A taxonomic review of the genus Zosterops in East Africa, with a revised list of species occurring in Kenya, Uganda and Tanzania

David J. Pearson and Donald A. Turner

Summary
Species limits among East African white-eyes Zosterops are reviewed. Recent molecular studies have revealed that arrangements such as those of Britton (1980), with just three species, and Fry (2000), with four species, are unsatisfactory. Most of the isolated highland forms which have been grouped under Z. poliogaster evolved independently and warrant treatment as full endemic species. Forms hitherto treated as subspecies of Z. senegalensis have been recovered within two divergent African clades. Within a northern clade Z. stuhlmanni appears best split pro tempore from Z. senegalensis (sensu stricto). Within a southern clade, stierlingi and anderssoni may be treated as subspecies of Z. anderssoni. The pale yellow-bellied forms, included until now within Z. abyssinus, were found in a different lineage from northeast African grey-bellied forms, and must be treated under Z. flavilateralis. With the inclusion of Z. vaughani of Pemba Island this results in a total of eleven East African species. These are listed with details of all constituent subspecies, distributions and synonyms. Occurrence within Kenya, Tanzania and Uganda is summarized in an appendix.

Introduction
The abundance of African white-eye forms, most of them morphologically similar, has long presented problems for taxonomists, in particular the placement of their species limits. Moreau (1957) admitted just three Zosterops species for the African mainland: Z. senegalensis, with yellow-bellied forms widespread in woodland; a duller Z. abyssinus with grey- or yellow-bellied birds in drier northeastern lowlands; and a rather dull southern Z. pallidus with belly grey, green or buff-and-white. The various isolated forms in the highlands of Ethiopia, eastern Kenya and northeast Tanzania with a rich green back, either a grey or bright yellow belly, and typically a broad eye-ring, he included within Z. senegalensis, as also did White (1963). But Hall & Moreau (1970) treated these together as a separate montane species Z. poliogaster, and this arrangement of four mainland Zosterops, each with a number of subspecies, was followed by Fry (2000), Dickinson (2003) and von Balen (2008). Following Oatley et al. (2012), Dickinson & Christidis (2014) separated a fifth species, Z. virens from Z. pallidus in South Africa.

Recent molecular genetic studies have brought into question the utility of traditional morphological characters in assessing African white-eye relationships. For example, three Gulf of Guinea species placed in the distinctive-looking genus Speirops have been found to be nested within Zosterops, each aberrant species more closely related to typical Zosterops than they are to each other (Melo et al. 2011). And the wide-ranging Z. senegalensis is clearly polyphyletic, for DNA analyses have recovered
subspecies *stenocricotus* and *stierlingi* in different major African white-eye lineages (Warren *et al.* 2006, Melo *et al.*, op. cit.).

In East Africa, Britton (1980) admitted three mainland species: *Z. senegalensis*, with three rich green and yellow-plumaged subspecies in Uganda and western Kenya and two more in Tanzania; the paler *Z. abyssinicus*, with two yellow-bellied subspecies in drier northern and eastern Kenya, extending to northeastern Tanzania; and *Z. poliogastrus*, comprising six isolated montane populations (each considered a subspecies), some yellow-bellied, others grey-bellied. The Pemba Island White-eye, treated as *Z. vaughani* by White (1963), was lumped with *Z. senegalensis* by Hall & Moreau (1970) and by Britton (1980), but returned to species status by Zimmerman *et al.* (1996) and later authors. Based on vocal differences and ecology, some of the highland isolates have recently been considered worthy of full species status, e.g. by Collar *et al.* (1994) and Borghesio & Laiolo (2004). The latest IOC World List (Gill & Donkster 2016) splits *Z. kikuyuensis* and *Z. sylvanus* (but not other forms) from *Z. poliogaster*.

The genetic phylogeny of East African white-eyes

DNA investigations of the East African *Zosterops* taxa have recently been published by Habel *et al.* (2013, 2015), Cox *et al.* (2014) and Meimberg *et al.* (2016). Studies using two mtDNA genes revealed extensive non-monophyly in all three mainland species (Cox 2013, Cox *et al.* 2014). Some endemic montane populations were shown to be more closely related to forms with other habitat and elevation preferences, and dispersal abilities, than to restricted populations in neighbouring forest fragments. Most would thus appear to have arisen independently as a result of niche divergence rather than as relics of an ancestral montane population. Most of the ‘sky island’ forms of Kenya and northern Tanzania were densely sampled, and strong support was found for the monophyly of each one. The forms *mbuluensis, silvanus, eurycricotus, winifredae* and *kikuyuensis*, all hitherto accommodated within *Z. poliogastrus*, formed independent well-supported clades, polyphyletic with respect to each other and to Ethiopian *poliogastrus*, and so should all now be treated as full endemic species. Northern Kenyan *kulalensis* was recovered close to Ethiopian *poliogastrus*, in a clade sister to *kikuyuensis*, and should be retained *pro tempore* as a subspecies of a restricted *Z. poliogastrus*. Meimberg *et al.* (2016) used DNA data from the entire mitogenome but from a restricted number of Kenyan taxa. Their findings were in agreement with those of Cox *et al.*, except that *sylvanus* emerged as basal to other montane populations. They confirmed that *kulalensis* is closely related to *poliogastrus*. But relationships between *sylvanus, kikuyuensis, kulalensis, poliogastrus* and Ethiopian *kaffensis* still require further research.

The various forms hitherto treated as subspecies of *Z. senegalensis* were recovered by Cox *et al.* (op. cit.) and Cox (2013) within two different major African clades. Within a ‘northern’ clade *senegalensis* and *jacksoni* may still be treated together under a restricted *Z. senegalensis*, but the forms *stierlingi* and *anderssoni* were recovered within a major ‘southern’ clade, as sister to *Z. virens* of South Africa (see also Oatley *et al.* 2012), and may be treated as subspecies of *Z. anderssoni*. Limited evidence on the east-central African forms (*stuhlmanni, toroensis* and *scotti*) indicates that these comprise a group within the northern clade, but polyphyletic with respect to *senegalensis*. We would therefore place them *pro tempore* within a separate species, *Z. stuhlmanni*. Evidence for placement of the South Sudan form *gerhardi* was conflicting, and requires further research. A specimen from the Imatong Mountains was recovered close to *poliogastrus*, but two more were recovered with *jacksoni*. Although this highland
subspecies is quite distinct from the smaller, paler nominate *senegalensis* of surrounding lowlands (G. Nikolaus, pers. comm.) we prefer to retain it as a subspecies of the northern *senegalensis* clade pending the latter’s further resolution.

Within *Z. abyssinicicus* (*sensu latu*), the similar yellow-bellied subspecies *flavilateralis* and *jubaeensis* were recovered by Cox (2013) in a different major clade from northeast African grey-bellied subspecies (including *omoensis*), and must therefore be treated under a separate species *Z. flavilateralis*. In genetic studies using nuclear microsatellite DNA (Habel et al. 2013) the Pemba Island form *vaughani* was shown to cluster quite separately from *Z. senegalensis*. With its addition as *Z. vaughani* the number of species occurring in Kenya, Uganda and Tanzania is now expanded to eleven. Details of these follow, and include some suggested new English names. The known distributions of highland and lowland taxa are shown in Figs. 1 and 2.

**Revised list of East African *Zosterops* species**

Order is based largely on the phylogeny of Cox *et al.* (2014). Also see Appendix. 1.

*Key to abbreviations*

RB: Breeding Resident. R(B): Resident, but breeding not confirmed
AMNH: American Museum of Natural History; GR: Game Reserve; NP: National Park; MCZ: Museum of Comparative Zoology, Harvard University, USA; NHM: Natural History Museum, Tring, UK; NMNH: National Museum of Natural History, Smithsonian Institute, USA; ZMB: Zoologisches Museum Berlin.

[Zosterops abyssinicicus] Guérin-Méneville 1843  **Abyssinian White-eye**

*Nomenclature*: Referred to as the White-breasted White-eye in Mackworth-Praed & Grant (1955). Attributed to Kenya and Tanzania by Hall & Moreau (1970) who at the time treated it as conspecific with *flavilateralis*, a course followed by several subsequent authors.

*Zosterops abyssinicicus omoensis* Neumann 1904. Type locality Senti-Tal, a valley between Uba and Gofa, southern Ethiopia.

K Although no records to date, it can be expected to occur in Ethiopian border areas near the southern end of Lake Stephanie.]

**Zosterops mbuluensis** Sclater & Moreau  **Mbulu White-eye**

See Taxonomic comments under the Taita White-eye *Z. silvanus*. Note that the specimens considered in the analyses of Cox *et al.* (2014) were all from the Chyulu Hills.

Monotypic species. **K** **T** **RB**. Northern Tanzania highlands from Mt Hanang and the Mbulu Highlands north to Oldeani, the Crater Highlands, Ketumbeine, the North Pares, Longido, Namanga Hill and the Chyulu Hills.


Zosterops flavilateralis Reichenow  

**Pale Scrub White-eye**

**Taxonomic comment:** formerly treated as a subspecies of *Z. abyssinicus*.

*Zosterops flavilateralis flavilateralis.* K T RB. Occurs over much of interior eastern and southern Kenya, and in lowland areas of northern, northeastern and central Tanzania, including much of Masailand, also from the Nairobi suburbs north to Samburu and Laikipia districts, and the central and northern Rift Valley. Birds described as *fricki* from Murang’a District and the Upper Tana north to the Ndotos are smaller and paler, but can hardly be described as intergrades with *jubaensis* (Friedmann 1937). Early specimens from Lotonok, South Turkana, were assigned here, and remain the only records west of the Rift Valley. (Includes *massaicus* and *fricki*.)


[Zosterops massaica* van Someren 1922. *Novitates Zoologicae* 29: 192. Type locality Sagala (south of Voi), Taita District, southeastern Kenya, c. 3°30’ S, 38°35’ E. Holotype in AMNH, collected by/for van Someren, 8 August 1918.]


K R(B). Mt Kulal and the Horr Valley, and birds in northern and northeastern border areas at Moyale, Mandera and El Wak also belong here. Some specimens from Kenya coastal lowlands south to Lamu, Manda, Witu and Ngomeni, and inland along the Lower Tana River to Baomo are reported to be *fricki x jubaensis* intergrades. Records from Wajir and Mombasa are not racially assigned.

*Zosterops silvanus* Peters & Loveridge  

**Taita White-eye**

**Taxonomic comment:** Cox (2013) and Cox *et al.* (2014) found strong support for *silvanus* as an independent evolutionary unit, quite separate from *mbuluensis* and *winifredae*. No hybrids are known between these forms.


*Zosterops winifredae* Sclater & Moreau  

**South Pare White-eye**

See Taxonomic comments under the Taita White-eye *Z. silvanus*.

Monotypic species. T RB. Confined to the South Pare Mts, northeastern Tanzania.

Zosterops anderssoni Shelley  Southern Yellow White-eye

**Taxonomic comment:** formerly treated as a subspecies of Z. senegalensis. The lowland (miombo) anderssoni is typically separate from the largely montane forest stierlingi, but Irwin (1981) referred to increasing intergradation between the two in areas of contact in Zimbabwe. There are also marked morphological differences: one pale yellowish-green above and bright yellow below with a narrow eye-ring (anderssoni), the other darker green above with a broader eye-ring (stierlingi). Here we treat stierlingi as a subspecies of Z. anderssoni. Meanwhile, molecular evidence in Oatley et al. (2012), Habel et al. (2013) and Cox et al. (2014) suggests that there may be a case for placing both anderssoni and stierlingi within the southern African Zosterops virens group. Further studies of both forms are warranted.


**Zosterops anderssoni anderssoni** T RB. Southern and southwestern savannas and woodlands. Birds in miombo in the Mpanda–Katavi–Rukwa region appear to belong here, as do others in Ruaha NP, the Selous GR, Songea District, the Rondo Plateau and some southeastern coastal forests, despite reported intergrades with stierlingi in several areas. (Includes niassae.)

[Zosterops niassae Reichenow 1904. Journal für Ornithologie 52: 133. Type locality Songea, Ruvuma Region, southern Tanzania, 10°41′S, 35°39′E. Type material in ZMB, collected by Dr N. Stierling, 28 July 1900.]

**Zosterops anderssoni stierlingi** T RB. Southern Tanzanian highlands from Mt Rungwe, the Poroto and Livingstone Mts, Matengo Highlands and Songea north to the Iringa Highlands and the Eastern Arc Mountains including the Udzungwas, Rubehos, Ulugurus, Ukagurus, Ngurus and the Usambaras. [Birds at Mahale Mountains NP (not satisfactorily assigned) require evaluation.]

Zosterops stierlingi Reichenow 1899. Journal für Ornithologie 47: 418. Type locality Iringa, Uhehe country, southern Tanzania, 7°47′S, 35°42′E. Type material in ZMB, collected by Dr N. Stierling, 1 May 1897. (Includes sarmenticius and usambarae.)


[Zosterops usambarae Reichenow 1909. Ornithologische Monatsberichte 17: 42. Type locality Mlalo, near Wilhelmstal, West Usambaras, northeastern Tanzania, 4°34′S, 38°19′E. Type material in ZMB, collected by Pastor K. Roehl.]

Zosterops vaughani Bannerman  Pemba White-eye

**Taxonomic comment:** Formerly treated by many authors as a subspecies of Z. senegalensis despite differing vocalizations, but proves to be genetically distinct (Habel et al. 2013). A molecular comparison is needed with stierlingi and anderssoni. Monotypic species. T RB. Common throughout Pemba Island including off-shore islets.

**Zosterops eurycricotus** Fischer & Reichenow  
**Tanzania Broad-ringed White-eye**


**Zosterops eurycricotus** Fischer & Reichenow 1884. *Journal für Ornithologie* 32: 55. Type locality base of Mt Meru (= Arusha NP), northern Tanzania, c. 3°14' S, 36°45' E. Holotype in Hamburg Museum, collected by G. Fischer, 17 July 1883. (Includes *perspicillatus* and *meruensis*.)

[Zosterops perspicillata Shelley 1889. *Proceedings of the Zoological Society* p. 366. Type locality 1520 m on Mt Kilimanjaro (east side), northern Tanzania, c. 3°04' S, 37°35' E. Syntypes (2) in NHM, collected by H.C.V. Hunter, 11 August 1888.


**Zosterops stuhlmanni** Reichenow  
**Green White-eye**

**Taxonomic comment:** Cox (2013) found that *stuhlmanni*, *toroensis* and *reichenowi* were recovered as a distinct evolutionary lineage, which we treat as *Z. stuhlmanni*. Included are birds which have been known as *Z. virens stuhlmanni* or *Z. senegalensis stuhlmanni*. Placement of the Albertine Rift montane form *scotti* remains tentative.

**Zosterops stuhlmanni stuhlmanni** **T U RB.** Ngara, Biharamulo, Mwanza and Bukoba Districts of northwestern Tanzania north to western and southern Uganda below 1700 m, including most Lake Victoria off-shore islands. **K.** Intergrades with *Z. senegalensis jacksoni* reported from Nyanza and Kakamega districts.

**Zosterops stuhlmanni** Reichenow 1892. *Journal für Ornithologie* 40: 54. Type localities Bukoba (1°19' S, 31°49' E) and Sesse Islands (0°20' S, 32°20' E), Lake Victoria. Syntypes ZMB, collected by Emin (Bukoba) November 1890, and F. Stuhlmann (Sesse Islands), December 1890.

**Zosterops stuhlmanni toroensis** Reichenow 1904. *Journal für Ornithologie* 52: 133. Type locality Kitamba, Semliki, DR Congo.

**U R(B).** Lowland areas of western and southwestern Uganda, notably the Bwamba lowlands and Semliki NP.

**Zosterops stuhlmanni scotti** **U RB.** 1850–3000 m in the Rwenzoris, also in the Bwindi-Impenetrable NP and above 3000 m in the Virunga Volcanos.

**Zosterops scotti** Neumann 1899. *Ornitologische Monatsberichte* 7: 24. Type locality 2440 m Yerua (= Yeriya Forest), east Rwenzori Mts, western Uganda, 0°31’ N, 30°06’ E. Holotype in NHM, collected by G.F. Scott-Elliott (mid-1890s).

**Zosterops kikuyuensis** Sharpe  
**Kikuyu White-eye**

Monotypic species. **K RB.** Central Kenya highlands from Meru and Embu Districts, Mt Kenya, and the Aberdares south to Nairobi.

**Zosterops kikuyuensis** Sharpe 1891. *Ibis* (6) 3: 444. Type locality Kikuyu forest, central Kenya, c. 1°00’ S, 36°40’ E. Holotype in NHM, collected by Sir F. Jackson, 15 August 1889. (Includes *somereni*.)

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D.J. Pearson and D.A. Turner
Zosterops virens somereni Hartert 1928. Novitates Zoologicae 34: 207. Type locality Mt Kenya, above Chuka, Embu District, 0°20′ S, 37°39′ E. Holotype AMNH, collected by Noel van Someren, 15 January 1921.

Zosterops poliogastrus Heuglin  Heuglin’s Montane White-eye

Taxonomic comment: Cox (2013) found that most of the former Z. poliogastrus subspecies formed independent clades polyphyletic with respect to each other. But kulalensis proved to be associated with Ethiopian montane forms, and is retained here within Z. poliogastrus. It was genetically close to kikuyuensis but more distant from the southern forms mbuluensis, sylvanus and winifredae.

Zosterops poliogastra Heuglin 1861. Type locality northern Ethiopia. Species name change from poliogastra to poliogastrus follows David & Gosselin (2002).

Zosterops poliogastrus kulalensis. K RB. Confinned to Mt Kulal, northern Kenya, where it seasonally favours areas of evergreen bush as well as forest.


Zosterops senegalensis Bonaparte  Northern Yellow White-eye

Taxonomic comment: Cox (2013) found that with the exception of jacksoni (Kenya highlands), all former East African senegalensis subspecies were recovered in clades independent from the nominate form.

Zosterops senegalensis Bonaparte 1850. Type locality Senegal.

Zosterops senegalensis senegalensis U RB. Northern Uganda south to lakes Albert and Kyoga. Savanna birds at Kidepo NP and elsewhere in Karamoja District may also belong here. (Includes superciliosus.)

[Zosterops superciliosa Reichenow 1892. Journal für Ornithologie 40: 193. [See also Chapin 1954: 180.] Type locality “Wadelai” but specimens came from Kiri (South Sudan) and Fadjulle (= Pajule, Acholi country, northern Uganda), 2°58′ N, 32°57′ E. Syntype from Pajule in AMNH, collected by Emin Pasha, 1881.]

Zosterops senegalensis jacksoni K RB. 1525–3050 m in the northern and western Kenya highlands from the Loima Hills, Mt Elgon, Cheranganis, southern Kerio Valley, Tugen Hills, Ndotos, Mathews Range and Mt Marsabit south to Laikipia, Mt Garguess and the lower slopes of Mt Kenya. In the west it occurs in Kakamega and Nandi districts, also the Gwissi Hills, and from Trans-Mara, Lolgorien and Mara GR east to the Loitas and the Ngurumans, the Mau, Gilgil, Naivasha and some western Nairobi suburbs. Meanwhile, birds in some western border areas appear to be intergrades with stuhlmanni. T RB. Known only from the Loliondo area of the northern Serengeti. Birds of the Mara Region and on Ukwerere Island (not racially assigned here) may be closer to Z. stuhlmanni. U RB. Birds in the south Elgon foothills around Mbale and Tororo appear to belong here, as do birds that reach 3400 m on the Mt Elgon moorlands. [A specimen collected from mist-forest at 2600 m on Mt Moroto (May 1963), and treated at the time as Z. senegalensis flavilateralis requires re-evaluation.]

Zosterops jacksoni Neumann 1899. Ornithologische Monatsberichte 7: 23. Type localities: the Mau, Guasso Massai, Nandi country and Mt Elgon. Syntypes ZMB, collected by
Neumann (November 1894) and Jackson (February 1890). (Includes garguensis, bayeri, elgonensis and yalensis.)

[Zosterops virens garguensis Mearns 1913. Smithsonian Miscellaneous Collections 61 (20): 7. Type locality 2165 m Mt Gargues (Uraguess), northern Kenya, 0°56’N, 37°24’E. Holotype in NMNH, collected by Edmund Heller, 25 August 1911.]

[Zosterops bayeri Lönnberg 1917. Arkiv för zoologi 11(5): 3. Type locality Londiani Forest, central Kenya, c. 0°10’S, 35°36’E. Holotype in RMCA, Tervuren, collected by Dr Leo Bayer, 29 March 1914.]

[Zosterops elgonensis van Someren 1922. Novitates Zoologicae 29: 191. Type locality Bukedi (= Bugwere), near Mbale, western side of Mt Elgon, eastern Uganda, c. 1°00’N, 34°00’E. Holotype in AMNH, collected by/for van Someren, 13 January 1916.]

[Zosterops yalensis van Someren 1922. Novitates Zoologicae 29: 191. Type locality Kaimosi, Kakamega District, western Kenya, 0°11’N, 34°47’E. Lectotype in AMNH, collected by Allen Turner (pp. Col. R Meinertzhagen) 22 January 1917.]


Discussion

In mainland East Africa, the treatment of some 16 recognized taxa within three white-eye species (Hall & Moreau 1970, Zimmerman et al. 1996, Fry 2000) has long seemed unsatisfactory. Species limits have partly been based on phenotypic characters such as the intensity of yellows and greens in the plumage and width of the eye-ring, yet grey-bellied forms have been lumped as sub-species with yellow-bellied ones. Habitat and altitude preferences have also been considered important in defining species. Thus, the grouping of the isolated eastern montane populations under a single species Z. poliogastus has assumed that all were derived from a forest ancestor which diverged into distinctive populations following retreat into isolated highland refugia during cool and arid climatic periods of the Plio-Pleistocene (Hall & Moreau op. cit., Diamond & Hamilton 2009). The continued placement of other highland taxa such as jacksoni, stierlingi and scotti with lowland Z senegalensis has therefore seemed far from logical.

Molecular genetics, which provided answers concerning the evolution of white-eyes in the western Indian Ocean (Warren et al. 2006) and the Gulf of Guinea (Melo et al. 2011), is now revealing relationships among mainland African forms, especially in East Africa. The traditional taxonomy no longer proves acceptable. Thus, most of the eastern ‘sky island’ forms have been found to represent independent species; the morphologically very similar forms inhabiting lowlands in southern Tanzania and northern Uganda have been recovered in quite separate lineages; and the paler yellow birds of the drier eastern Kenyan and northeast Tanzanian lowlands prove not to be allied to grey-bellied Ethiopian forms. In East Africa we must thus recognize at least five additional highland species, Z. sylvanus, Z. winifredae, Z. kikuyuensis, Z. eurycricotus and Z. mbuluensis, and at least one new lowland species Z. anderssoni (and preferably a second, Z. stuhlmanni), while our former Abyssinian White-eye becomes Z. flavilateralis.
Our understanding of the distribution of some white-eye taxa in East Africa has been obscured by difficulties of separation and correct identification in the field. Specimens are lacking from some areas where forms potentially come into contact or overlap. Thus the range of *anderssoni* in Tanzanian lowlands, and the extent of its contact, if any, with *stuhlmanni* and *flavilateralis*, remain to be clarified. The absence of white-eyes from wide areas of arid northern and eastern Kenya needs to be confirmed. And the limits of *senegalensis* and *toroensis* in Uganda require further definition. The restricted ranges of the highland taxa are better known, but questions remain regarding birds that occupy the Mahali and Gombe Stream National Parks in western Tanzania, and highlands near the northeast Uganda/northwest Kenya border. Good photographs from some of these lesser explored areas are likely to be essential to answer pending questions.
Figure 1. East African distribution of highland taxa: 1-mbuluensis, 2-sylvanus, 3-winfredae, 4-stierlingi, 5-eurycricotus, 6-scotti, 7-kikuyuensis, 8-kulalensis, 9-jacksoni, 10-gerardi, ?-taxon undetermined.
Figure 2. East African distribution of lowland taxa: 1–flavilateralis, 2–jubaensis, 3–anderssoni, 4–vaughani, 5–stuhlmanni, 6–toroensis, 7–senegalensis, x–reportedly flavilateralis/jubaensis intergrades, ?–undetermined.
Acknowledgements

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References


### Appendix 1. East African Zosterops taxa

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