

Proposal to split taxon *halophila* as a monotypic species from *Oenanthe lugens* as *Oenanthe halophila* (Tristram 1859)

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This is a slight adjusted version of a pre-proposal submitted to the Palearctic RAG on 11.9.2025.

The *lugens*-complex has traditionally been considered to comprise eight to nine taxa in three groups (Tye 1989; Dean et al. 1992; Collar 2005, Table 1, Figure 1). Apart from the *lugens*-group (see above), the *lugubris*- group from northeast Africa and the *lugentoides* group from the Arabian Peninsula have been included in this complex on the basis of morphological similarities. However, molecular phylogenetic analyses including analyses of genome-wide data have revealed that these three groups do not form a monophyletic clade (Schweizer and Shirihai 2013; Alaei Kakhki et al. 2016, 2023). Instead, the *lugens*-group is more closely related to *O. finschii*, *O. chrysopygia* and *O. xanthoprymna* (Alaei Kakhki et al. 2023).

Taxa of the *lugens* complex and their distribution range. The nine taxa usually included in the *lugens* complex are divided into three groups.

<i>lugens</i> complex	
<i>lugubris</i> group	
<i>O. l. lugubris</i> (Rüppell, 1837)	Highlands of Eritrea, north and central Ethiopia
<i>O. l. vauriei</i> R. (Meinertzhagen, 1949)	North-east Somalia
<i>O. l. schalowi</i> (G. A. Fischer & Reichenow, 1884)	Southern Kenya, north-east Tanzania
<i>lugentoides</i> group	
<i>O. l. lugentoides</i> (Seebohm, 1881)	Highlands of south-west Saudi Arabia, western Yemen
<i>O. l. boscaweni</i> (G. L. Bates, 1937)	North-east Yemen, southern Oman
<i>lugens</i> group	
<i>O. l. lugens</i> (M. H. C. Lichtenstein, 1823)	Levant south to north-west Saudi Arabia, eastern Egypt, north-east Sudan
<i>O. l. halophila</i> (Tristram, 1859)	North Africa roughly from Morocco east to Libya
<i>O. l. warriai</i> (Shirihai & Kirwan, 2011)	Basalt deserts of eastern Jordan and southern Syria
<i>O. l. persica</i> (Seebohm, 1881)	Southern and western Iran, wintering mostly in eastern Arabia

Tabel 1. Taxa included in the *lugens*-complex and its subdivision in three groups and their distribution taken from Schweizer and Shirihai (2013).

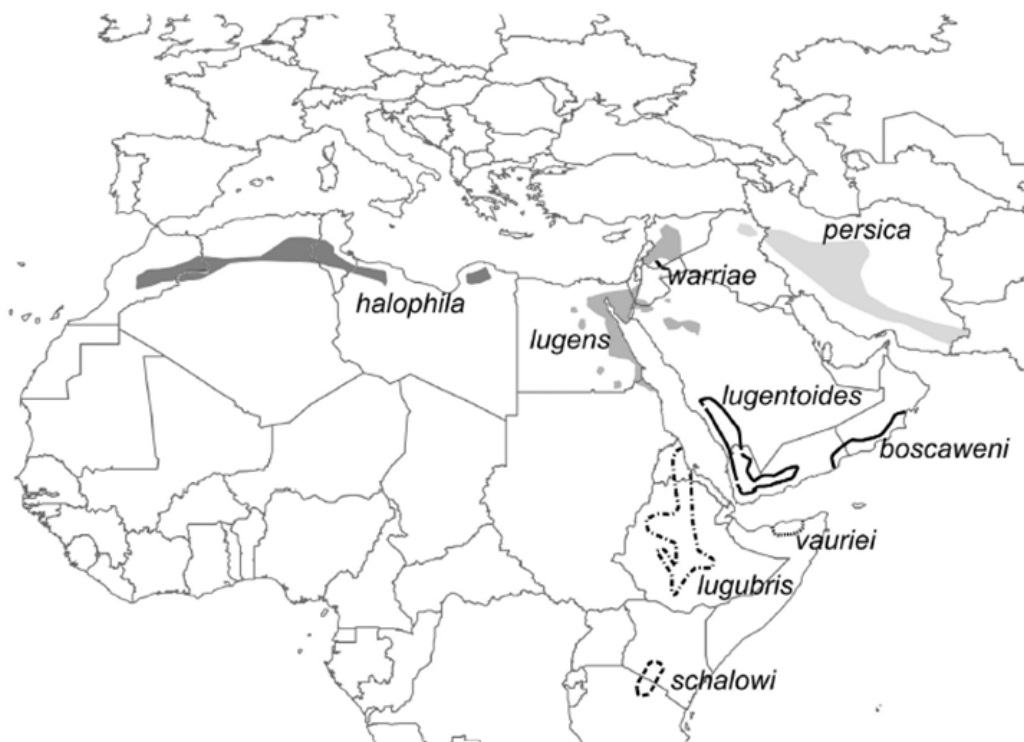


Figure 1. Distribution of the taxa within the *lugens*-complex taken from Schweizer and Shirihai (2013).

The three groups traditionally included in the *lugens*-complex are now widely treated as three different species, including Avilist v2025, although during the process of preparing the latter, the relevant paper presenting a phylogenetic hypothesis based on genome-wide data (Alaei Kakhki et al. 2023) does not seem to have been considered. However, the results of this paper strongly support this treatment.

Species level taxonomy within the *lugens*-group has been differently interpreted in the last years. The last versions of IOC (including the latest version, Gill F, D Donsker & P Rasmussen (Eds). 2025. IOC World Bird List v15.1) accepted three species *O. halophila*, *O. lugens* (incl. *O. l. lugens*, *O. l. persica*) and *O. warriae*, a treatment that was earlier proposed by Shirihai and Svensson (2018). Avilist v2025 treats the entire group as single species, however, during the decision process, the important results of Alaei Kakhki et al. (2023) were not considered (see discussion issue#453 for the AviList v2025)

I will first introduce phenotypic and genomic variation in the *lugens* group partly extracted with complements from my previous publications (Schweizer and Shirihai 2013; Alaei Kakhki et al. 2023). Then I will argue that the allopatric taxon *halophila* is best split as a monotypic species under an integrative version of the biological species concept.

Phenotypic variation

Within the *lugens* group, sexes are virtually identical in *lugens* and *persica* and differ only slightly in *warriae*, whereas *halophila* shows a pronounced sexual dimorphism (Shirihai et al. 2011; Shirihai and Svensson 2018; Table 2). Moreover, *lugens* and *persica* are morphologically only subtly differentiated. Male *halophila* on the other hand, although similar, can be readily separated from both *lugens* and *persica* (Shirihai et al. 2011; Shirihai and Svensson 2018).

The taxon *warriae* has until recently been considered as a dark morph of *lugens*, but Shirihai et al. (2011) demonstrated that this range restricted almost entirely black wheatear is not a morph of *lugens* and should be better treated as a taxon of its own.

For the separation of males of *halophila* ('Maghreb Wheatear') and *lugens* ('Mourning Wheatear'), Shirihai and Svensson (2018) write the following:

"[male] Maghreb is likely to be confused only with *Mourning Wheatear* (sexes alike), especially in areas where both allegedly mix in winter (e.g. in W Egypt), or where they could occur as vagrants. Thus, [male] Maghreb hardly differs from Mourning, except in flight by narrower and greyer (more subdued, not so pale and contrasting) basal area to flight-feathers (notably strongly reduced on primaries) and by usually rather indistinct (sometimes almost lacking) cream-pink wash to ventral region (never as deep buff, rufous or cinnamon as in many Mourning). Also tends to have pale areas of lower back, rump and belly less pure white (greyish pink-cream in some), while crown and hindneck when fresh are less pure whitish, being dirty ash-brown."

"Song [of 'Maghreb Wheatear'] based on own impressions and several recordings (e.g. from Morocco, Algeria, Tunisia and Libya) perhaps slightly different from Mourning Wheatear (*lugens*) being a little slower or even staccato-like, a little drier and more mechanical, yet can include a recurring clear yodelling *yalala* with slightly falling pitch and more warbling trills. At times more extended song, being more varied, jumbled and richer, a continuous sweet, unhurried warbling (alternately ascending and descending), with each strophe sounding like a ringing trill mixed with brief whistles and metallic calls. Appears to show stronger individual variation than Mourning *lugens*, but this requires confirmation. Some appear more imitative."

There are claims of presumed phenotypically intermediates individuals between *halophila* and *lugens* or even a cline within *halophila* with females progressively becoming more male like towards the eastern part of its range. However, this was interpreted by Shirihai and Svensson (2018) as a consequence of "apparently underestimated natural variation and the occurrence of a darker female morph"

in *halophila*, and they noted: "We, at least, have been unable to find any confirmed [female] *halophila* with fully [male]-type plumage, nor have we seen a tendency for [female] to become darker in the east." Earlier, Shirihai et al. (2011) stated the following accordingly:

"Guichard (1955) reported that of four females collected in Tripolitania, Libya, one was typical pale *halophila*, but two others were principally male-like, while the fourth seemed intermediate between male and female plumage. Apparently similar intermediates reported from Egypt by Baha el Din & Baha el Din (2000), who also reported birds with *halophila*-like plumage but with extensive white in wing like *O. l. lugens*. However, neither of these references acknowledged the extreme variation in female *halophila* described above. Baha el Din & Baha el Din (2000) confirmed the lack of overlap in breeding ranges of *halophila* and *lugens* in Egypt, which are separated by the Nile (and even suggested that they favour different habitats). *O. l. halophila* is constant in its plumage characteristics and clear sexual differences exist across its range."

I know the variation of female *halophila* quite well from several visits to the Maghreb, especially from southern Tunisia, where the taxon is quite common. There is variation in female plumage, however, I have never seen a female that strongly appeared male-like. Moreover, it has to be taken into account that first winter males of *halophila* appear not black-and white overall than ad males, which could be confusing for the unaware observer. Note additionally, that female *halophila* can be very similar to females of Finsch's Wheatear *O. finschii*. Their breeding ranges are widely disjunct, and a co-occurrence during winter is not likely.

Table 2. Morphological characterization of the taxa comprised in the *Oenanthe lugens* complex taken from Schweizer and Shirihai (2013)

Taxon	No clear sexual dimorphism			Clear sexual dimorphism			clear sexual dimorphism & dimorphic male plumage			
	No clear sexual dimorphism	Clear sexual dimorphism	Dimorphic male plumage	All-black plumage, white wing flashes in open wings strongly reduced and rufous pectal patch is lacking	Black-and-white plumage, white wing flashes in open wings and rufous pectal patch well developed	Black-and-white male and grey-brown female, reduced white wing flashes in open wings, rufous ventral patch reduced (pinkish cream)		Black-and-white male and grey-brown female, reduced white wing flashes in open wings, rufous ventral patch well marked in both sexes, female has streaked throat and/or body, and both sexes have rounded wing shape similar to African taxa	overall between Arabian and remaining African taxa, with male's black area on breast/flanks not as extensive as the latter but has characteristic dusky and streaky brown crown; females paler, approaching the Arabian taxa in having paler underparts with thinner dark streaks and greyer lined upperparts	Black-and-white male and deep-brown female, with strongly reduced white wing flashes in open wings; rufous ventral patch well marked and deep in both sexes
<i>krabarti</i> (Bischoff, 1937)		X	X							X
<i>vauriei</i> R. Meinertzhagen, 1949		X						X		
<i>schaferi</i> (G.A. Fischer & Reichenow, 1894)		X							X	
<i>lugens</i> (Seeborn, 1881)		X					X			
<i>boscareni</i> G.L. Bates, 1937		X					X			
<i>lugens</i> (M.H.K. Lichtenstein, 1923)	X				X					
<i>halophila</i> (Tristram, 1859)		X				X				
<i>warniei</i> Shirihai & Kirwan 2011	X			X						
<i>pectoralis</i> (Seeborn, 1881)	X				X					

Genetic variation

In analyses chiefly dominated by mtDNA variation (two mitochondrial genes and one nuclear Intron (Schweizer and Shirihai 2013), *O. finschii* was revealed to be the sister lineage of a clade consisting of the members of the *lugens* group as well as *O. xanthoprymna* and *O. chrysopygia* (Figure 2). Even the *lugens* group turned out not to be monophyletic. The taxon *persica* was found to be more closely related to a cluster consisting of the taxa *O. chrysopygia* and *O. xanthoprymna* than to the remaining members of the *lugens* group, although the cluster of the two *persica* samples was not robustly supported. *Halophila* was found to be the sister group of a clade comprising *lugens* and *warriæ*. The samples of the latter were nested within *lugens*. Within *lugens*, two clusters were robustly supported. However, they could not be associated with a particular locality or region and revealed no obvious geographic structure. The non-monophyly of the *lugens* complex with *persica* being more closely related to *O. chrysopygia* and *O. xanthoprymna* was also shown in dataset with one individual per taxon using three nuclear and five mtDNA markers (Aliabadian et al. 2012; Alaei Kakhki et al. 2016).

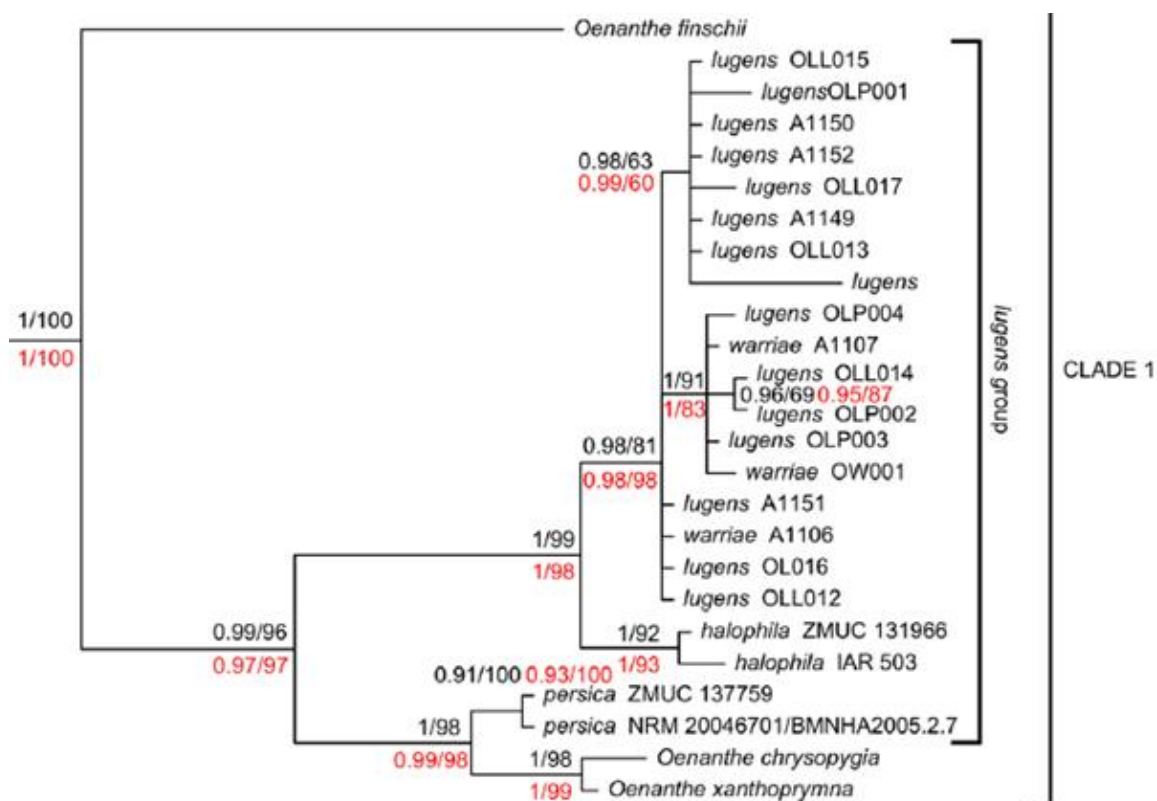


Figure 2. 50% Majority rule consensus tree of the BI with MrBayes on the basis of the two mtDNA genes and one nuclear intron of the *lugens* group from Schweizer and Shirihai (2013). Clade credibility values and bootstrap values of the maximum likelihood inference with RAxML above 0.5 or 50 respectively are indicated at each node. Moreover, BI clade credibility values and ML bootstrap values for the mtDNA dataset are indicated in red at each node.

However, the *lugens* group was corroborated as monophyletic group when whole-genome-resequencing data was analysed (Alaei Kakhki et al. 2023. Figure 3).

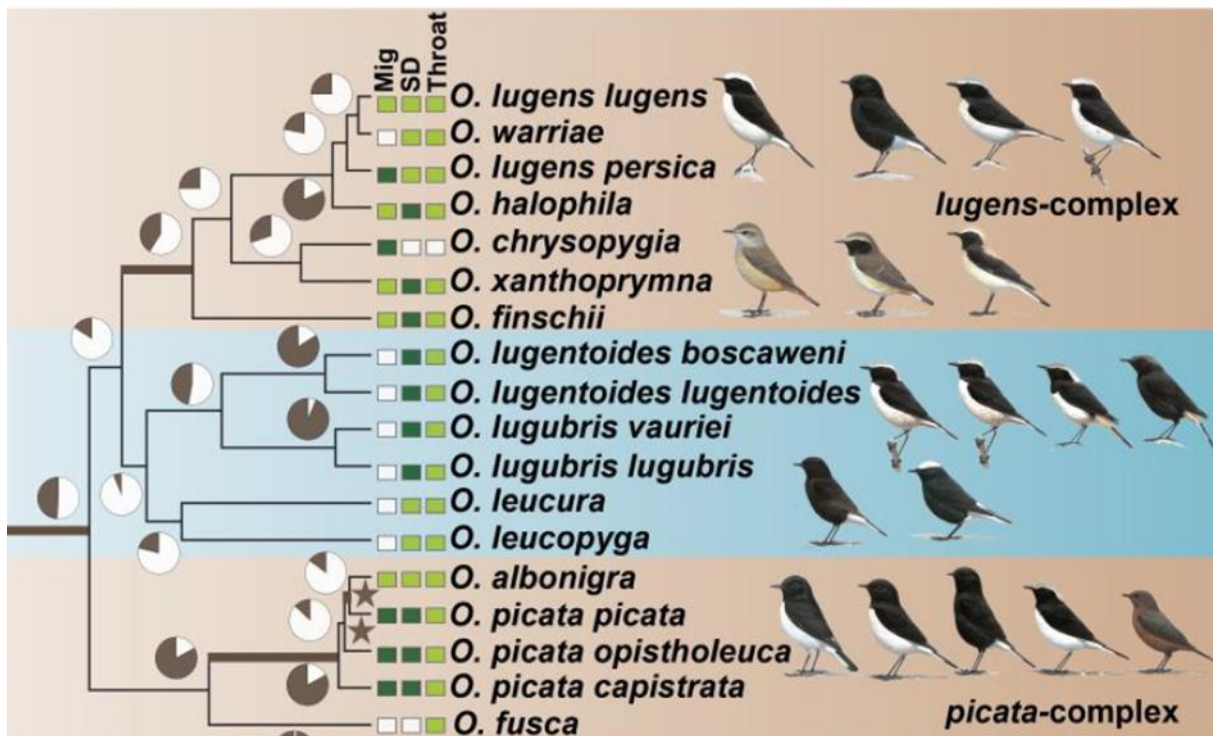


Figure 3. Part of a Time-calibrated phylogenetic tree of open-habitat chats and levels of ILS from Alaei Kakhki et al. (2023). All nodes are supported by bootstrap values of 100. Pie charts depict the gene tree heterogeneity for each internal branch, with the dark proportion indicating the proportion of concordant gene trees (gCF). Bold branches indicate internal branches for which ILS alone is statistically sufficient to explain the observed gene tree heterogeneity. Stars indicate branches that are in the phylogenetic anomaly zone. The character states of three selected characters: Sexual dimorphism (SD), monomorphic female-type (white), monomorphic male-type (pale green), dimorphic (dark green); Migratory behavior (Mig), sedentary (white), short-distance migrant (pale green), long-distance migrant (dark green); and throat coloration (throat), white (white), black (pale green), and polymorphic (white and pale green). Drawing courtesy of Chris Rose (www.chrisrose-artist.co.uk) with permission from Bloomsbury Publishing Plc.

So, within the *lugens* complex there is a clear discordance between mitochondrial and genome-wide data. However, as revealed by Alaei Kakhki et al. (2023) the evolution of the *lugens* complex was marked by two incidences of introgression that likely underpins this mito- nuclear discordance observed in this complex (Figure 4). Introgression occurred between *O. xanthoprymna* and the *O. lugens* ancestor and between north-African *O. halophila*. Alaei Kakhki et al. (2023) explain:

"Introgression occurred between *O. xanthoprymna* and the *O. lugens* ancestor and between north-African *O. halophila* and the middle eastern *O. l. lugens* -- *O. warriae* ancestor. Both incidences of introgression make sense in the light of biogeography, as they occurred between geographically neighboring taxa (fig. 4). Together they can explain the close mitochondrial relationship of *O. l. persica* with *O. xanthoprymna* and *O. chrysopygia*: *O. xanthoprymna* mitochondria were introduced into the *O. lugens* ancestor by hybridization and may at

first have segregated in the *O. lugens* lineage but then have been lost in *O. halophila*. Mitochondrial replacement with *O. halophila* variation upon genetic exchange of the latter taxon with the *O. l. lugens*--*O. warriae* ancestor would have left *O. l. persica* the only taxon with a **O. xanthoprymna*-*like mitogenome."

Alaei Kakhki et al. (2023) also shed shed first genomic light on the divergence of *warrie* 'Basalt Wheatear':

"...a species with a very restricted range that is interesting from the perspective of phenotypic evolution: this species turns out to be highly similar to *O. l. lugens* at the genomic level, which contrasts with its marked phenotypic divergence (fig. 4). This result is similar to the situation observed, for instance, in Hooded and Carrion Crows (*Corvus cornix* and *Corvus corone*, respectively) (Poelstra et al. 2014) and opens interesting questions on the evolutionary history of this taxon's coloration."

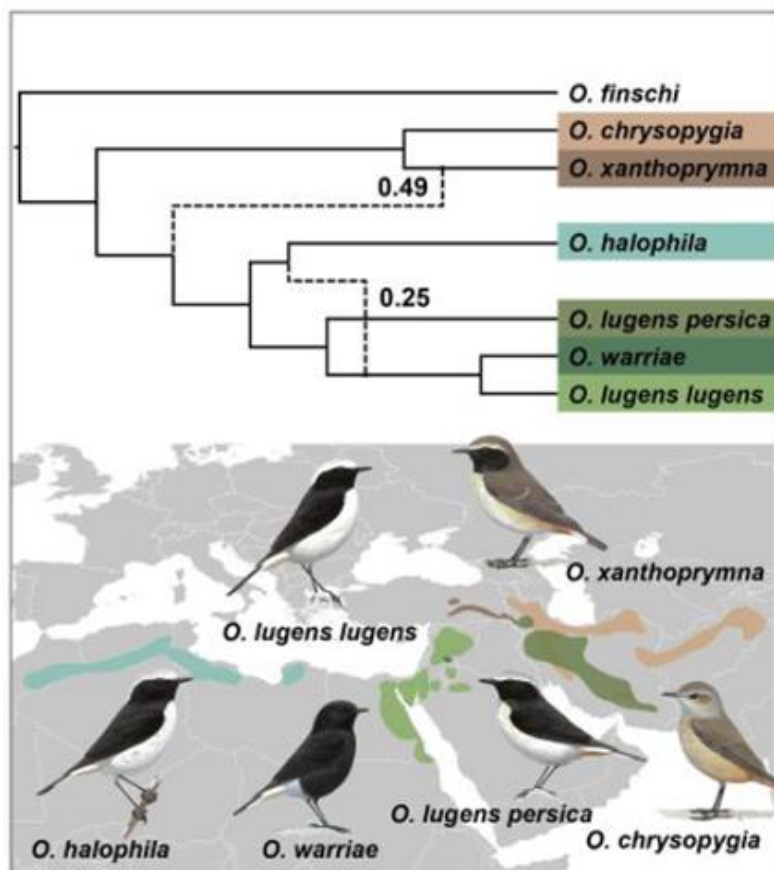


Figure 4. Phylogenomic networks and distribution ranges for the *lugens* complexe from Alaei Kakhki et al. (2023). Phylogenomic networks were estimated under the maximum pseudolikelihood approach implemented in phyloNet. Numbers on the edges indicate the inheritance probabilities, which correspond to the proportion of gene trees supporting the reticulate relationship. Drawings courtesy of Chris Rose (www.chrisrose-artist.co.uk) with permission from Bloomsbury Publishing Plc. Distribution ranges modified from BirdLife International and the Handbook of the Birds of the World (2016).

Given the mito-nuclear discordance, the time estimates for the splits of the different lineages chiefly based of mtDNA variation provided by Schweizer and Shirihai (2023) are of limited use, however, they indicated that the *lugens* group diversified during the last 500k years. The time calibrated tree in Alaei Kakhki et al. (2023) indicated that their diversification might even be more recent. However, unpublished MSMC2 (Multiple Sequentially Markovian Coalescent, Schiffels and Wang 2020) analyses indicate that *halophila* had an independent demographic history for the last 500k years (own data, Niloofar Alaei Kakhki in litt.).

Taxonomic consequences

The phylogenetic history of wheatears of the genus *Oenanthe* has been shaped by repeated phases of introgression in different evolutionary lineages (Alaei Kakhki et al. 2023), and this is likely responsible for the mito-nuclear discordance observed in the *lugens* group, which clearly influenced recent taxonomic interpretations -- chiefly, the non-monophyly of the *lugens* group in mtDNA.

As revealed by genomic data, *halophila* first split with in the *lugens* group. Although its separation is rather recent, this is in line with the timeframe of well accepted species level split within *Oenanthe* (Lutgen et al. 2025, Alaei Kakhki et al. 2023). For example, species within the *hispanica-pleschanka -melanoleuca-cypriaca* complex are also rather young and diversified in the last 700'000 year (note that this was estimated based on a huge population level data set using state of the art methods) (Lutgen et al 2025).

In issue #453 for the AviList v2025, one of the arguments against splitting *halophila* was that this would make *O. lugens* polyphyletic. However, as explained above, genome wide data show that there is a mito-nuclear discordance, and if *halophila* was split, *O. lugens* would still comprise a monophyletic clade. (Notwithstanding this, one has to bear in mind that polyphyletic taxa in mtDNA can be expected in clades with a history of introgression throughout their evolutionary history such as *Oenanthe* wheatears).

Halophila is unique among the taxa of the *lugens* group in showing strong sexual dimorphism. Dimorphic sexes can be found in *O. finschii*, and *O. xanthprymna*, hence in two consecutive sister groups of the *lugens* group (Figure 3). Moreover, males can be separated by plumage characteristics from *lugens* and *persica* (and also *warriae*, of course) and *halophila* differs slightly in vocalizations from *lugens*.

Wheatears of the genus *Oenanthe* are a very peculiar, though highly interesting radiation. Convergent phenotypic evolution is prevalent on different levels (Aliabadian et al. 2012; Alaei Kakhki et al. 2023; Lutgen et al. 2025), and species from separate evolutionary lineages can be very similar in plumage and difficult to separate in the field. Songs are often very similar among different wheatears species -- e.g. in the *Oenanthe* the *hispanica-pleschanka* complex, which is now broadly considered as comprising four species level taxa, and with the exception of that of *O. cypriaca*, songs

and other vocalisations of the other species are extremely similar in this complex (Lengacher and Schweizer in prep.).

By taking into account the peculiarities of the genus and applying a consistent taxonomic treatment within the group, the genomic and morphological data and available information on vocalisation clearly suggest that the taxon *halophila* should be treated as a species level taxa, *Oenanthe halophila* (Tristram 1859), based on an integrative version of the biological species concept and by applying a prospective approach. In such an approach, as Schweizer et al. (2023) elaborate: "Species delimitation decisions are thus made on the basis of present-day or potential future processes or interactions among lineages. To evaluate whether lineages are likely to fuse in the future, our approach relies on integrating multiple lines of evidence by evaluating all present data. Consequently, species delimitation decisions concern hypotheses that need to be documented and reevaluated when new evidence becomes available.».

Voting

Seven members (me included) support the split of the taxon *halophila* as a monophyletic species from *Oenanthe lugens*. One member, however, did not strongly oppose against the split, but would like the entire *lugens* complex to be treated including particularly *warriae*, would like to have included more sample in the genomic analyses especially individuals at the eastern and western end of the ranges of *halophila* and *lugens* s. str. to test for admixture, and a quantification of geographic variation of difference female plumage types in *halophila*.

I have the following objections to this.

- As argued by Alaei Kakhki et al. (2023) and described above, *warriae* might be similar to the *C. c. corone* / *C. c. cornix* case which are not split by AviList.
- As stated above, there is - in my opinion solid - qualitative information that there is no geographic cline of female plumage types in *halophila*.
- The ranges of *halophila* and *lugens* s. str. are not in contact, however, a better (population level) genomic sampling could potentially infer that there was gene flow recently and/or occasionally today. However, this would not affect the overall conclusion, otherwise, the *hispanica-pleschanka-melanolecua-cypriaca* complex should then be partly lumped as well and probably also *O. chrysopygia* and *O. xanthopyrmyna* to be consistent, and I am quite sure that this would not get wide support.

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