

Appendix A

Taxonomic recommendations

On the basis of the findings from this study, previous published studies, and also incorporating unpublished findings based on morphometric data, we suggest a number of changes in the taxonomic treatment of African-Arabian mainland *Zosterops*, including those from the islands of Pemba and Socotra, relative to the classification used in van Balen (2019).

Comprehensive inclusion of African subspecies revealed widespread mainland taxa *Z. abyssinicus* and *Z. senegalensis* as non-monophyletic (Fig. 2), supporting previous findings (Cox et al., 2014), who included a small subset of these taxa (three and five subspecies respectively). The exceptionally widespread *Z. senegalensis* (Fig. 1B) occupies a diversity of habitats from acacia woodland to evergreen forest (Moreau, 1957) and, despite its remarkably homogenous appearance (yellow-bellied birds with a green back, see Plate 1A), fourteen subspecies tend to be recognised (Dickinson, 2003), based largely on plumage, which inter-grade widely across the species range (Clancey, 1967; Moreau, 1957). Based on the results of our study we suggest major revision to the current taxonomy is required. We therefore make the following recommendations of twenty lineages that should be treated at species rank as independent taxonomic units. However, we take a conservative approach to this, as several taxa require substantial further research to establish their appropriate ranking.

African yellow white-eyes “*Zosterops senegalensis*” *sensu lato* (see Plate 1A)

Our molecular phylogenetic analyses showed nominate *Z. s. senegalensis* Bonaparte, 1850, itself to be polyphyletic, occurring in the phylogeny as two independent clades within the larger clades B₂ and B₅ respectively (Fig. 2). Our West African samples (from Liberia, Ghana and Nigeria) therefore comprise a separate taxon from Central African ones (from Uganda and the Democratic Republic of Congo (DRC)). As the type locality is Senegal, the name *senegalensis* should apply to the West African taxon only, but the boundary between the taxa remains to be established in detail.

- 1) *Zosterops senegalensis* Bonaparte, 1850
 - a) *Z. s. senegalensis* Bonaparte, 1850
 - b) *Z. s. demeryi* Büttikofer, 1890

Species delimitation analyses (bGYMC thresholds >0.1) grouped the west African *Z. s. senegalensis* with *Z. s. demeryi* Büttikofer, 1890 (single sample from Liberia), with which it intergrades across this region; the two together form a monophyletic grouping within the larger clade B₅ (Fig. 2). Based on this, we suggest these taxa be treated as a single species comprising two subspecies, with more in depth sampling across the ranges of both being required to determine if *demeryi* in fact merits separate subspecific status.

- 2) *Zosterops stenocricotus* Reichenow, 1892

This proposed species, from the island of Bioko and southeast Nigeria to Gabon, placed within clade B₃ (Fig. 2), differs from other mainland “*senegalensis*” based on mtDNA genetic differentiation. It was resolved as monophyletic and it was distinct based on all species delimitation analyses implemented. It has previously been recommended for full species status in recognition of its distinctive song (Fry et al 2000).

3) *Zosterops stuhlmanni* Reichenow, 1892,

Our museum samples identified as *Zosterops s. stuhlmanni* from Uganda form a strongly supported clade (1.00 BPP) with other East-Central African “*senegalensis*” samples from Uganda and eastern DRC (Kivu), which were collected in the field and identified as *Z. s. senegalensis* (Fig. 2, nesting within clade B₂). Although these taxa are reciprocally monophyletic in our phylogeny (1.00, and 0.90 BPP respectively), molecular species delimitation methods cluster them together as a single species. Based on their genetic similarity and close geographic location e.g. museum sample BMNH 1913.7.16.140 was collected from Mpumuru and field samples ZMUC 145103 and ZMUC 145211 were collected from nearby Mt Rwenzori, they are likely to represent a single taxon. However, more in-depth investigation within this region is required to clarify these relationships.

- 4) *Zosterops quanzae* Meyer de Schauensee, 1932
- a) *Z. q. quanzae* Meyer de Schauensee, 1932
 - b) *Z. q. kasaicus* Chapin, 1932
 - c) *Z. q. heinrichi* Meise, 1958

Z. q. quanzae from central Angola intergrades with *heinrichi* from northwest Angola and *kasaicus* from northeast Angola and southwest DRC, and the three form a well-supported clade within the larger clade C₂ (Fig. 2). All species delimitation analyses group these Angolan taxa together, and as they not reciprocally monophyletic and the ranges of the samples included here also overlap, we suggest taxa from this region represent a single species (the name *quanzae* takes priority over *kasaicus*). However, as sampling is based on limited numbers of museum specimens identified to subspecies on unstated criteria from a relatively small geographical area, we strongly recommend more detailed investigation to clarify precise relationships between them.

- 5) *Zosterops jacksoni* Neumann, 1899
- a) *Z. j. jacksoni* Neumann, 1899
 - b) *Z. j. gerhardi* van den Elzen & König, 1983

Z. jacksoni, from the Kenyan highlands, was resolved with the singleton of *Z. gerhardi*, from the highlands of south Sudan and north-east Uganda, as a clade within the larger clade B₅ in our phylogenetic analysis (Fig. 2), where they are sister to the *Z. senegalensis* clade (species 1 above). Species delimitation for our concatenated mtDNA sequence data suggested these taxa as distinct from *Z. senegalensis* (species 1) at all bGYMC thresholds >0.1, while Cytb pairwise distances are 1.5%, which is just below the 2% threshold for taxa to be conspecific (Appendix C, Table S1). Together *Z. jacksoni* and *Z. gerhardi* were also combined based on molecular species delimitation analyses (thresholds 0.2-0.7). Formerly, these highland taxa were included in the “*Z. poliogaster*” *sensu lato* species complex (van den Elzen and König 1983), but as a result of their resemblance to *demeryi*, *stuhlmanni* and *stierlingi* were later placed in “*Z. senegalensis*” (Fry et al., 2000). Morphometric data (N=5 per taxon, Day, et al. unpublished) placed *jacksoni* and *gerhardi* closely together along PC1-PC3. Based on our results we suggest that *jacksoni* is elevated to species status, but further assessment is needed to validate the status of *gerhardi*.

- 6) *Zosterops anderssoni* Shelley, 1892
- a) *Z. a. anderssoni* Shelley, 1892
 - b) *Z. s. stierlingi* Reichenow, 1899
 - c) *Z. s. tongensis* Roberts, 1931

Samples of *stierlingi* included in our phylogeny are reciprocally monophyletic (0.99 BPP), but nest within a larger, well-supported clade that also contains samples of *anderssoni* and the single *tongensis* analysed and that itself forms part of clade C₂ (Fig.2). The latter taxa are unresolved as a group, with *tongensis* embedded in one of the *anderssoni* subclades. Molecular species delimitation analyses grouped all three taxa together at thresholds 0.5-0.9 (lower thresholds included additional taxa – see section 3.3 in the main article) and pairwise distances from Cytb are <0.4% (see Appendix C, Table S1), considerably lower than the 2% threshold for taxa to be considered conspecific. Based on these analyses we cannot recommend that each of these taxa be elevated to species level; however, they warrant further investigation since morphometric data (Day et al, unpublished) suggests *anderssoni* (N=11) to be distinct from *stierlingi* (N=5) and *tongensis* (N=4) across PC axes 1-3. In contrast to the other two taxa, *stierlingi* is restricted to highland habitats across southern East Africa, including east Zambia, south and east Tanzania, Malawi and north-western Mozambique (van Balen, 2019). The lowland birds *anderssoni*, widespread across the savannahs of Southern Africa, and *tongensis*, from northern-eastern Southern Africa, intergrade. As a group, the three taxa are clearly distinct genetically from other Afrotropical white-eyes, but further in-depth study is required to resolve the relationships between them.

7) *Zosterops vaughani* Bannerman, 1924

Z. vaughani, from Pemba Island, is currently recognized as a species (van Balen, 2019), although some previous authors regarded it as conspecific with “*Z. senegalensis*” *sensu lato*. Habel et al. (2013) showed this taxon to be distinct based on population genetic analyses (microsatellites) of a small subset of four taxa, but it has not previously been included in a broader phylogenetic analysis. Our results identified *Z. vaughani* to be a highly distinct species with respect to all other Afrotropical taxa, being resolved within clade C as sister to the Indian Ocean ‘*maderaspatanus*’ clade, as opposed to any mainland species, though without strong support for this placement.

Taxa whose status requires further assessment - *Z. s. reichenowi* and *Z. s. toroensis*

The taxa *Z. s. reichenowi* Dubois, 1911, and *Z. s. toroensis* Reichenow, 1904, are only represented by single archival samples, which were collected from Uganda and the Democratic Republic of Congo respectively. Together these taxa form a clade in our phylogeny, albeit with weak support (0.53 BPP), within the larger well supported clade B₂ (Fig. 2), and are closely related to *Z. stuhlmanni*. Molecular species delimitation analyses indicate that these taxa comprise distinct species, supported by Cytb pairwise distances that are >2% (Appendix C, Table S1), however, further focused sampling from the region is needed to confirm their status.

Abyssinian white-eyes “*Zosterops abyssinicus*” *sensu lato* (see Plates 1A and B)

In the dry lowlands of north-east Africa, “*Z. senegalensis*” *sensu lato* is replaced by “*Z. abyssinicus*” *sensu lato* (Fig. 1B), which has a duller green back and locally can have either a yellowish or whitish belly. This taxon is confined to lowland (<1000m) scrubland or semi-desert habitat of North-east Africa, but is also found outside mainland Africa on the island of Socotra in the Gulf of Aden and in the southern tip of the Arabian peninsula (Moreau, 1957). There are currently four recognised subspecies of *Z. abyssinicus* (Dickinson, 2003), although previously this group was thought to represent two separate species based on belly colour (‘white or pale-bellied’ - *Z. abyssinicus*; and the ‘yellow-bellied’ - *Z. smithi* Sclater (1930)).

- 8) *Zosterops flavilateralis* Reichenow, 1892
a) *Z. f. flavilateralis* Reichenow, 1892
b) *Z. f. jubaensis* Erlanger, 1901

This is a yellow-bellied bird from southern Ethiopia, Kenya and north-east Tanzania and was formerly considered to be an *abyssinicus* subspecies. (Cox et al., 2014) revealed this taxon to be distinct from white-bellied forms, and it is currently a recognised species (van Balen, 2019). Both Cox et al. (2014) and Habel et al. (2015) showed *flavilateralis* to be indistinguishable from *Z. jubaensis* Erlanger, 1901, and our species delimitation analyses further support the concept of synonymising these taxa, which form a monophyletic group within clade B₆.

- 9) *Zosterops abyssinicus* Guérin-Méneville, 1843
a) *Z. a. abyssinicus* Guérin-Méneville, 1843
b) *Z. a. arabs* von Lorenz & Hellmayr, 1901
c) *Z. a. omoensis* Neumann, 1904

We are cautious regarding the status of these white-bellied taxa that together comprise a monophyletic grouping within clade A₂ in our phylogenetic analysis. They appear to have distinct ranges, with *arabs* occurring on the Arabian peninsula (SW Saudi Arabia, Yemen and S Oman), *abyssinicus* from north-east Sudan, Eritrea and north and central Ethiopia, and *Z. omoensis* from west Ethiopia (and possibly north-east South Sudan) (van Balen, 2019). Three distinct groupings were identified in our study using species delimitation methods (bGYMC 0.1-0.9), although these three lineages have Cyt b pairwise distances of between 0.8-1.5%, which is lower than the 2% threshold considered for taxa to be conspecific, and *Z. a. abyssinicus* is polyphyletic. Although species delimitation analyses identified the grouping of *abyssinicus* samples from Eritrea and Sudan as distinct, several samples from Ethiopia group conversely grouped with those of *arabs*; further investigation is thus needed to fully determine the affinities of Ethiopian birds. The samples of *omoensis* from southern Ethiopia are reciprocally monophyletic, were identified as a distinct grouping based on species delimitation analyses (bGYMC 0.1-0.9) and therefore the taxon could be a candidate for elevation to species status. Notably, all white-bellied taxa cluster closely together in morphospace based on morphometric trait data (Day et al. unpublished).

- 10) *Zosterops* sp. nov.

A major finding from our analyses is the exceptionally deep genetic divergence between insular (Island of Socotra, Yemen) and mainland populations (northern Somalia) of what has been known as *Zosterops abyssinicus socotranus* Neumann, 1908, since the review of Moreau (1957). These taxa are far apart on the phylogenetic tree, being embedded within clades A₂ and C respectively (Fig. 1), and each is a distinct and highly supported entity, despite their plumages being exceptionally similar (see Plate 1A). As the type locality of *socotranus* is Socotra and there is no available name for the northern Somalia population, we record it here as a sp. nov. that we are in the process of describing and naming.

- 11) *Zosterops socotranus* Neumann, 1908

The taxon *socotranus* (*sensu stricto*) from the island of Socotra forms a well supported clade that is supported as a distinct species based on species delimitation analysis across all thresholds (bGYMC 0.1-0.9). This island population of *Zosterops abyssinicus socotranus* is sister to the other white-bellied taxa comprising *Z. abyssinicus* (species 9), within clade A₂, and merits species status, although Cytb pairwise distances are <2% (Appendix C, Table S1).

Montane white-eyes “*Zosterops poliogastrus*” sensu lato (see Plate 1B)

Montane white-eyes previously referred to as “*Z. poliogastrus*” are comparatively large birds with rich green backs, yellow or grey bellies and some with very broad white eye rings and bright golden feathers (Plate 1B). They are forest endemics of the mountains of Ethiopia through the Kenyan Highlands and several isolated mountains in southern Kenya and northern Tanzania. These non-intergrading montane populations were traditionally treated as eight subspecies of a wider species complex (Dickinson, 2003). Cox et al. (2014) demonstrated the polyphyly of five of these taxa and recommended their elevation from subspecies to species rank. All former subspecies of *Z. poliogastrus* are currently recognised as species (van Balen, 2019). Based on the results from our molecular phylogeny and species delimitation analyses, unpublished morphometric data, genetic findings from Cox et al. (2014), and song data (Husemann et al., 2014), we consider that the following five taxa each rank as monotypic species, spread in widely separated parts of our phylogenetic tree (Fig. 2), whereas the remaining three taxa pose greater uncertainty that will require further research to unravel.

12) *Zosterops mbuluensis* Sclater and Moreau, 1935

A highly supported monophyletic grouping that is sister to *Z. flavilateralis* in clade B₆ (Fig. 2).

13) *Zosterops eurycricotus* Fischer and Reichenow, 1884

A highly supported monophyletic grouping that is sister to *Z. melanocephalus* in clade B₄ (Fig. 2)

14) *Zosterops kikuyuensis* Sharpe, 1891

A highly supported monophyletic grouping embedded in clade B₅ (Fig. 2), but clearly distinct from *Z. poliogastrus* (species 17, below).

15) *Zosterops silvanus* Peters and Loveridge, 1935

A highly supported monophyletic grouping embedded in clade C₂ (Fig. 2).

16) *Zosterops winifredae* Sclater, 1934

Another highly supported monophyletic grouping embedded in clade C₂, but well separated from *silvanus* (Fig. 2).

17) *Zosterops poliogastrus* Heuglin, 1861

a) *Z. p. poliogastrus* Heuglin, 1861

b) *Z. p. kulalensis* Neumann, 1902

c) *Z. p. kaffensis* Williams, 1948

Despite the widespread *kaffensis* from south-west Ethiopia and the restricted *kulalensis* from Mt Kula, northern Kenya, each being resolved as monophyletic in our phylogenetic analysis, and found to be divergent regarding morphometric data (Day et al. unpublished), species delimitation analyses suggested they form a single lineage along with samples referred to as *Z. aff. poliogastrus* (also from Ethiopia), being only considered separate species at the highest thresholds of 0.8–0.9 using bGYMC. This is supported by the Cyt b pairwise distance which at only 0.4% (see Appendix C, Table S1) is considerably lower than the 2% threshold considered for taxa to be conspecific. In our tree *Z. p. poliogastrus* (Ethiopia and Eritrea) and samples referred to as *Z. aff. poliogastrus* are also non-

monophyletic. However, these may all comprise a complex of very young species that further study using more rapidly evolving markers, such as SNPs, as well as additional vocalization and morphometric analysis, would provide key evidence as to their status.

Southern African white-eyes

The taxonomic affinities of southern African *Zosterops* have long been a source of disagreement and have led to numerous taxonomic revisions (e.g. Clancey, 1967; Gill, 1936; Moreau, 1957; Oatley et al., 2011; Oatley et al., 2012). We showed that the southern African white-eye species *Z. pallidus* Swainson, 1838 and *Z. virens* Sundevall, 1850 are distinct, supporting (Oatley et al., 2012), who also confirmed hybridisation in areas where they occur in sympatry. However, contrary to that study, we found they are not sister taxa, although they are closely related (both group within clade C₂, see Fig. 1), which confirms the finding from Cox et al. (2014). The detailed molecular study of Oatley et al. (2012), along with vocalisation data (Oatley et al., 2011), did not support the separation of the subspecies *Z. v. virens* and *Z. v. capensis*, despite distinct plumages, but both Dickinson and Christidis (2014) and del Hoyo and Collar (2016) retain them. Our data indicated that although they are reciprocally monophyletic, bGYMC only supports their separation at a threshold of >0.8 (Cytb b pairwise distances are much less than 2%, Appendix C, Table S1).

18) *Zosterops pallidus* Swainson, 1838

19) *Zosterops virens* Sundevall, 1850

a) *Z. v. virens* Sundevall, 1850

b) *Z. v. capensis* Sundevall, 1850

The name *virens* has priority over *capensis* (Thompson and Taylor 2014).

Gulf of Guinea white-eyes ('mainland clade' sensu Melo et al. 2011)

Zosterops melanocephalus Gray, 1862, from Mount Cameroon was formerly placed in the genus *Speirops*. This is an phenotypically aberrant *Zosterops* species, hence previous taxonomic assignment, but based on genetic studies (Cox et al., 2014; Melo et al., 2011) both found it to be embedded within *Zosterops* as a highly divergent lineage, which is further supported in the current study.

20) *Zosterops melanocephalus* Gray, 1862

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Plate A: Africa-Arabia mainland *Zosterops*, including the Islands of Pemba and Socotra.

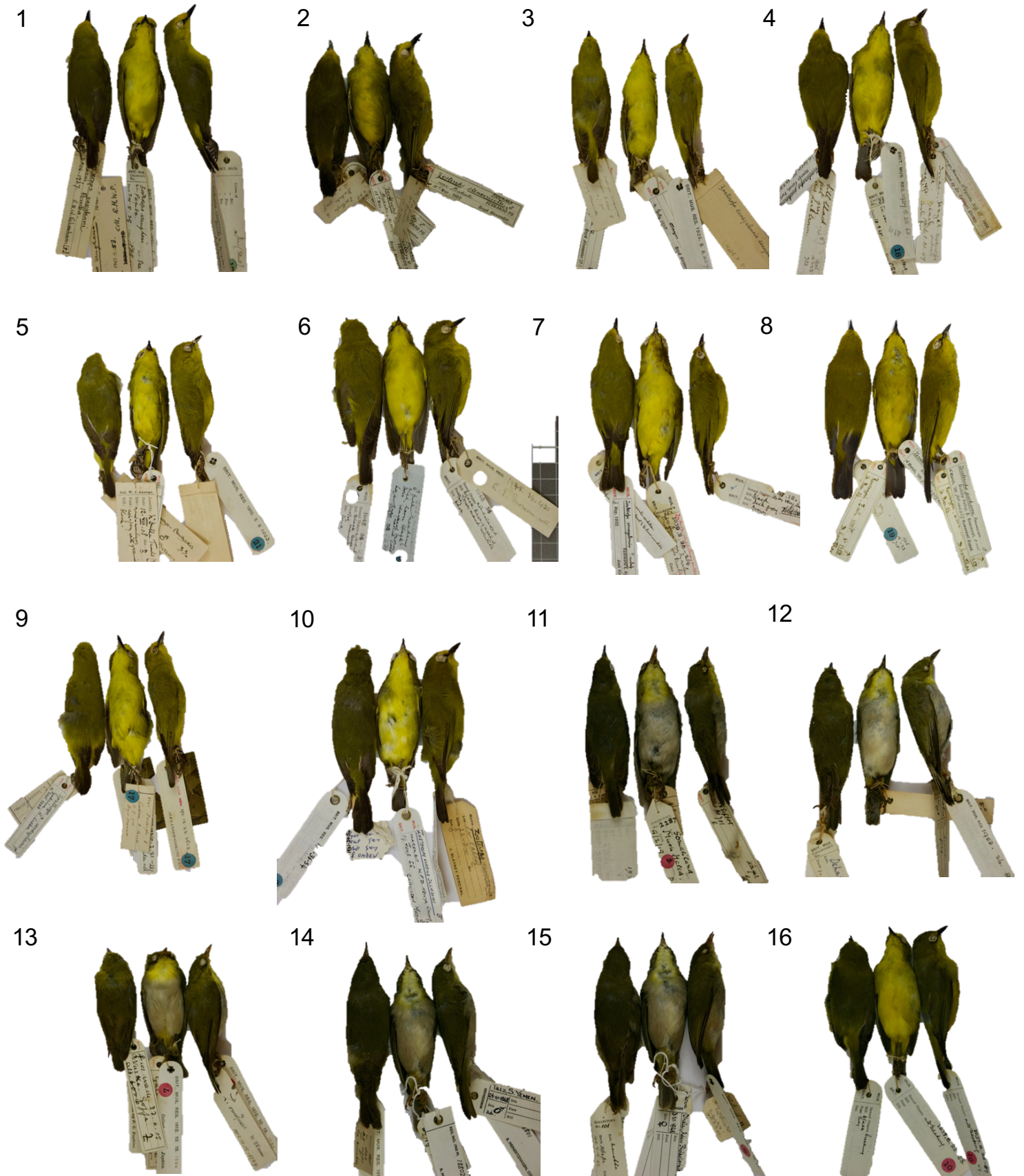
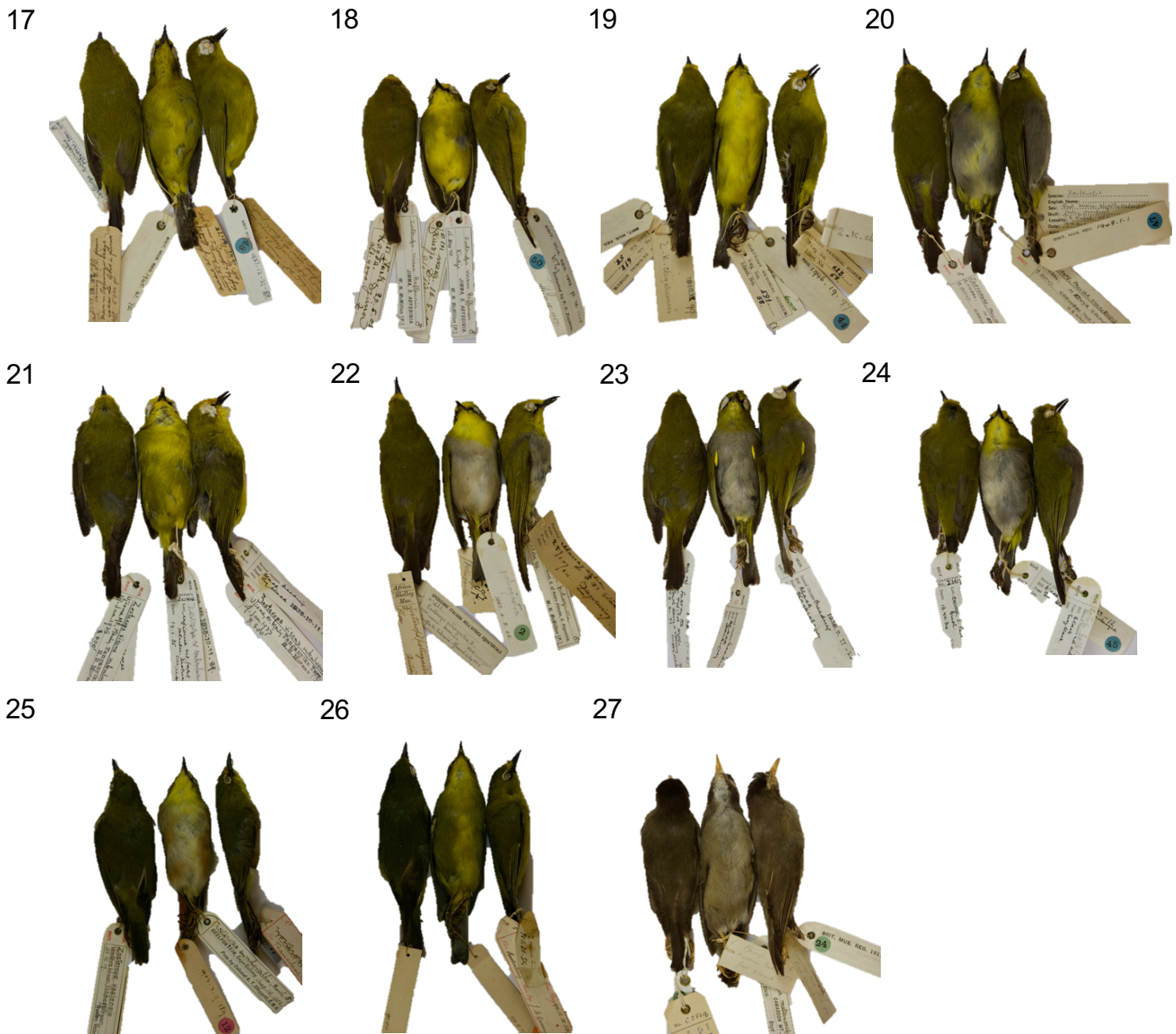
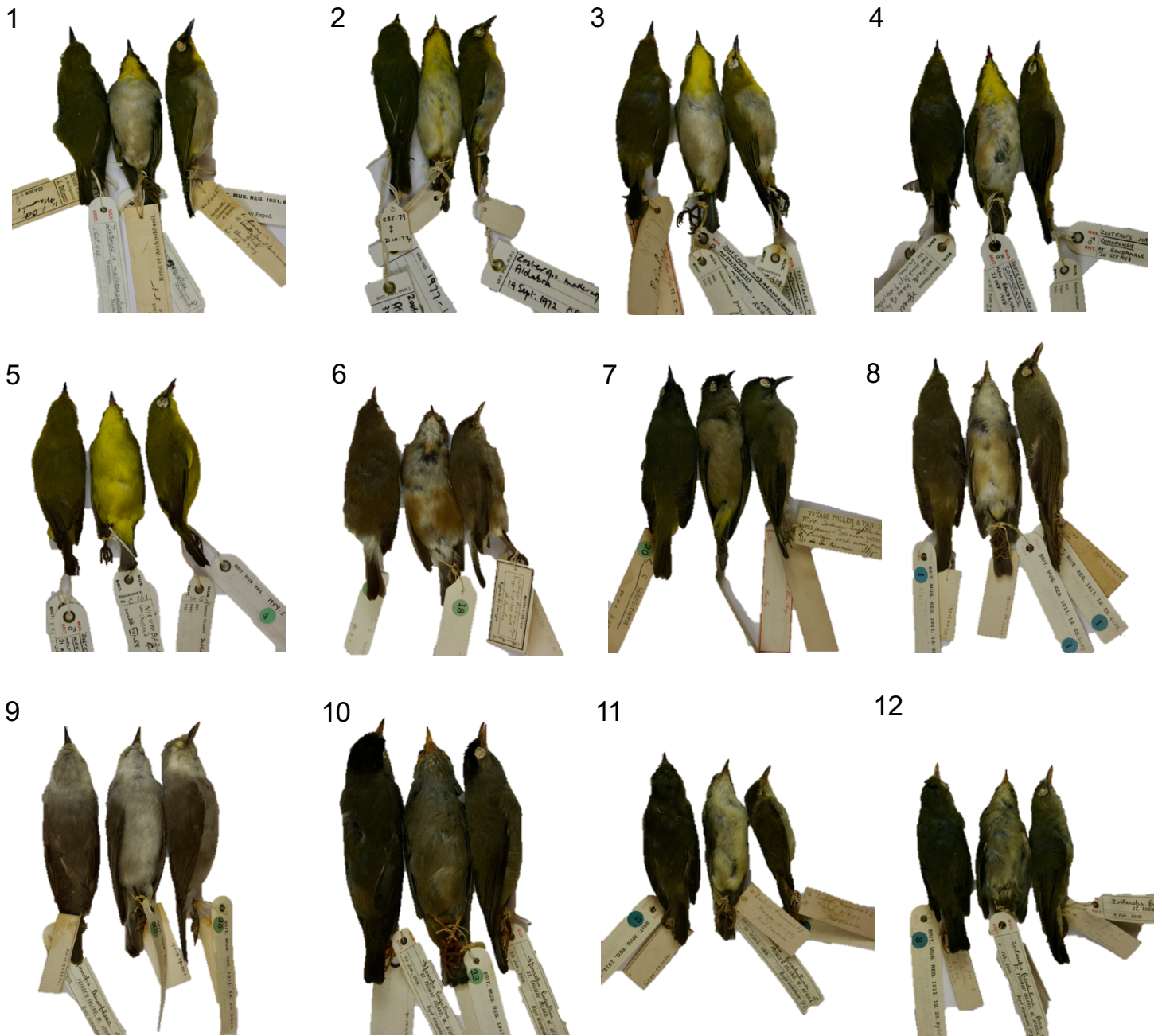


Plate B: Africa-Arabia mainland *Zosterops*, including the Islands of Pemba and Socotra.



Photographs of dorsal, ventral and lateral views of BMNH specimens: 1. *Z. vaughani*; 2. *Z. stenocricotus*; 3. *Z. senegalensis*; 4. *Z. stuhlmanni*; 5. *Z. quanzae*; 6. *Z. s. stierlingi*; 7. *Z. anderssoni*; 8. *Z. s. reichenowi*; 9. *Z. s. toroensis*; 10. *Z. jacksoni*; 11. *Z. socotranus*; 12. *Z. sp. nov.*; 13. *Z. a. omoensis*; 14. *Z. a. abyssinicus*; 15. *Z. a. arabs*; 16. *Z. flavilateralis*; 17. *Z. eurycricotus*; *Z. p. kaffensis*; 19. *Z. kikuyuensis*; 20. *Z. p. kulaensis*; 21. *Z. mbuluensis*; 22. *Z. poliogastrus*; 23. *Z. silvanus*; 24. *Z. winifredae*; 25. *Z. pallidus*; 26. *Z. virens*; 27. *Z. melanocephalus*.

Plate C: Western Indian Ocean and Gulf of Guinea Island *Zosterops* (not all species included in Figure 2 are shown).



Photographs of dorsal, ventral and lateral views of BMNH specimens: 1. *Z. maderaspatanus maderaspatanus*; 2. *Z. maderaspatanus aldabrensis*; 3. *Z. maderaspatanus anjuanensis*; 4. *Z. maderaspatanus comorensis*; 5. *Z. kirki*; 6. *Z. borbonicus*; 7. *Z. olivaceus*; 8. *Z. griseovirescens*; 9. *Z. leucophaeus*; 10. *Z. lugubris*; 11. *Z. ficedulinus*; 12. *Z. feae*.

5 cm