by codon positions (partition strategies $P_3$, $P_4$) has the largest effect on the harmonic mean $-\ln L$. Partition strategy $P_3$, which does not partition the 16S by stems and loops, results in posterior likelihood values very close to those of the full partition strategy $P_4$, whereas partitioning stems and loops of 16S only as in $P_2$ has a considerably weaker effect (Table 2).

### 3.3. Bayesian analysis

The consensus tree topologies inferred from all four analyses differed, yet all of the differences involved alternative placements of weakly supported nodes (i.e., <0.95). There were notable differences in posterior probabilities between the analyses depending on whether the cox1 sequences were partitioned by codon position ($P_3$, $P_4$; Table 2). The analysis that did not include any codon position partitions ($P_1$, $P_2$) and the third partition analysis (strategy $P_3$) are generally representative of these two partitioning strategy groups. The two analyses that did not partition the cox1 gene by codon inferred weak support for the relationships of two major clades (A and B in Fig. 2). In contrast, the two analyses that partitioned cox1 by codon position inferred greater support for these same clades, with posterior probabilities increasing from <0.55 to close to significant ($0.90 \leqslant P_p < 0.95$). The analysis using four partitions was a decisively better explanation of the data than all other analyses according to the Bayes factor (Table 5). Thus, it is our preferred hypothesis of the phylogeny of wheatears, and subsequent discussion will be limited to this tree which agrees with the ML and the MP trees except some poorly supported relationships within species, and differing from the MP tree in the placement of clades B and C as sister groups (Fig. 2).

### 3.4. Morphometrical distances between species

There was a significant correlation between the genetic and morphometric distances matrices (i.e., Mahalanobis

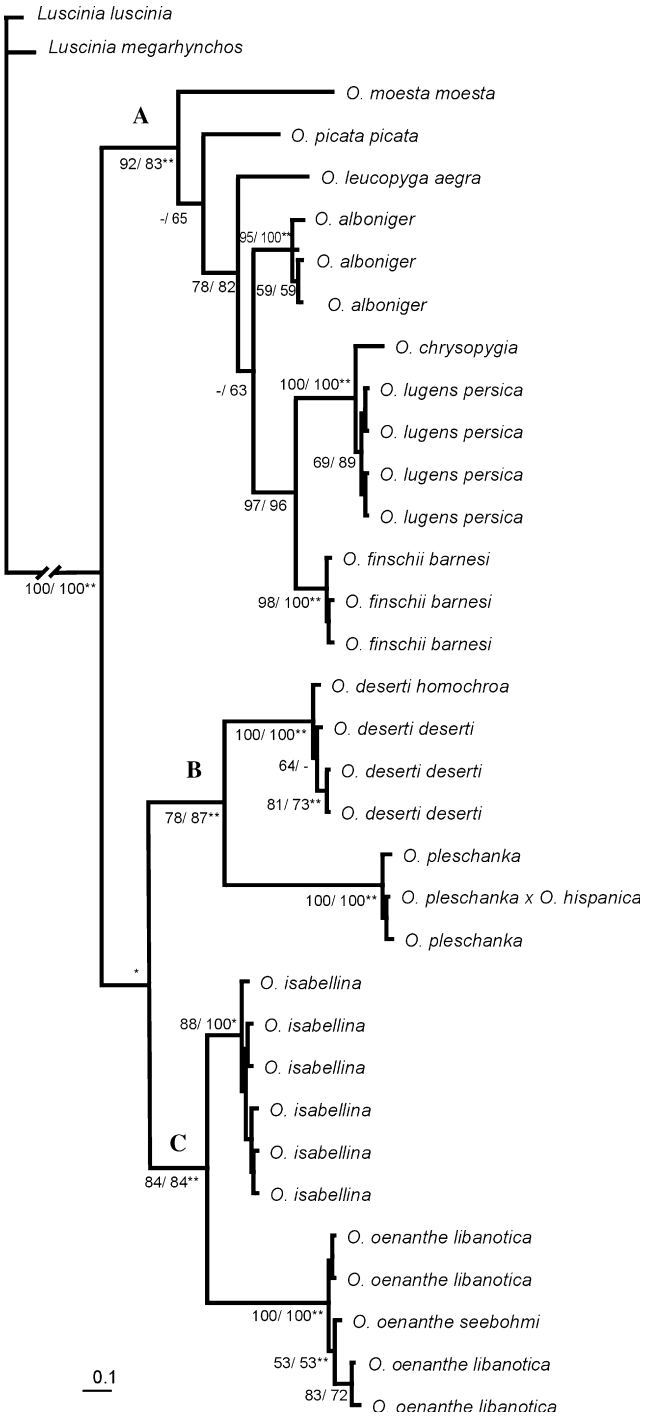


Fig. 2. Ninety-percent majority-rule consensus tree sampled from the posterior distribution of the most-partitioned analysis (strategy $P_4$). Posterior probability values from the Bayesian analysis are indicated at the >99% (**) >95% (*) significance levels. Numbers represent ML and MP bootstrap values (500/5000 replicates; given only if >50%). Clades A, B, and C are discussed in the text.

distances calculated on all the primary variables plus the ratios, reflecting an overall dissimilarity in size and shape) between species ($Z = 2.058$; $P = 0.02$; Mantel's test, 10,000 permutations). The topology of the morphological tree (Fig. 3) remains almost the same when the size-factor is removed (PCA analysis), apart from *O. chrysopygia* and

Table 5
2ln Bayes factors of comparisons of all partitioning strategies

| | $P_4$ | $P_3$ | $P_2$ |
|---|---|---|---|
| $P_1$ | 697.1 | 650.1 | 140.3 |
| $P_2$ | 556.8 | 509.8 | |
| $P_3$ | 47.0 | | |

The values indicate support for the column model over the row model.

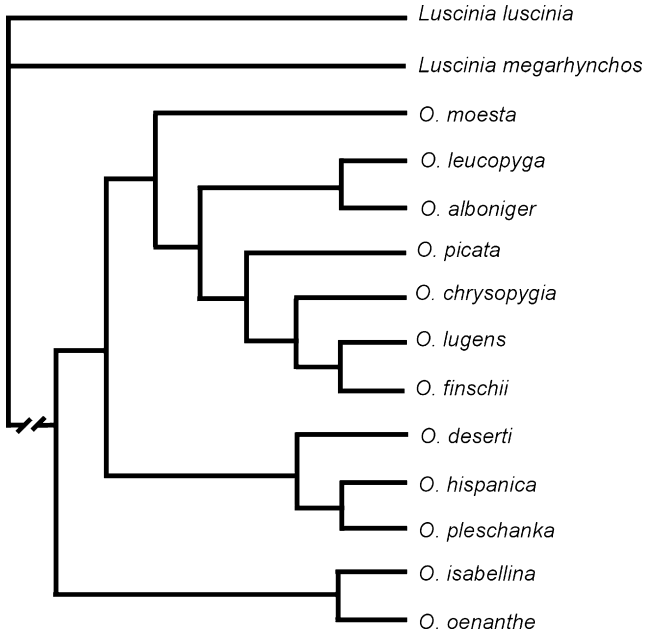


Fig. 3. Dendrogram based on morphometrical distances (21 variables and six ratios).

*O. finschii* swapping positions (not shown). Among the morphological traits that were individually regressed on the genetic matrix, we found a significant phylogenetic effect ($r = 0.21$, $P = 0.032$) of length of the emargination of second primary in proportion to the wing length (Sp2/WL, see Appendix A for details).

Comparing five alternative trees (the preferred molecular topology, the morphometric tree, and three alternative hypotheses from the literature; Table 6) with a reduced set of terminal taxa (one per species) and the molecular data matrix using Shimodaira–Hasegawa tests, the likelihood values for the morphometric topology did not result to be significantly different from the preferred molecular topology, whereas all three literature hypotheses were rejected with high significance (Table 6). Comparing the topology of the molecular tree to the other hypotheses with partition metric and quartet statistics, all of these alternatives were significantly different, but the difference values were lowest for the morphometric tree (Table 6).

## 4. Discussion

### 4.1. Systematics of wheatears

The phylogenetic arrangement of the wheatear species resulting from the analysis of our data set largely differs

Table 6
Difference measures of the molecular tree (Fig. 2; only one sequence per taxon) compared to the tree from morphometric data (Fig. 3) and three alternative topological hypotheses from the literature (Panov, 2005; Tye, 1989)

| Molecular tree | | | | | | |
|---|---|---|---|---|---|---|
| Phenetic tree[a] | Partition metric | *P*-value in Partition metric | Symmetric difference (in Quartet measure) | *P*-value in Quartet measure | Likelihood differences | *P*-value in Shimodaira–Hasegawa test |
| 1 Present study | 6 | <0.01 | 0.17 | <0.01 | 3.99 | 0.674 |
| 2 Panov (2005) | 16 | <0.01 | 0.40 | 0.01 | 84.57 | 0.000 |
| 3 Tye (1989) | 16 | <0.01 | 0.58 | 0.01 | 145.16 | 0.000 |
| 4 Tye (1989) | 16 | <0.01 | 0.54 | 0.01 | 145.10 | 0.000 |

Trees were compared using partition and quartets measures in Component (Page, 1993). Tree likelihoods were calculated in PAUP* (Swofford, 2002) based on the genetic data set and compared statistically by a Shimodaira–Hasegawa test. The likelihood ($-\ln L$) of the best (= molecular) tree was 3598.47.

[a] Phenetic tree 3 and 4 differ in their position of *O. oenanthe* (see Fig. 1).

from previous hypotheses on the structure of the genus *Oenanthe*. Several of the relationships suggested by our analysis support arrangements on which a certain consensus has been reached in the literature, but they only concern the terminal nodes of the tree. Most of the more-inclusive clades found in the present study (Fig. 2) differ from the previously suggested arrangements.

The very close relatedness of *O. hispanica* and *O. pleschanka* has been unambiguously assumed since long due to their ability to hybridize in their contact zone (Haffer, 1977; Panov, 2005). Our hybrid specimen is nested in the *O. pleschanka* group, despite a plumage pattern close to *O. hispanica*. Our analysis further suggests, with >95% support, that *O. lugens* and *O. finschii* are not sister-taxa, whereas they were treated as conspecific by Dementiev et al. (1968); their non-conspecificness is further shown by the broad geographical overlap the two species have in the Middle East (Aliabadian et al., unpublished data). We confirm, with a high posterior probability and bootstrap support, the much more disputed proximity of *O. isabellina* and *O. oenanthe*. These two species are part of the same species-group according Roselaar (1988), but were considered unrelated by Haffer (1988), Tye (1989) and Panov (2005). The position of *O. deserti*, placed near *O. pleschanka* in our analyses with strong support, is novel as well. *O. deserti* has previously been placed either in the same species-group as *O. finschii* and *O. lugens* (Vaurie, 1949; Roselaar, 1988), close to the *O. picata*, *O. finschii*, and *O. lugens* group by Tye (1989), or as basal to the other wheatears (Panov, 2005).

The strongly supported sister relationship between *O. chrysopygia* and *O. lugens* that emerges from our analyses had remained completely overlooked until now; in fact the amount of divergence between the two is the smallest we found among all species included in our analysis. *O. chrysopygia* was generally considered as a relative of *O. moesta* (e.g., Haffer, 1988; Mayr and Stresemann, 1950; Tye, 1989), or was considered a sister species to *O. xanthoprymna*, with *O. xanthoprymna* and *O. chrysopygia* being sister to a large clade that included *O. moesta*, *O. finschii* and *O. lugens* (Panov, 2005). Lastly, we confirm *O. oenanthe seebohmi* as a subspecies of *O. oenanthe*, and, considering the small amount of genetic divergence, *O. deserti homochroa* as a subspecies of *O. deserti*.

Several other problems remain in need of further clarification. In accordance with the view of Panov (2005), *O. picata* appears to be less closely related to *O. lugens* than previously thought (e.g., Hall and Moreau, 1970; Mayr and Stresemann, 1950; Tye, 1989), but its exact position within our clade A is unclear. *O. moesta* occupies a basal position of the clade A in our analyses remaining relatively isolated from the other species. The basal relationships between the three well-defined clades remain somewhat questionable, even if the posterior probability of a B–C node is >95%. The pattern of well-defined species groups with less supported internal nodes is commonly observed in birds, where it suggests rapid initial cladogenesis followed by more recent speciation events (Crochet et al., 2000).

### 4.2. Phylogeny, morphology, and ecology

There is a remarkably good agreement between our morphological and molecular trees (Figs. 2 and 3), especially if the unsupported clades in the molecular tree are collapsed. The genetically supported relationships of the species pairs *O. hispanica–O. pleschanka*, *O. finschii–O. lugens*, *O. chrysopygia–O. lugens*, *O. leucopyga–O. alboniger*, and, to a lesser extent, *O. picata–O. lugens* (in order of decreasing morphological similarity), correspond well to shape similarities as reported by Kaboli et al. (unpublished manuscript). The distance tree reported here (Fig. 2), which is restricted to the same species available for molecular analysis, confirms these similarities, and further (i) clusters *O. isabellina* with *O. oenanthe*, (ii) positions *O. deserti* not far from the group of *O. pleschanka* and *O. hispanica*, and (iii) defines a group including *O. picata*, *O. lugens*, *O. finschii*, *O. chrysopygia*, *O. leucopyga*, and *O. alboniger* (Fig. 3). This topology shows clear similarities with the phylogenetic tree.

Hence, there is a remarkable match between the molecular phylogeny and the morphometric distances among species, extending even to deep branches of the trees, the main difference being the position of *O. deserti–O. pleschanka* clade in the morphological tree. This concordance is

Table 7
Ecological and ethological characters for different divisions in three main clades A, B, and C as suggested by the molecular tree in Fig. 2

| | The three main clades | | |
|---|---|---|---|
| | A | B | C |
| Constituting species | *O. moesta*, *O. picata*, *O. leucopyga*, *O. alboniger*, *O. chrysopygia*, *O. lugens*, *O. finschii*, | *O. deserti*; *O. pleschanka*, *O. hispanica* | *O. isabellina*, *O. oenanthe* |
| Colour female and juvenile | Highly variable (pale brown, brownish, or dark-brownish or black-and-white as in the male) | Buff-brown, without black patches (except tail) | Buff-brown, without black patches (except tail) |
| Wing shape | Rounded (longer in desert species *O. alboniger* and *O. leucopyga*) | Pointed | Pointed |
| Migration | Resident, or partial migrant | Long distance migrant | Long distance migrant |
| Main perch sites | Stones (except *O. moesta*) | Vegetation | Ground |
| Main foraging mode | Perch-and-pounce and aerial sallying | Perch-and-pounce and aerial sallying | Hop-and-peck |
| Typical nest site | In a hole (rock crevice or burrow) | On the ground, under a bush or a stone | On the ground, under a bush or a stone |
| Nest platform | Small stones (except *O. moesta*) | Twigs | Twigs, or absent |
| Typical movement pattern | Aerial | Aerial | Cursorial |

also supported by the higher measures of tree congruence among these topologies as compared to hypotheses from the literature, and by the fact that the DNA data did not significantly reject the morphometric tree topology in a Shimodaira–Hasegawa test (Table 6). In birds, at least at within-genus level, such congruence between morphometry and phylogeny seems to be the exception rather than the rule. It is widely assumed that characters directly involved in locomotion and foraging, among others, are particularly susceptible to convergence, and that plumage characteristics in general are too labile for use in systematics (reviewed in Omland and Lanyon, 2000). In *Sylvia* warblers, ecologically relevant morphological traits show only weak relationships with phylogeny (Böhning-Gaese et al., 2003), and in gulls, morphometrical patterns (Schnell, 1970) appear unrelated to the molecular phylogeny (Crochet et al., 2000). Our results are at variance with the preceding ones, and suggest that, in the genus *Oenanthe*, morphometric patterns are subject to strong phylogenetic constraints. As the morphology of wheatears is closely correlated with eco-ethological traits (Kaboli et al., unpublished manuscript), ecological niches of wheatears appear phylogenetically conservative. Interestingly, the arrangement in three main clades shown by the molecular and morphometric trees is in full agreement with several ecological and ethological character states of the species included (Table 7).

### 4.3. Phylogeny and colour patterns

The study of the relationships between wheatear species has been obscured until now by the too exclusive attention on chromatic characters. Chromatic characters may sometimes carry a strong phylogenetic signal (e.g., Bridge et al., 2005), but they are most often misleading and unusable to infer phylogenetical relatedness between bird species (e.g., Cibois et al., 2004; Crochet et al., 2000; Olsson et al., 2005). As stated by Panov (2005), colour patterns in wheatears are not sufficiently conservative, and should be used with great caution in looking for species relationships. This is obvious in the convergence observed in colour pattern of species belonging to different clades, e.g., *O. finschii* and *O. lugens* vs. *O. pleschanka* and *O. deserti*. Our results tend to support the hypothesis that, in the genus *Oenanthe*, certain colour characters (e.g., a black throat, or a white cap) can appear, disappear and reappear independently in different lineages (see Cibois et al., 2004; Olsson et al., 2005; Price and Pavelka, 1996; and references therein). The question remains whether evolution in *Oenanthe* progresses from highly contrasting black-and-white patterns toward grey–brown plumages (Mayr and Stresemann, 1950; Tye, 1989), or, on the contrary, whiteness in the plumage is an evolutionary innovation (Panov, 2005). Our molecular tree supports the former hypothesis, since none of the grey–brown birds are in a basal position. However, since some rather dull African species are missing from our study, this question cannot be confidently answered.

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## Appendix A. List of the morphological variables (21 primary variables) measured on 189 museum skins, and the 6 ratios calculated from these variables

| | |
|---|---|
| (a) *Flight apparatus* | |
| Sp2 | Length of emargination of the second primary |
| Sp3 | Length of emargination of the third primary |
| WL | Wing length |
| P1L | Length of first primary |
| P1P2 | Tip of first primary to tip of second primary |
| P1P3 | Tip of first primary to tip of third primary |
| P1P4 | Tip of first primary to tip of forth primary |
| P1P5 | Tip of first primary to tip of fifth primary |
| P2Wt | Tip of second primary to wing tip |
| GtWt | Greatest cover tip to wing tip |
| AtWt | Alula tip to wing tip |
| TL | Tail length |
| (b) *Feeding apparatus* | |
| BL | Bill length |
| BD | Bill depth |
| BW | Bill width |
| MRB | Maximum length of rictal bristles |
| (c) *Foot–leg complex* | |
| TaL | Tarsus length |
| HTL | Hind toe length |
| HTNL | Hind toe nail length |
| MTL | Middle toe length |
| MTNL | Middle toe nail length |
| (d) *Ratios* | |
| SP2/WL | Length of emargination of the second primary/wing length |
| WingRI | Wing roundness index = (Wing length − P1 tip to wing tip)/wing length |
| TL/WL | Tail length/wing length |
| BL/BD | Bill length/bill depth |
| Tal/WL | Tarsus length/wing length |
| FootS/TaL | Foot span (= HTL + HTNL + MTL + MTNL)/tarsus length |

## Appendix B. Male mean values (in mm) for the measured external morphology in 202 specimens studied

| *Species* | *N* | Sp2 | Sp3 | WL | P1L | P1P2 | P1P3 | P1P4 | P1P5 | P2Wt | GtWt | AtWt | TL | BL | BD | BW | MRB | TaL | HTL | HTNL | MTL | MTNL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *O. alboniger* | 20 | 28.2 | 27.3 | 103.9 | 26.3 | 47.6 | 55.3 | 55.5 | 54.1 | 8.0 | 61.1 | 81.6 | 69.8 | 12.1 | 4.3 | 5.0 | 8.5 | 27.00 | 8.8 | 7.1 | 10.7 | 5.5 |
| *O. d. deserti* | 10 | 25.2 | 23.4 | 93.7 | 19.8 | 50.9 | 55.2 | 55.0 | 51.9 | 4.4 | 54.0 | 74.7 | 65.2 | 11.4 | 3.7 | 4.2 | 7.9 | 25.99 | 6.3 | 6.1 | 8.9 | 5.1 |
| *O. d. homochroa* | 7 | 25.1 | 22.0 | 90.1 | 20.5 | 48.0 | 52.2 | 52.2 | 49.4 | 4.1 | 51.9 | 72.2 | 64.7 | 11.1 | 4.0 | 5.0 | 8.1 | 26.11 | 6.1 | 5.8 | 9.1 | 4.8 |
| *O. finschii* | 20 | 25.9 | 23.6 | 89.7 | 22.7 | 41.5 | 47.6 | 47.9 | 46.4 | 6.3 | 51.2 | 71.1 | 62.4 | 11.2 | 4.4 | 4.7 | 8.2 | 25.90 | 7.2 | 6.5 | 10.0 | 5.3 |
| *O. hispanica melanoleuca* | 10 | 25.8 | 24.1 | 91.3 | 21.6 | 45.7 | 51.6 | 51.4 | 48.0 | 4.9 | 52.9 | 73.1 | 62.9 | 11.0 | 4.0 | 4.3 | 7.4 | 23.66 | 7.0 | 5.7 | 10.1 | 5.2 |
| *O. isabellina* | 20 | 25.6 | 22.0 | 98.3 | 19.7 | 54.4 | 57.6 | 57.1 | 53.4 | 3.2 | 54.6 | 78.5 | 59.8 | 13.0 | 4.8 | 5.0 | 8.7 | 30.47 | 7.2 | 7.3 | 10.2 | 6.0 |
| *O. leucopyga aegra* | 15 | 28.6 | 26.3 | 104.0 | 26.6 | 49.5 | 55.9 | 55.8 | 54.3 | 6.5 | 60.1 | 83.0 | 73.3 | 13.3 | 4.8 | 5.0 | 10.8 | 26.95 | 8.1 | 6.7 | 11.2 | 5.3 |
| *O. lugens persica* | 20 | 26.4 | 24.2 | 95.1 | 22.3 | 45.7 | 51.5 | 51.9 | 50.6 | 6.7 | 54.8 | 75.5 | 64.3 | 11.7 | 4.2 | 4.6 | 8.1 | 25.52 | 7.5 | 6.6 | 9.8 | 5.5 |
| *O. moesta moesta* | 15 | 27.4 | 26.1 | 92.4 | 24.2 | 43.3 | 48.3 | 48.3 | 47.4 | 5.2 | 53.1 | 72.7 | 67.1 | 13.3 | 5.1 | 5.4 | 9.8 | 30.14 | 8.5 | 6.9 | 10.4 | 5.4 |
| *O. oenanthe libanotica* | 20 | 24.7 | 22.1 | 98.0 | 16.7 | 57.2 | 60.7 | 59.4 | 53.5 | 3.5 | 56.6 | 78.7 | 57.8 | 11.6 | 4.0 | 4.5 | 6.8 | 27.65 | 7.2 | 7.4 | 9.8 | 6.3 |
| *O. o. seebohmi* | 5 | 25.0 | 21.4 | 92.9 | 19.7 | 50.8 | 54.0 | 53.7 | 50.5 | 3.3 | 52.2 | 73.6 | 57.3 | 11.9 | 5.0 | 5.1 | 7.7 | 28.59 | 8.0 | 7.1 | 10.7 | 5.7 |
| *O. p. Picata* | 8 | 25.3 | 24.5 | 91.4 | 24.5 | 40.2 | 46.6 | 48.1 | 47.1 | 9.8 | 53.1 | 71.8 | 66.8 | 10.8 | 4.3 | 4.4 | 7.6 | 24.92 | 8.0 | 6.0 | 10.3 | 5.1 |
| *O. pleschanka* | 20 | 24.7 | 21.8 | 92.6 | 20.9 | 47.8 | 53.2 | 53.2 | 50.4 | 5.7 | 53.1 | 74.1 | 63.2 | 10.3 | 3.8 | 4.1 | 6.9 | 23.51 | 6.3 | 5.9 | 9.4 | 5.1 |
| *O. chrysopygia* | 12 | 24.6 | 23.1 | 91.9 | 23.7 | 43.3 | 49.0 | 49.3 | 48.1 | 6.0 | 52.7 | 72.9 | 58.9 | 11.9 | 4.2 | 4.5 | 7.0 | 25.46 | 7.2 | 6.5 | 10.0 | 5.2 |

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