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Author: Wells, D. R.

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Zosterops white-eyes in continental South-East Asia. 1: proposed refinements to the regional definition of Oriental White-eye *Z. palpebrosus*

by D. R. Wells

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Summary.—Grounds exist for accepting that the previously unrecognised paratypes of *Zosterops* (*palpebrosus*) *auriventer* Hume *in* Hume & Davison, 1878, from a population inhabiting the coastal lowlands of the Malacca Straits, are all still held by the Natural History Museum, Tring, and that the overall type series is a taxonomic composite. Comparative morphology and a re-reading of original collecting details combine to revise Hume's identification of his paratypes. Their population is re-named and its geographical range redefined, with suggested outcomes for species limits. The term 'continental' here includes the islands of South-East Asian shelf waters, i.e., as far the Greater Sundas and their satellites.

In a report on collections from Tenasserim (modern Thanintharyi state), south-east Myanmar (Hume & Davison 1878), A. O. Hume, leading Indian empire ornithologist of his day, announced the collection near Tavoy (modern Dawei) town (14ºN), 'of a *Zosterops*, which I believe should be referred to *palpebrosus*, as an accidental variety, but which may indicate a new species. It is the same size as [Indian Subcontinent, ?including nominate] *palpebrosus*, but is greener and more olive above, and beneath, instead of having only the lower tail-coverts yellow has the whole of the feathers of the vent and a broad band right up the middle of the abdomen on to the lower breast, of this same yellow …. Should other similar specimens be hereafter obtained, the bird will of course require to be specifically separated, and might then stand as *auriventer*.' This Hume soon claimed to have managed: 'I now find that I have five similar specimens from different parts of the Malay Peninsula' (Hume 1878), and (Hume 1879b) duly confirmed a species *Zosterops auriventer*.

Less than a decade later, Hume's vast skin collection was acquired by the British Museum (Natural History) (BMNH; now the Natural History Museum, NHMUK) (Collar & Prŷs-Jones 2012). Nothing in his writings identifies these additional specimens individually, but his collectors in the Thai-Malay Peninsula had worked just its western edge, and NHMUK still holds five expedition skins dated 1878 or earlier, all from west coast localities. NHMUK 1886.12.1.1727, labelled Malacca (town at 02º12'N), is typical of the Malacca Straits mangrove and deforested subcoastal strip population of *Z. palpebrosus* but has the regional trade specimen make-up of the time and is guessed to have been market-purchased. The rest are from 'Penang', meaning at that time just the island off the west side of the Peninsula (05ºN). Three of these, NHMUK 1886.12.1.1728–1730, match the same southern population; the fourth, NHMUK 1886.12.1.1745, unexpectedly, shows most of the characters of the north-east Peninsular / Gulf of Thailand coastal subspecies *Z. p. williamsoni* Robinson & Kloss, 1919. Whatever may have been intended by 'different parts' of the Peninsula, it is the case that Malacca and Penang are the only localities that Hume himself (Hume 1879a) published, and no other critically dated white-eyes were accessioned from his collection. Dates and the match in numbers thus make it a reasonable assumption that these are the

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specimens Hume referred to in his description, forming the balance of the *Z. auriventer* type series.

Background

BMNH curator R. B. Sharpe (Sharpe 1887a) was the first to apply Hume's combination *Zosterops auriventer*, to a white-eye collected by local museum curator L. Wray in montane forest of the Bintang (Larut) range, on the mainland of the Peninsula south-east of Penang. Hume's material in its entirety would by then have been available to Sharpe in London, and might have excited comment had Wray sent a specimen (none found or registered) rather than, as suspected, just a description. Nor could Sharpe have known that Wray's collecting ground lay outside the habitat range of Hume's paratype population. In fact, nothing from the literature implies any awareness of more than one white-eye taxon in the Thai-Malay Peninsula prior to Ogilvie-Grant (1905) distinguishing *Z. aureiventer* [*sic*] on inland forested Kala Kiri (Besar) peak (06º37'N), Yala / Pattani provincial border, from birds taken in the same month on the nearby coast of Pattani, east side of the Peninsula—identified by him as *Z. palpebrosa* [*sic*] and which in an appended note the collector H. C. Robinson aligned with mangrove-zone breeders of the Malacca Straits. A year later, Ogilvie-Grant (1906) introduced a third name, *Z. tahanensis*, for specimens from Mount Tahan, 250 km south-southeast of Kala Kiri.

Having himself been the source of most of this new material, Robinson was quick to adopt a two-species (one inland, one coastal) arrangement for the Peninsula. Evidently having realised that Kala Kiri and Tahan birds were one and the same (*cf*. Robinson & Kloss 1911), however, he (Robinson 1907, 1909, 1910) chose to revert the name *auriventer* to coastal birds, replacing Ogilvie-Grant's *palpebrosus*. In London, Sharpe (1909) did the same despite having earlier (Sharpe 1887b, 1889) described inland forest white-eyes collected by J. Whitehead on Mount Kinabalu, north-west Borneo, as '*Z. aureiventer* [*sic*] Hume ... Not to be separated from a Tenasserim type specimen'. Like Ogilvie-Grant, he should also have been aware of Hartert's prior determination of Tahan white-eyes, as '*auriventer* Hume: Tavoy, Tenasserim' (Hartert 1902).

Robinson's views continued to waver. He and C. B. Kloss (Robinson & Kloss 1919) returned coastal forms to *Z. palpebrosus*, including as subspecies their Gulf of Thailand mangrove bird *williamsoni* and western *auriventer*, although characterisation of 'the true *Z. auriventer*' as having bright, yellowish-toned upperparts and 'extremely pale' flanks (Robinson & Kloss 1918), implied they had knowledge only of southern populations, not of the holotype itself (see below). A next, more radical step (Robinson & Kloss 1924) then decided that whereas *williamsoni* remained a subspecies of *Z. palpebrosus*, Malacca Straits and inland forest white-eyes together joined Hume's Tavoy type as members of species *auriventer*, by then with three subspecies recognised: coastal Tenasserim and Malacca Straits nominate, *tahanensis* inland in the Peninsula, and *medius* Robinson & Kloss, 1923, inland in Borneo. Robinson's ultimate tweak to this arrangement (Robinson 1927) appeared after he had retired to London (and to the BMNH collections). With it, he removed *williamsoni* from *Z. palpebrosus* and imposed a single-species concept whereby all of the above taxa, independent of habitat, became subspecies of *Z. auriventer*.

Following up in the 1930s, F. N. Chasen (Chasen 1931, 1935, 1939) maintained Robinson's one-species arrangement, but took the ultimate step of returning everything to species *palpebrosus*. Over the same period, Stresemann (1931) first considered there to be two species, re-recognising *palpebrosus* on Peninsular and Gulf coasts and leaving inland populations aligned with Hume's holotype as *Z. auriventer*. This insight he (Stresemann 1939) then overturned (a) by removing *tahanensis* and Bornean *medius* from the equation and

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making them subspecies of *Z. atricapilla* (Black-capped White-eye, otherwise endemic to the montane forests of Sumatra and Borneo), and (b) by reverting the Tavoy type to species *palpebrosus*, re-deploying *auriventer* as a subspecies name to cover populations through to the Malacca Straits.

In re-assigning *tahanensis* and *medius*, it is assumed that Stresemann would have been unaware of the overlap in altitudinal ranges of *medius* and *atricapilla* on Borneo (*cf*. Mann 2008). It must be doubted also whether he or Chasen, any more than Kloss or (before his retirement to London) Robinson, had personally examined Hume's holotype (Stresemann appears to have relied on information sent from London by N. B. Kinnear). In his monograph on Asia-Pacific white-eyes (Mees 1957), however, G. F. Mees stated that he had seen it and, although he brought himself to believe that it belonged with species *palpebrosus* only after 'ample consideration and re-examination', to date (*cf*. Mayr 1967, Medway & Wells 1976, Wells 2007, van Balen 2008, Dickinson & Christidis 2014, Gill & Donsker 2016) the name *auriventer* (original spelling) has been maintained where Stresemann settled it.

The facts—a closer look

Some of the reasoning applied by Stresemann and Mees (see also Mayr 1967), and perhaps by earlier investigators, may have resulted from Tavoy's position on the lower reaches of a large river running south just inland of the Andaman Sea coast, allowing the 'near the town' of the holotype's field label to imply that it had been collected close to the coast. This alignment with habitats occupied by Oriental White-eyes in the Thai-Malay Peninsula (see Mees 1957: 73) nevertheless overlooked what Hume & Davison (1878, Appendix 1) had reported concerning the collector W. R. Davison's visit to Tavoy district in March–April 1878. In this account, they reported forest evidently continuous with that of the interior as reaching near the town; also, and more directly to the point, that a fledgling Maroon-breasted Philentoma *Philentoma velata*—a vangid strictly dependent on the interior of closed-canopy rainforest—was taken 'in the neighbourhood of Tavoy' on the same day (19 April) as the holotype. Hume's holdings at NHMUK in fact include three other bird species collected 'at', 'near' or 'in the neighbourhood of' Tavoy on that day, 11 more if a day either side is added, all of them typical of inland evergreen forest or forest edge, vs. only one or two near these dates that could have come from any other habitat. It follows that expedition collectors had visited inland forest over the period in question, shifting probability towards *auriventer* having itself come from this habitat, which is one that Hume's paratype population in the Thai-Malay Peninsula routinely avoids (Wells 2007).

Inquiry into why, even without that information, there had been such uncertainty about applying species-group names began with a fresh examination of the entire re-assembled *auriventer* type series, plus additional Malacca Straits coast material. Recorded as a male, by its relatively dull yellow chin and throat, and only slight tonal contrast between uppertail-coverts and rump / back possibly not fully adult (although it has black lores), apart from tail damage (rr1–4 lost bilaterally) the holotype is still in fair condition, as are all five claimed paratypes. Max. (flattened) chord wing and tail length measurements (Table 1) of the holotype and a Malacca Straits coast sample (n = 29), paratypes included (LKCNHM, NHMUK, RMNH, USNM; see Acknowledgements for museum acronym definitions), overlapped totally, whereas tail / wing ratios did so only narrowly: 68 vs. 59–68 (mean 64.3), with just one Malacca Straits representative at 68. Wingtip shape (*cf*. Mees 1957) also differed: shortfall of the holotype's outermost large primary (p9 descendant) behind the tip 1.2 mm, vs. 2.3–4.1 mm (mean 3.1), and wingtip p7 = 8 whereas nearly 70% of the Malacca Straits sample had p6, 7 and 8 sub-equal.

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TABLE 1
Morphometrics (in mm; range and mean) of the *Zosterops* populations discussed herein. Wing and tail lengths, and primary shortfall behind wingtip measured as max. (flattened) chord, tarsus from tarso-tarsometatarsal notch to third toe flexure point, bill from anterior edge nasal groove to tip; sexes combined (label determinations discounted). With the exception of data on Borneo coastal specimens in the WFVZ collection supplied by R. Corado, all measurements by the author.

Taxon	*n*	Wing	Tail	Tail / wing ratio (×100)	P9 < wingtip	Tarsus	Bill
auriventer (Tenasserim)	2	52, 52	35.6, 36.7	68, 71	1.2, 1.2	14.3, 14.7	6.8, 7.1
erwini (South Natuna Islands)	14	50–56 (52.7)	31.5–35.5 (33.5)	60–66 (63.0)	3.6 (*n* = 1)	13.8–15.8 (14.6)	6.9–8.0 (7.3)
erwini (Malacca Straits)	29	50–54 (52.2)	30.4–35.6 (33.6)	59–68 (64.3)	2.3–4.1 (3.2)	14.2–16.0 (14.9)	6.5–7.7 (7.2)
Unidentified (Borneo coast)	8	48.0–50.5 (49.5)	28.1–33.8 (32.0)	59–69 (64.8)	2.3, 5.5	12.0–14.9 (13.6)	6.2–7.0 (6.7)
buxtoni (Sumatra)	3	50–52 (51)	31.2–34.4 (32.8)	62–66 (64.0)	3.6–4.0 (3.8)	13.2–14.5 (13.8)	5.7–6.3 (6.0)

Hume had focused mainly on the development of mid-ventral yellow. A more inclusive colour comparison covering all specimens from the Malacca Straits sample that share the holotype's curatorial history, made by eye against colour standards (Smithe 1975) on a non-reflective, neutral ground in uniform-intensity 'artificial daylight', on the other hand, produced consistent differences.

Upper body, measured at mantle level: in all Malacca Straits specimens bright, yellowish green, nearest to Smithe's Citrine (no. 51), cap the same except at least the base of feathers bordering the dark loral streak and variably onto lower forehead, clear yellow; vs. in the holotype: olive-tinged mid green, between Smithe's Greenish Olive (no. 49) and Yellowish Olive-Green (no. 50), paling only slightly on cap, uniformly to bill base and above lores, with no evidence of frontal or supra-loral yellow.

Anterior flanks, representing grey of flanks to sides of breast, narrowly linked across upper breast: in all Malacca Straits birds distinctly pale, silvery tinged, between Smithe's Light Neutral Gray (no. 85) and Pale Neutral Gray (no. 86); vs. in the holotype, opaque lead grey, between Smithe colours Medium Plumbeous (no. 87) and Pratt's Payne's Gray (no. 88).

Underwing-coverts: washed pale yellow in Malacca Straits birds, but, excluding leading edge, white in the holotype.

A second Tenasserim specimen (MSNG 16990) of the same era (see Figs. 1–2 in Wells 2017), collected by L. Fea in the interior *c*.190 km north of Tavoy on 13 March 1887 and identified as *auriventer* by Salvadori (1888), is a black-lored adult, also sexed as a male, with chin to throat brighter yellow and uppertail-coverts slightly brighter vs. rump/back. Otherwise, apart from being soiled, it is a fair match for Hume's holotype in all respects, including extent of green on outer webs of the latter's surviving rectrices. Wing and tail lengths (52 mm and 36.7 mm, ratio 71) along with shortfall of p9 only 1.2 mm and wingtip p7 = 8 descendant affirm the proportional shape divergence from Malacca Straits birds. If this eliminates Hume's 'accidental variant' option, it follows that Oriental White-eyes of the Malacca Straits and neighbouring coasts (Fig. 1) cannot reasonably be identified as *auriventer* (*cf*. Fig. 2)—given also that the potentially interposed (see below) *Z. p. williamsoni*, characterised by its fuller yellow supra-loral to frontal stripe but less, individually to hardly any, mid-ventral yellow, diverges even further. As such, independent of possible species-limit issues, the Malacca Straits population needs a replacement name.

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Figure 1. *Zosterops* (*palpebrosus*) '*auriventer*' (= *erwini*), mangrove zone, Khlong Thom district, Krabi Province, peninsular Thailand, i.e., at the proven end-point of *erwini* range closest to the type locality of nominate *auriventer* (© P. D. Round / Wetlands Trust)

Figure 2. *Zosterops* '*tahanensis*', Keledang Sayong Forest Reserve, inland Perak state, Peninsular Malaysia; differs from nominate *auriventer* (which is unknown in life) only by average measurements (see Wells 2017, this issue) (© Amar-Singh HSS)

Outcomes for taxonomy

A search of synonymies in Mees (1957) found one appropriate alternative for Malacca Straits birds: *erwini* (honouring Stresemann) Chasen, 1934, from the South Natuna archipelago, South China Sea. Chasen's text failed to record where his comparative material came from, but the type series of *erwini* (holotype and 13 paratypes: LKCNHM, NHMUK)

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displays the characters understood to separate Malacca Straits birds from north-east Peninsular / Gulf of Thailand *williamsoni*. On some Natuna specimens, yellow of the mid-ventral stripe suffuses slightly further onto the breast, and those still safely measurable show a marginally broader range of wing lengths, up to 56 mm although with nearly the same sample mean, 52.4 mm vs. 52.7 mm. However, these variables (others claimed by Chasen himself not confirmed) hardly warrant introduction of another name. As such, the Oriental White-eye of coastal and non-forested subcoastal habitats of the south-west and southern Thai-Malay Peninsula, the eastern seaboard of Sumatra (where recorded up to 48 km inland in lowland plantation country of Utara province: RMNH 15957–958), and on associated islands south to Bangka (but see below for mainland Borneo), hitherto known as *Z. p. auriventer*, is re-named:

> ***Zosterops palpebrosus erwini*** Chasen, 1934: holotype NHMUK 1947.60.60, adult male (label data), collected by P. M. de Fontaine on Panjang Island (02°45′N, 108°54′E), South Natuna archipelago, South China Sea, on 19 August 1931. Described on pages 96–97 of Chasen, F. N. 1934. Nine new races of Natuna birds. *Bull. Raffles Mus*. 9: 92–97.

Uncoupling the name *auriventer* from Malacca Straits coastal-zone white-eyes forces the northern limit of the population now to be called *erwini* to retreat south by *c*.800 km, to Khlong Thom district, Krabi province, on the west side of the Thai-Malay Peninsula (based on mangrove-zone birds photographed in the hand at 07°43′N by P. D. Round). North of Malaysia, west-coast *Z. palpebrosus* specimens are very few, but one (USNM 154055) from Libong Island, near to the Khlong Thom range limit, is typical *erwini*. A second (NHMUK 1936.4.12.2544), from Ra Island close to 09°N, Mees (1957) identified as *auriventer* (= *erwini*) but Robinson & Kloss (1924) had been sufficiently confused by this same individual that in the one publication they also identified it as *Z. p. williamsoni*. A fresh identification exercise conducted 'blind' (without benefit of labels) keyed it as *williamsoni*, albeit with less than the usual extent of yellow on the forehead and above the lores, but not dissimilar to some *williamsoni* at this subspecies' southern limit in Pattani province, east coast of the Thai-Malay Peninsula. Given that white-eyes have been seen in west-coast mangrove forest north to near 10°N in Ranong province, opposite the southern tip of Tenasserim, it is possible that *williamsoni* replaces *erwini* northward on both coasts, rather than on the east side of the Peninsula alone. The 'out-of-place' individual (NHMUK 1886.12.1.1745) from Penang Island presents a potential difficulty, but its exceptionally pointed wing (p8) suggests dispersal mobility. Where, or indeed whether, the ranges of *williamsoni* and *erwini* meet north to south along the east coast of the Peninsula also remains to be ascertained as the thin scatter of sight records (Wells 2007, Round 2008) south of the southernmost confirmed *williamsoni* locality identified white-eyes only to species level.

The still-surprising upshot is that no white-eye has been reported reliably from anywhere on the long Andaman Sea coastline of Tenasserim (continuous with that of the Thai-Malay Peninsula) until virtually its northern limit near the head of the Gulf of Martaban (Mottama). There, near 17°N in December 1876, W. R. Davison (Hume & Davison 1878; NHMUK) collected several yellow-bellied *Z. p. siamensis* in mangrove forest, through which they may have been transient, as this is not regular habitat (P. D. Round *in litt*. 2011). East into the Gulf of Thailand and Cambodia, *Z. p. williamsoni* has barely emerged out of the mangrove zone (P. D. Round *in litt*. 2015, F. Goes *in litt*. 2016). As such, the combined breeding range of the *erwini* / *williamsoni* subspecies pair appears separated (a) from now-restricted *auriventer* and (b) from other conventionally accepted, mostly upland, *Z.*

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palpebrosus populations on the continent by a latitude gap that, coupled with other classes of evidence, habitat selection included, could indicate a species boundary.

The situation on Sumatra, where *erwini* and inland forest and forest edge Z. (*p.*) *buxtoni* are described as being partitioned by altitude (Mees 1957, van Marle & Voous 1988) but, at least until recently, are more likely to have been directly parapatric by habitat, also invites attention. Particularly so as a molecular survey that included nominate *palpebrosus* from Nepal and Indonesian *Z. p. unicus*, from Flores, in the Lesser Sundas (very similar morphologically to Z. *p. melanurus* of Bali and Java, into which, in far-western Java, *buxtoni* grades), recovered these two within separate, apparent species-level clades (Moyle *et al*. 2009).

Attention is also drawn to Borneo. Mangrove coasts at least on the western side of the island have long been presumed to be occupied by *auriventer* (= *erwini*) (e.g., Mees 1957, Smythies & Davison 1999, Mann 2008), but Baker (1922) and Stresemann (1931, 1939) had both claimed that a form identifiable as, or similar to, *buxtoni* occurred. Chasen (1935) was aware of this and acknowledged having examined 'old and faded' specimens from the lowlands near Kuching, south-west Sarawak, but made no final identification. What appears to have been at least Stresemann's evidence has been re-examined: specimens NHMUK 1893.6.24.18 and 1893.7.4.14 collected by A. H. Everett at 'Poeh' (Pueh) (habitats not recorded), in far south-west Sarawak in 1892. Colour tones and pattern are non-Bornean *erwini*-like, except that the underwing-coverts are white, rather than lemon-tinged, with uppertail-coverts slightly too brightly and contrastingly yellow-tinged. They also average shorter winged: 48 mm and 50 mm (vs. 50–56 mm, mean 52.3 mm in *erwini*). Two other apparent adults, YPM ORN 063503–504, dated 20 September 1951 from a lowland inland locality, Stapok road, close to Kuching town (around which Fogden 1966 reported regular evening flights of white-eyes in the direction of nearby mangroves) are similar, except that the underwing-coverts are *erwini*-like pale lemon, rather than white, and neither shows any contrasting supra-loral yellow. They too are small: wings 48 mm and 50 mm. Another four individuals, WFVZ 41715–718, collected from foraging flocks in a sea-level woodland / buffalo pasture mosaic on the Klias Peninsula, south-west Sabah state in May 1983 (Sheldon *et al*. 2001), were measured, described and photographed by R. Corado. They are

Figure 3. Unidentified coastal white-eye, Damai, Santubong Peninsula, south-west Sarawak, western Borneo (© D. N. Bakewell)

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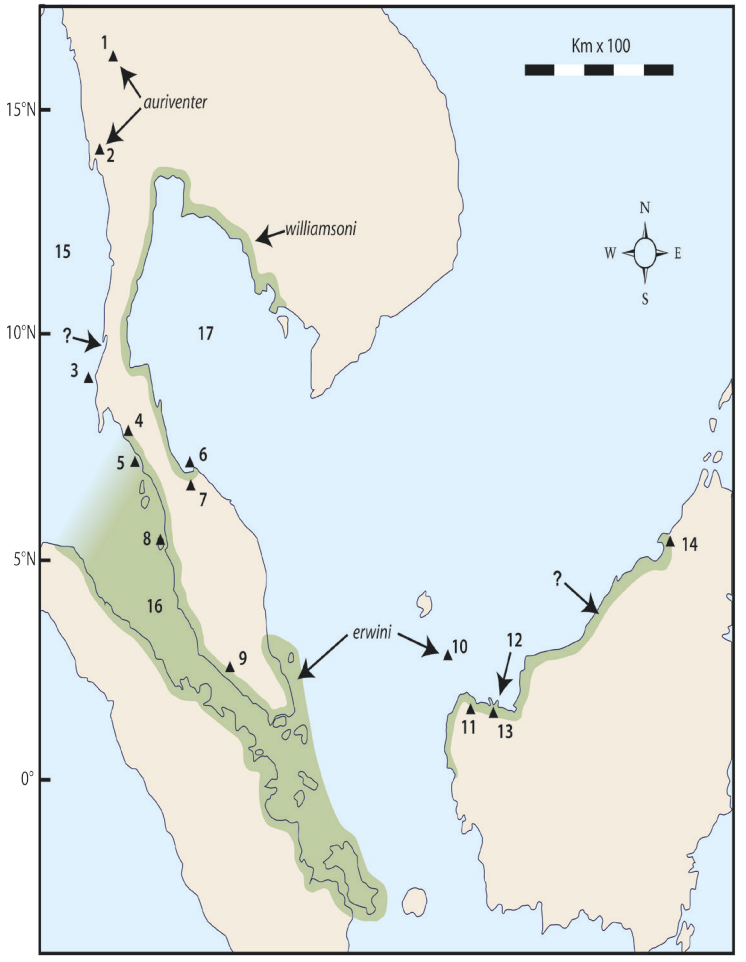

Figure 4. Currently understood range limits of western South-East Asian white-eye taxa conventionally grouped in *Zosterops palpebrosus*. Key: 1—Mount Mulayit; 2—Tavoy; 3—Ra Island; 4—Khlong Thom district; 5—Libong Island; 6—Pattani Bay; 7—Mount Kala Kiri; 8—Penang Island; 9—Malacca; 10—Panjang Island; 11—Pueh Range; 12—Santubong Peninsula; 13—Kuching; 14—Klias Peninsula; 15—Andaman Sea; 16—Malacca Straits; 17—Gulf of Thailand.

in the same size category (wing 49.0–50.5 mm) and a fair match for Pueh specimens (with white underwing-coverts), except that two of the four appear to approximate a *buxtoni* amount of supra-loral yellow, more than in *erwini*. Finally, close-range photographs (www.orientalbirdimages.org) taken by D. N. Bakewell in a coastal garden at Damai, Santubong Peninsula, also near Kuching, in December 2004, show a white-eye (Fig. 3) with bold yellow mid-ventral stripe and pale grey lateral body, but otherwise unlike any non-Bornean *erwini* specimen handled during this work. Full yellow supra-loral streak, all-yellow uppertail-coverts merging with rump and back but strongly contrasting with green of mantle and entirely black upperside of the tail, and slender bill are all characters of Indonesian *buxtoni* / *melanurus* / *unicus*.

Eight decades after Chasen dropped the issue, it is still safe only to conclude that mainland Bornean populations supposedly of *Z. palpebrosus*, despite being separated by only a short stretch of sea from the type locality of *erwini* (Fig. 4), are not true *erwini*. The current best provisional choice appears to be between (a) variable intergradation of *erwini* and a *buxtoni*-like taxon, implying (recent?) double invasion of Borneo from different sources, or (b), given that Bornean birds average shorter-winged than either hypothetical parent (Table 1), a separate, as yet un-named form in which definitive plumage characters develop apparently over more than one moult.

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Conclusion

Moyle *et al*. (2009) published genetic evidence of one or more species boundaries between the Indian Subcontinent and Lesser Sundas range extremes of conventionally identified *Z. palpebrosus*. One proposal draws on morphology and habitat-based arguments for uncoupling the name *auriventer* from supposed Oriental White-eyes inhabiting the Malacca Straits and neighbouring coasts, and the consequent retraction of the re-named population's mainland range southward. This opens a large, terrestrial range gap between inner tropical, mangrove-haunting *erwini* and *williamsoni*, and northern, mainly upland forest *siamensis*. Attention is also drawn to likely habitat-based parapatry between mainly coastal *erwini* and inland forest *buxtoni* 'subspecies' in eastern Sumatra, and to previously undescribed morphological differences between *erwini* and the neighbouring coastal white-eye population of western mainland Borneo.

These potential taxonomic boundaries all require more data from the field, particularly on vocalisations, especially song; also sampling for more phylogenetic analysis—to be undertaken before degradation of habitats that could be crucial to understanding finally eliminates such opportunities. It is proposed that sampling be broad enough to address at least: (1) the level of relatedness of coastal *erwini* and *williamsoni*, and of this pair with *siamensis*, the nearest neighbouring mainland taxon currently accepted as part of true western and northern continental *Z. palpebrosus*, against the proposition that they are not conspecific; (2) relatedness of *erwini* and *buxtoni* on Sumatra, against the proposition that they are not conspecific; and (3) status of the coastal Bornean population, relative to both *erwini* and *buxtoni*.

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Address: Serendip, Illington, Thetford, Norfolk IP24 1RP, UK, e-mail: davidrwells.wells1@gmail.com

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