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A comprehensive phylogeny and taxonomic evaluation of the waxbills (Aves: Estrildidae)

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ABSTRACT

We present a revised taxonomy of Estrildidae based on the first time-calibrated phylogeny of the family Estrildidae estimated from a data set including the majority of the species, and all genera except the monospecific *Paludipasser*, using two mitochondrial and five nuclear markers. We find that most differences in current taxonomy reflect alternative opinions among authors regarding inclusiveness of genera, which are usually not in conflict with the phylogeny. The most notable exception is the current circumscriptions of the genera *Neochmia, Nesocharis* and *Taeniopygia*, which are incompatible with the phylogeny.

Estrildidae is subdivided into six well supported subclades, which we propose be recognized as the subfamilies Amandavinae, Erythrurinae, Estrildinae, Lagonostictinae, Lonchurinae and Poephilinae.

1. Introduction

The waxbills, (Aves: Estrildidae, Bonaparte, 1850) is a speciose group of small seed-eating songbirds naturally distributed in Africa, southern Asia and Australasia (Payne, 2010). The family contains both nondescript birds and extremely colorful ones, and several species are popular as cage birds. This has also contributed to some species having been introduced to other parts of the world, such as southern Europe, Pacific islands and the West Indies. The pet trade is negatively influencing several species, including at least five species classified as Near Threatened or Vulnerable (IUCN, 2018). The Zebra Finch *Taeniopygia guttata* is one of the commonest birds in the pet trade, and was only the second bird species to have its entire genome sequenced (Warren et al., 2010), making it one of the most well studied model species, from a genomic perspective.

The waxbills have been the subject of much taxonomic attention, but a consensus has been hard to achieve. A major difficulty facing taxonomists over the years has been to accurately define the limits between Estrildidae and other groups, and the inclusivity has varied substantially. Also the subdivision of the group has been problematic. Chapin (1917) discovered that palate markings of nestlings differed between groups, and other morphological characters such as natal down, sexual dimorphism, wing shape, skeletal characters, and muscle morphology have been used to group species into taxonomic entities (e.g. Bentz, 1979; Delacour, 1943; Webster, 2007). The waxbills are also characterized by an array of behavioral traits related to nestling begging behavior, singing posture and courtship behavior, which have been used to inform taxonomic decisions (e.g. Delacour, 1943).

The systematics of the Estrildidae has been the subject of relatively few comprehensive molecular phylogenetic studies. Early attempts to elucidate relationships were made by Christidis in a series of studies that used karyotyping and electrophoresis for a limited number of taxa (Christidis 1986a, 1986b, 1987a, 1987b, 1987c). There have been a few subsequent studies based on DNA sequence data, but these have suffered from limited taxon sampling and low support for internal nodes, and have thus not succeeded in resolving biogeographic questions or relationships between larger clades. A study by Sorenson and Payne (2001) found that the Estrildidae and Viduidae constituted well supported sister clades, and that this clade in turn was sister to Ploceidae and Prunellidae. This topology was corroborated by van der Meij et al. (2005) based on the mitochondrial cytochrome *b* and the nuclear ß-fibrinogen intron 7. SS Studies focusing on Viduidae also provided insights into the phylogeny of Estrildidae (Sorenson et al., 2003, 2004), largely corroborating conclusions of previous molecular studies. Arnaiz-Villena et al. (2009) presented a biogeographic study based on 58 taxa, proposing that the split between Viduidae and Estrildidae occurred around 20 million years ago (mya), and that the most recent common ancestor (MRCA) of the Estrildidae lived around 16.5 mya. They

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speculate that this coincided with critical phases of the uplift of the Tibetan plateau, which would have triggered the radiation of estrildids in the Indian subcontinent, from which they later dispersed to Africa in the west, and towards Australia and the South Pacific in the east. Their detailed phylogeny also allowed for a number of taxonomic proposals, but a shortcoming of the study is the complete lack of support for all basal nodes making all conclusions concerning relationships between genera tentative.

A recent study based on 4000+ nuclear loci confirmed the sister relationship between Estrildidae and Viduidae, and also found Ploceidae to form the sister clade to these two groups (Oliveros et al., 2019). These authors estimated the divergence time between Estrildidae and Viduidae at c. 15.5 mya, but as only one species per family was included, it was not possible to estimate the age of the MRCA of Estrildidae. Hooper and Price (2017), based on a multilocus data set, estimated the crown age of Estrildidae to 12.5 Ma, and found Ploceidae in a sister position. The most comprehensive phylogenetic and taxonomic review available was presented by Payne (2010) based on an unpublished phylogeny. In brief, the Estrildidae is divided into three subfamilies, Estrildinae (mainly African waxbills), Lonchurinae (grassfinches, mannikins and munias), and Erythrurinae (parrotfinches), where Lonchurinae and Erythrurinae are presumed to be sisters.

Until now, no species level phylogeny based on both mitochondrial and nuclear loci has been published for the whole family, besides for subsets of species, like van der Meij et al. (2005) and Hooper and Price, 2017and comprehensive analyses of munias of the New Guinea area by Stryjewski (2015) and Stryjewski and Sorenson (2017). Here, we present the first time-calibrated phylogeny of the family Estrildidae based on a data set including all genera except the monospecific *Paludipasser* (*P. locustella,* Locust Finch), and the majority of the species, using two mitochondrial and five nuclear markers. This is to our knowledge the most comprehensive publicly available phylogeny of Estrildidae to date. We evaluate the structure of the phylogeny and based on our results propose a revised taxonomy at the generic level.

2. Material and methods

2.1. Study group

There is no consensus concerning the number of species in Estrildidae. Gill and Donsker (2019) and del Hoyo and Collar (2016) both list 141 species, but the total number of taxa recognized at species level in these two references combined are 145. Dickinson and Christidis (2014) lists 131 species, of which two were not recognized by the two former references, bringing the grand total to 147 taxa recognized as full species by at least one of these authorities. We studied 103 estrildid species and 2 geographically separated subspecies based on a multilocus data set. We assembled a single locus analysis (SLA) of nicotinamide dehydrogenase section 2 with some additional Estrildidae sequences (n = 122), including those from Stryjewski and Sorenson (2017), available from GenBank, bringing the total number of waxbill species, sensu Gill and Donsker (2019), considered in this study to 117. For a few taxa we also included representatives from different geographical areas, to assess degree of divergence, if any (Supplementary Table S1). We also used a wide variety of Passeroidea as outgroups, as well as *Menura novaehollandiae* and *Acanthisitta chloris,* based on Claramunt and Cracraft (2015), Moyle et al. (2016), Oliveros et al. (2019), Prum et al. (2015) and Selvatti et al. (2015) and own unpublished data. In total, our data set included 172 species (Supplementary Table S1). We followed the nomenclature according to Gill and Donsker (2019), except that sequences obtained from GenBank have retained their original designations in the trees.

2.2. Lab work

DNA was extracted from fresh material (muscle, blood or feathers) using the Qiagen DNA Mini Kit and following the manufacturer's protocol, but with 30 µl DTT added to the initial incubation step for the extraction from feathers. We sequenced the mitochondrial cytochrome *b* (cyt*b*) gene and nicotinamide dehydrogenase 2 (ND2), and five nuclear regions: ß-fibrinogen intron 5 (fib5), glyceraldehyde-3-phosphodehydrogenase intron 11 (G3P), myoglobin intron 2 (myo), ornithine decarboxylase (mainly) introns 6–7 (ODC) and transforming growth factor beta 2 (TGF). Amplification and sequencing followed the protocols described in Fregin et al. (2012) for cyt*b*, G3P, myo and ODC. For TGF we followed Primmer et al. (2002) and for fib5 Marini and Hackett (2002).

2.3. Phylogenetic analyses

The sequences were aligned and trimmed using MegAlign 4.03 in the DNAstar package (DNAstar Inc.). For the nuclear loci, heterozygous sites were coded as ambiguous. Substitution models were selected based on the Bayesian Information Criterion calculated in jModeltest 2.1.7 (Darriba et al. 2012). The GTR + Γ + I model was selected for cyt*b*, ND2 and TGF, GTR + Γ for fib5, HKY + Γ for ODC and K80 + Γ for G3P and myo. Trees were estimated by Bayesian inference using BEAST 1.10.4 (Suchard et al. 2018). XML files were generated in the BEAST utility program BEAUti version 1.10.4. All loci were analysed concatenated under an uncorrelated lognormal distributed relaxed clock, best-fit models and a "birth-death incomplete sampling" tree prior with a normal distribution, and partitioned by locus. Substitution and clock models were unlinked.

The analyses of extended mitochondrial SLAs were run for 150 million generations and sampled every 10,000 generations, and the concatenated data for 250 million generations, sampled every 10,000 generations. Convergence to the posterior distributions of the parameter estimates was evaluated by monitoring the effective sample size (ND2, ESS > 1000; concatenated data, ESS > 500) and trace plots in Tracer 1.7.1 (Rambaut et al., 2018). We also examined convergence and reproducibility by running each analysis at least twice, with random starting points. Trees were summarized using TreeAnnotator version 1.10.4 (included in BEAST package), choosing "Maximum clade credibility tree" and "Mean heights", and displayed in FigTree version 1.4.4 (Rambaut 2018). 10% of the trees, determined by the nature of the trace plots in Tracer, was discarded as "burn-in", and the posterior probabilities (PPs) were calculated from the remaining samples.

2.4. Dating

We calibrated the phylogeny based on the age of a single node, the split between *Menura novaehollandiae* from the rest of the ingroup. The estimate was based on a number of recent studies attempting to provide time trees for birds (Claramunt and Cracraft, 2015; Moyle et al., 2016; Hooper and Price, 2017; Oliveros et al., 2019; Prum et al., 2015; Selvatti et al., 2015). All these studies have come to different results regarding this split, ranging from 33 to 47.5 mya. As there is no consensus on the exact age of the divergence of *Menura* from the rest of the ingroup, we chose to use the node age 39 *mega annuum* (Ma) suggested by Prum et al. (2015), which was closest to the median between the above mentioned studies. We applied a normal prior with a mean of 39 and a standard deviation set to 0.51, making this a relatively hard prior of 95% HPD 38–40 mya.

3. Results

3.1. Phylogeny

Not all loci were obtained for all species (Supplementary Table S1). All sequences have been deposited in GenBank (Supplementary Table S1). Sequences of mitochondrial genes showed no double signal in the electropherograms, the alignment showed no stop codons, insertions or

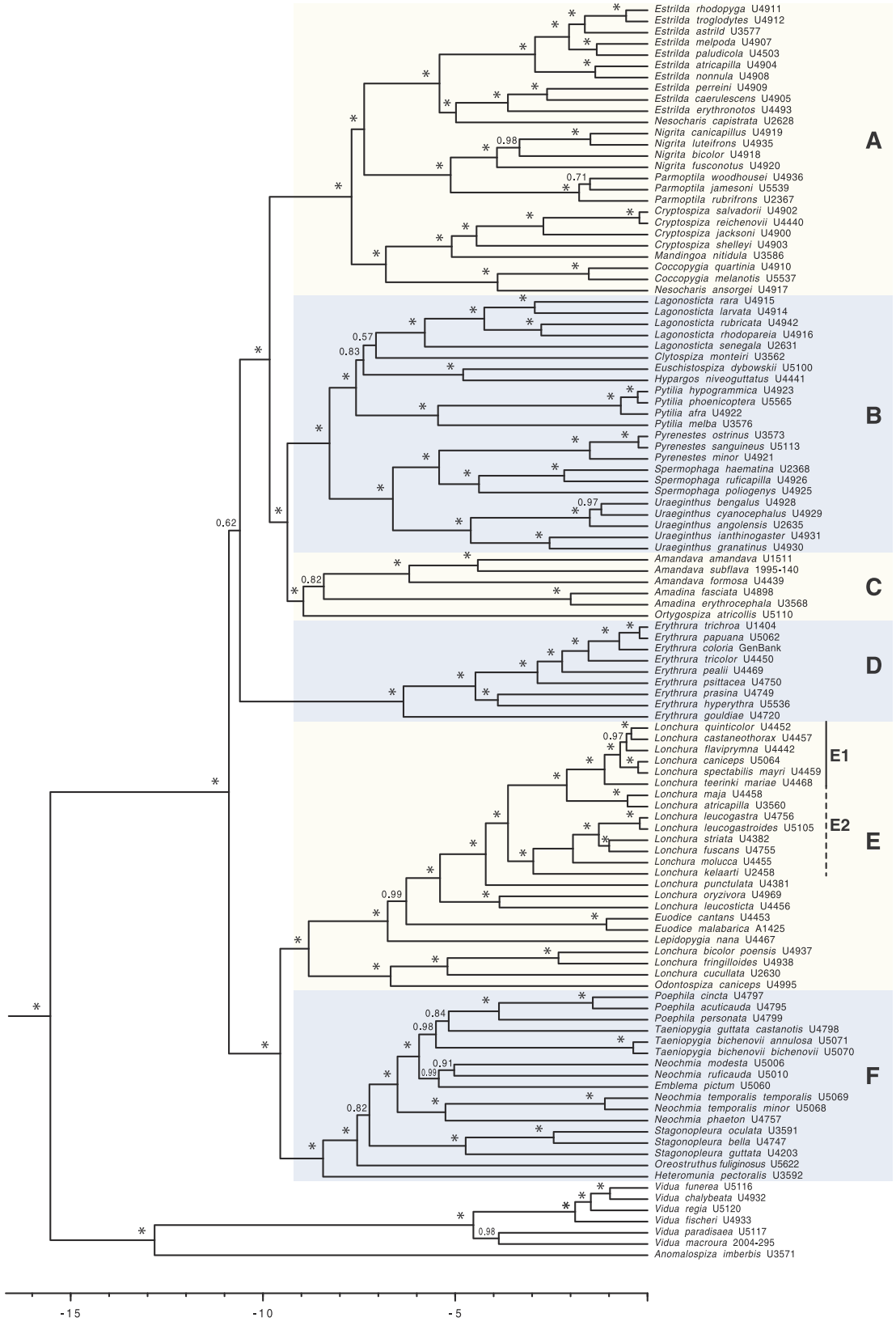

Fig. 1. Phylogeny of Estrildidae based on the multilocus data set of the mitochondrial cytochrome *b* and ND2, and the nuclear fib5, G3P, myoglobin, ODC, and TGF introns inferred by BEAST, calibrated by the split of *Menura* from Eupasseres at 39 mya. Values at nodes indicate posterior probabilities (PP); * indicates PP = 1.00. Clades referred to in the text are labelled with letters. Names follow Gill and Donsker (2019). Outgroups have been pruned.

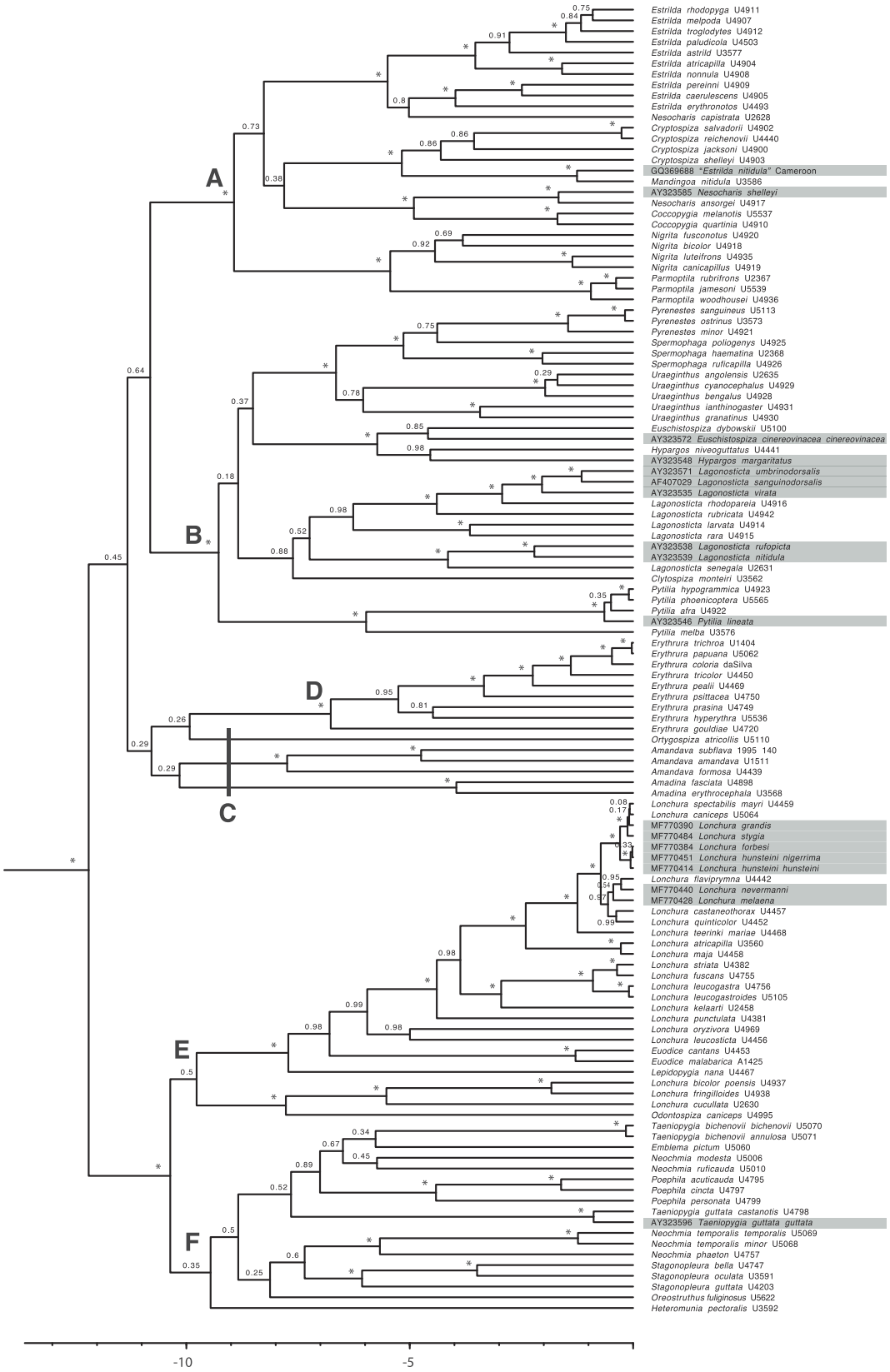

Fig. 2. Phylogeny of Estrildidae based on ND2, inferred by BEAST and calibrated by the split of *Menura* from Eupasseres at 39 mya. Values at nodes indicate posterior probabilities; * indicates PP = 1.00. Samples not included in the concatenated analysis (Fig. 1) are highlighted in green. Outgroups have been pruned. Clades recovered in the multilocus analysis (Fig. 1) are indicated, although clade C is not recovered as monophyletic here. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

deletions, and a vast majority of nucleotide substitutions were found in the 3rd codon position and resulted in few amino acid substitutions.

The multilocus analysis is summarised in Fig. 1, and the ND2 tree (with some additional species not included in the multilocus analysis) in Fig. 2. All primary clades (A–F) within Estrildidae and the relative positions of these were strongly supported in the multilocus analysis, with the exception of clade D. Most currently recognized genera were recovered as monophyletic and congruent with the phylogeny, except for the positions of *Nesocharis capistrata* in clade A, *Taeniopygia bichenovii* and *Taeniopygia guttata castanotis* in clade F, and *Neochmia ruficauda*, *N. modesta*, *N. temporalis* and *N. phaeton* in clade F (Fig. 1).

There were no strongly supported incongruences between the concatenated analysis and the ND2 tree, except for the position of *Estrilda astrild*. In the ND2 tree the branching order of many nodes differed compared to the phylogeny based on the concatenated data, but all such conflicts lacked support. The three genera in clade C (Fig. 1) were placed as incremental sisters to clade D in the ND2 tree, with negligible support.

3.2. Dating

Estrildidae was estimated to have diverged from Viduidae 15.5 mya (95% HPD 13.5–17.6), and the most recent common ancestor (MRCA) of Estrildidae is estimated to have lived about 10.9 mya (95% HPD 9.5–12.3). The six major clades (A–F, Fig. 1) were inferred to have diverged in rather rapid succession during a period of about 1.6 Ma, at approximately 9.3–10.9 mya. The major radiations within these clades were inferred to have begun at different times in different areas, earlier in Africa and Australia (approximately 7.7–8.9 mya), and slightly later in Asia and Wallacea (approximately 4.5–6.3 mya) (Table 1, Fig. 1).

4. Discussion

4.1. Phylogeny

4.1.1. Relationships among clades

The phylogeny is overall well supported and well resolved. The taxonomic arrangement by Payne (2010), dividing Estrildidae into three subfamilies, is fully corroborated, clades A, B and C together corresponding to his subfamily Estrildinae; clade D corresponding to his subfamily Erythrurinae; and clades E and F together corresponding to his subfamily Lonchurinae. The position of the genus *Vidua* together with *Anomalospiza* as the sister clade of Estrildidae is corroborated.

4.1.2. Relationships within closely related species groups

In clade A (Fig. 1) a subclade contains the genus *Estrilda*, as well as *Nesocharis capistrata*. The species currently in *Estrilda* have previously been suggested to be divided into a number of genera (e.g. Wolters, 1957; Steiner, 1960). Their divisions are consistent with the phylogeny.

The genus *Coccopygia* has sometimes been subsumed in *Estrilda,* but is here shown to be deeply divergent from that genus in a position that would make *Estrilda* polyphyletic. Furthermore, *Coccopygia* differs from other taxa in clade A by reduced palate markings in nestlings (Steiner, 1960).

Table 1
Divergence times and 95% highest posterior density (HPD), both in million years, estimated in the same analysis as in Fig. 1.

Node	Age	HPD
MRCA of clade Estrildidae (clades A-F)	10.9	95% HPD (9.5–12.3)
MRCA of Estrildidae and Viduiidae	15.5	95% HPD (13.5–17.6)
MRCA of clade A	7.8	95% HPD (6.6–8.8)
MRCA of clade B	8.3	95% HPD (7.2–9.4)
MRCA of clade C	9.0	95% HPD (7.8–10.3)
MRCA of clade D	6.4	95% HPD (5.2–7.6)
MRCA of clade E	8.8	95% HPD (7.6–10.1)
MRCA of clade F	8.5	95% HPD (7.3–9.8)

Cryptospiza reichenovii and *C. salvadorii,* the two morphologically most similar species in the genus, show a very slight divergence, which may signify either recent divergence or recent gene flow, which may challenge species status and calls for further study. In the ND2 tree (Fig. 2) two samples of *Mandingoa nitidula*, both presumably of the subspecies *schlegeli* based on range, are more diverged than expected and may indicate unrecognized cryptic divergence. One of these is a GenBank sequence, and we have no information concerning morphological differences between these samples. However, the amount of divergence suggests that further investigation may be warranted.

In clade B, much of the topology is uncontroversial. A poorly resolved clade includes the genus *Lagonosticta,* the single-species lineage *Clytospiza monteiri,* one clade containing *Hypargos* and *Euschistospiza,* and one clade containing four *Pytilia* species. In the ND2 tree, the split between *Hypargos margaritatus* and *H. niveoguttatus* is surprisingly deep, judging from their slight morphological difference, but is consistent with treating them as different species. In *Pytilia*, a sister clade to *Pytilia melba* contains four apparently closely related species (Figs. 1, 2). These four species may be divided into two morphologically similar pairs, *P. lineata* and *P. phoenicoptera,* and *P. afra* and *P. hypogrammica*, respectively. The species within both these pairs are allopatric, while at the same time at least partly sympatric with one of the species of the other pair. Counterintuitively, the morphologically different *P. phoenicoptera,* and *P. hypogrammica*, which are widely sympatric in West Africa, are inferred to be more closely related to each other than to the respective morphologically similar species *P. afra* and *P. hypogrammica* (Figs. 1, 2). A possible explanation for this could be ongoing or recent gene flow, indicated by low divergence in both mitochondrial and nuclear phylogenies.

Pyrenestes ostrinus and *P. sanguineus* are inferred to be closely related. In both these species, populations of different body size and bill shape and size are known from many parts of their ranges, without apparent signs of assortative mating (Smith, 1993; Smith and Girman, 2000). Their ranges overlap only in the Ivory Coast, but the 0.5% (uncorrected p) divergence between these two species is smaller than what seems to be required to reach a stage in the speciation process where gene flow does not occur upon secondary sympatry (Price, 2008). It is possible that introgression may be responsible for the slight divergence, and further research is needed into both possible gene flow as well as the intraspecific morphological size variation present in both species. The prospect that individuals with different body size and bill shape within populations of both species carry ancestral genetic variants that have evolved in parallel in independent lineages, as suggested for a group of species in the genus *Lonchura* (Stryjewski and Sorenson, 2017), is another possible avenue of inquiry.

The genus *Uraeginthus* contains two species (*U. granatinus* and *U. ianthinogaster*) that have often been allocated to the genus *Granatina*, and treating these two as part of a different genus than *Uraeginthus* is consistent with morphological differences and the deep split in the clade, estimated to having occurred more than 4.5 mya.

Clade C consists of the genera *Amadina, Ortygospiza* and *Amandava,* which are inferred to have diverged from each other very early in the history of Estrildidae. The unsampled *Paludipasser* is often placed close to these, but evidence is scarce, and Payne and Sorenson (2003), argue for no close relationship with any particular Estrildidae.

Clade D consists of the parrotfinches *Erythrura,* in which *E. gouldiae*, which is often placed in *Chloebia,* is sister to the remainder of the clade. In *Erythrura,* there is a basal split between species occurring to the west of the Wallace line, as drawn by Huxley (1868), and those restricted to the east of this line. In the ND2 tree, the haplotypes of the GenBank *E. trichroa* and our *E. papuana* are identical. There may be several explanations for this: taxonomy may be wrong in that *E. trichroa* and *E. papuana* are not separate species but conspecific size morphs; alternatively the sequence similarity may be due to introgression; or one or

more samples may have been misidentified. We have not been able to access the specimens to evaluate this.

Clade E1 is a conglomerate of extensively hybridizing *Lonchura* species mainly from New Guinea and the Bismarck archipelago, with one species from east Nusa Tenggara, Indonesia and two species from Australia. A subsection of this group of species has been studied in depth by Stryjewski (2015) and Stryjewski and Sorenson (2017), who inferred that they represented a very recent radiation that had not yet developed reproductive isolating barriers, as evidenced by extensive introgression. Our study incorporated mitochondrial sequences from Stryjewski (2015) and corroborates the pattern of rapid radiation. We refer to Stryjewski and Sorenson (2017) for further details of the complex evolution of this clade. The part of clade E labelled E2 contains species that are morphologically similar to those in clade E1. Among these, *L. leucogastra* and *L. leucogastroides* show very low degree of divergence. We do not have enough data to evaluate whether this is a result of very recent divergence or gene flow, but further study is warranted. *L. punctulata* is inferred to be sister to E1 and E2. The morphologically very different species *L. leucosticta* and *L. oryzivora* are inferred to be sisters. According to unpublished data, *L. tristissima* and *L. fuscata* are also part of this clade (Fig. A.1. in Stryjewski, 2015). *Euodice*, *Lepidopygia nana* and *Odontospiza caniceps* are often included in *Lonchura*, whereas the three African species currently in *Lonchura*, have often been placed in *Spermestes*. The deep divergence in clade E makes treatment as different genera plausible for some of these clades.

Heteromunia pectoralis is morphologically similar to the genus *Lonchura*, but is here shown to belong in the grassfinch clade (F, Fig. 1), suggesting that this plumage pattern may be plesiomorphic and that the more colorful plumages of many other species in clade F may have evolved under a different selective regime than that acting on the mannikin sister clade E (Fig. 1). To explore the apparent low level of recent diversification in this clade, in two cases we included samples representing distinct subspecies. In *Taeniopygia bichenovii,* the subspecies *bichenovii* and *annulosa,* that vary mainly in rump colour, are only slightly diverged, indicating a separation of less than 0.5 Ma. The two subspecies *Neochmia temporalis temporalis* and *N. temporalis minor,* on the other hand, are inferred to have diverged around 1.2 mya. There are more than a dozen pairs of taxa in Estrildidae, treated as full species, that share a MRCA younger than this, e.g. *Euodice cantans* and *E. malabarica*, and species in *Lonchura*, *Pyrenestes* and *Pytilia*. Diagnosable plumage differences between *Neochmia temporalis temporalis* and *N. temporalis minor* are present both on the head and the undertail-coverts, and sexual dimorphism occurs only in *N. temporalis minor* (Payne, 2019). Further research is required to determine whether these two taxa deserve to be treated as a separate species.

4.2. Dating

All the recent studies that addressed the age of the Aves or Passeriformes radiation (Claramunt and Cracraft, 2015; Jarvis et al., 2014; Moyle et al., 2016Hooper and Price, 2017; Oliveros et al., 2019; Prum et al., 2015; Selvatti et al., 2015) came to different results, and this needs to be taken into consideration when interpreting the evolution of the waxbills. We prefer to use a calibration based on fossils, as the age of nodes as old as the inferred age of the MRCA of Estrildidae are difficult to estimate by mtDNA divergence, due to increasing saturation. The advantage of using a single calibration point gleaned from larger phylogenies including many fossil calibration points is reproducibility and potentially also scaling to other calibration points.

The calibration point used by Sorenson et al. (2003) was 20 Ma for the age of the split between Viduidae and Estrildidae, estimated by Sorenson and Payne (2001) based on an assumed 2% of sequence divergence per million years (Klicka and Zink 1997, 1999; Avise et al. 1998). We estimated the age of the MRCA of Viduidae and Estrildidae to approximately 15.6 Ma, which is very similar to the approximately 15.5 Ma estimated by Oliveros et al. (2019), who used 13 fossil calibration points and extensive cross reference to geological and climatic events. The estimated age of 10.9 Ma of the MRCA of Estrildidae in this study is similar to the age estimated by Sorenson et al. (2003), although the ages of most other nodes differ to some extent. For example, the age of the MRCA of *Lagonosticta* was estimated to approximately 7.2 Ma by Sorenson et al. (2003) and to approximately 5.8 Ma in this study. Hooper and Price (2017) estimated the crown age of Estrildidae to approximately 12.5 Ma, which is slightly older than our estimate, but consistent with their higher estimate of the divergence of *Menura* from other Oscines to just over 42 mya.

Arnaiz-Villena et al. (2009) estimated the divergence between Estrildidae and Viduidae to 20 mya, and the MRCA of Estrildidae to 16.5 mya, compared to our estimates of 15.6 mya and 10.9 mya, respectively. They estimated the age of their nodes A–J (Fig. 1 in Arnaiz-Villena et al., 2009) to between 7.1 and 11 Ma, whereas the age of the corresponding nodes in this study were estimated to approximately 2–6.3 Ma, but both calibration points and methods for estimating ages differed significantly. Arnaiz-Villena et al. (2009) used the divergence between *Fringilla coelebs* and *Carduelis chloris*, estimated to 16.5 mya by Arnaiz-Villena et al. (1998) as a calibration point. These two species were not included here, but the age of that split would be expected to correspond to the split between *Fringilla montifringilla* and *Carduelis carduelis*, here estimated to having occurred approximately 12.6 mya (Supplementary Fig. S1).

4.3. Taxonomic remarks

4.3.1. Taxonomy at the subfamily level

Estrildinae is divided into three well supported clades and Lonchurinae into two, which all diverged during a relatively short span of time approximately 9.3–10.9 mya. These five clades together with Erythrurinae may be arranged as three subfamilies consisting of one, two and three tribes, respectively (D and E + F and A + B + C), or as six subfamilies. There is no consensus regarding how to determine whether a clade should be regarded as a family, subfamily or tribe, and each of these treatments have their own merits. In our opinion, the relatively similar age of the six clades is a strong argument for treating them at the same taxonomic level. However, in the radiation of estrildids, homoplasy is abundant, and particularly clades A-C identified in Fig. 1 are not possible to define based on morphological synapomorphies. Previous taxonomists (cf. Delacour 1943, Steiner, 1960, Wolters 1957) have struggled with this, and in the light of our molecular phylogeny it becomes clear that the characters proposed, like palate markings of nestlings, vocal and courtship characteristics, body proportions, and muscular organisation, are not reliable markers of phylogenetic relationship. For example, the tribe Amadine (Delacour, 1943) was a conglomerate of all species from our clade E, *Heteromunia* from clade F, and only *Amadina* from clade C.

In our opinion, taxonomic recognition of six groups of equal hierarchical standing is reasonable for clades A–F in Fig. 1. If so, the name Estrildinae Bonaparte, 1850 is available and suitable for clade A, in a more restricted circumscription than currently used (Mayr et al., 1968); the name Lagonostictinae (Steiner, 1960) is available and suitable for clade B; the name Amandavinae (Steiner, 1960) is available and suitable for clade C (as stated above, the name Amadinae has been in previous use, but using a name based on *Amadina* for any clade is now unsuitable, due to its previous polyphyletic usage); the name Erythrurinae (Delacour, 1943) is in current use for clade D; the name Lonchurinae (Steiner, 1960) is available and suitable for clade E, in a more restricted circumscription than currently used (Mayr et al., 1968); and the name Poephilinae (Mayr, Paynter & Traylor, 1968) is available and suitable for clade F.

We propose to recognize the following subfamilies.

- Estrildinae (Bonaparte, 1850-1851) (clade A). Referred taxa: *Brunhilda, Coccopygia, Cryptospiza, Estrilda, Delacourella, Glaucestrilda,*

Mandingoa, Nesocharis, Nigrita and *Parmoptila.*

- Lagonostictinae (Steiner, 1960) (clade B). Referred taxa: *Clytospiza, Euschistospiza, Granatina, Hypargos, Lagonosticta, Pyrenestes, Pytilia, Spermophaga* and *Uraeginthus*.
- Amandavinae (Steiner, 1960) (clade C). Referred taxa: *Amadina, Amandava, Ortygospiza* and possibly *Paludipasser*.
- Erythrurinae (Delacour, 1943) (clade D). Referred taxa: *Chloebia* and *Erythrura*.
- Lonchurinae (Steiner, 1960) (clade E). Referred taxa: *Euodice, Lepidopygia, Lonchura, Mayrimunia, Padda,* and *Spermestes*.
- Poephilinae (Mayr, Paynter & Traylor, 1968) (clade F). Referred taxa: *Aidemosyne, Bathilda, Emblema, Heteromunia, Neochmia, Oreostruthus, Poephila, Stagonopleura, Stizoptera* and *Taeniopygia*.

4.3.2. Taxonomy at the genus level

In our results, there are a number of cases where the phylogeny is incompatible with the current taxonomy, suggesting revision might be warranted (Supplementary Fig. 2). In clade A, the two species in *Nesocharis* are not part of the same clade, rendering both *Nesocharis* and *Estrilda* non-monophyletic, as *Nesocharis capistrata* is part of the *Estrilda* clade with high support. As with division into subfamilies, also delimitation of genera is subjective. We propose that genera in addition to being compatible with the phylogeny, should represent divergences of fairly equal age range and preferably be made up of morphologically, ecologically reasonably intuitive and identifiable groups of species. All genera proposed here are at least 4 million years old. The two oldest nodes representing a MRCA of a genus are those of *Amandava* and *Spermestes*, which are about 6 million years old. We propose that the deep branches and the morphological heterogeneity among major lineages and clades in *Estrilda* justifies dividing the genus into three previously proposed genera, *Estrilda* Swainson, 1827, *Brunhilda* Reichenbach, 1862, and *Glaucestrilda* Roberts, 1922, and that *Nesocharis capistrata* is transferred to the genus *Delacourella* Wolters, 1949. All these proposed genera represent sufficiently old splits and morphologically intuitive units. *Brunhilda* is characterized by a combination of black ear coverts and chin, and strongly barred wing coverts and tertials. *Glaucestrilda* is predominantly pearly grey with a red rump. *Delacourella* differs from *Nesocharis* by its unique head pattern, and is characterized by a black chin patch narrowly extending to delimit the rear of the ear coverts.

The taxonomy of Gill and Donsker (2019) differs to some extent from that of Payne (2010), adopted in del Hoyo and Collar (2016), and in a number of cases the taxonomy of the latter seems preferable to us. For example, the topology of Clade B is entirely congruent with the taxonomy of Payne (2010) and del Hoyo and Collar (2016), and we propose that the deep divergence and morphological differences between the two parts of the *Uraeginthus* clade is recognised by resurrecting the genus *Granatina* Sharpe, 1890. *Granatina* differs from *Uraeginthus* by darker plumage with extensive cinnamon or chestnut areas, blackish tail and stronger reddish bill. The palate marking in nestlings are bolder and more extensive (Steiner, 1960).

Clade C is congruent with the taxonomy of both Gill and Donsker (2019) and Payne (2010), and in no need of a revision of the genera included here.

Clade D consists of the parrotfinches *Erythrura* and the Gouldian Finch, which is included in *Erythrura* by Gill and Donsker (2019) but in *Chloebia* by Payne (2010) and del Hoyo and Collar (2016). *Chloebia* differs from *Erythrura* in having a shorter and higher pale bill, purple breast, yellow belly and a blue rump. In view of its morphological distinctness, and the relatively old age of the divergence from the parrotfinches, we advocate transferring it to the genus *Chloebia* Reichenbach, 1863.

Clade E is made up of species that at one time or another have all been included in the genus *Lonchura.* However, these species are parts of different groups that share significant evolutionary or morphological characteristics that set them apart from other groups. We propose that the name *Lonchura* is restricted to clade E1 and the part of clade E marked E2 (Fig. 1). *Lonchura oryzivora* and *L. leucosticta* constitute a clade that is sister to E1 and E2, and Stryjewski (2015) also include *L. fuscata* and *L. tristissima* in this clade (Fig. A.1. in Stryjewski, 2015). *Lonchura oryzivora* and *L. fuscata* make up a morphologically distinctive pair, and have previously been placed in the genus *Padda* Reichenbach, 1850. Delacour (1943) described the genus as large, with very large bill, both mandibles slightly convex, and pointed out their black head and throat, with only cheek white. We propose that this name is reinstated for these two species. *L. tristissima* and *L. leucosticta* are sisters to *Padda*, and can thus not be retained in the genus *Lonchura* if *Padda* is recognised. They are characterized by their unique pure yellow rump, and exhibit vocal characteristics that differ from other munias (Wolters, 1949), and we propose that they are transfered to the genus *Mayrimunia* Wolters, 1949. *Euodice* and *Lepidopygia nana* (sometimes *Lemurestes nana*) have often been included in *Lonchura*. Delacour (1943) defined *Euodice* as medium sized, with thick and short silver gray bill; comparatively long blackish or purplish, rounded tail, sometimes with central tailfeathers elongated; no ornamental decomposed fringes on rump or tail feathers. *Lepidopygia* is recognized by black throat, bill with black upper and pinkish lower mandibles, and pink legs. We concur that upholding two genera for these species is warranted, and supported by phylogenetic and morphological characteristics. Four species in clade E, three currently in *Lonchura* and one in *Odontospiza,* are restricted to Africa. They are morphologically quite similar to those labelled E1 and E2, but lack ornamental decomposed fringes on rump or tail feathers. Retaining any of these species in *Lonchura,* with *Euodice* and *Lepidopygia* upheld, would render *Lonchura* polyphyletic, and we propose that the genus *Spermestes* Swainson, 1837 is reinstated. Both Güttinger (1970) and Baptista (1973) came to the conclusion that *Odontospiza* resembles *Spermestes* in behavior, and argued these two genera were closely related. When this species was first transferred to *Lonchura,* the original species epithet was changed to *griseicapilla* as *caniceps* was preoccupied. The name *caniceps* is now invalid for this species (IZCN, 1999). We consider arguments for upholding *Odontospiza* insufficient, and advocate that *Odontospiza* is subsumed in *Spermestes* under the name *Spermestes griseicapilla*.

A majority of the divergences in clade F are relatively old, and recent diversification has been limited. Maybe as a result of this, most species in the clade are rather unique in appearance and difficult to intuitively unite into larger genera compatible with the phylogeny. We recover the genera *Neochmia* and *Taeniopygia* as non-monophyletic, further enhancing the impression of uniqueness among the lineages. As the splits are so deep, we take the position of treating a majority of lineages as different genera, and advocate the previously proposed names shown in Table 2. This means transferring *Taeniopygia bichenovii* to the genus *Stizoptera* Oberholzer, 1899, *Neochmia modesta* to the genus *Aidemosyne* Reichenbach, 1862–63, and *Neochmia ruficauda* to the genus *Bathilda* Reichenbach, 1862–63.

4.3.3. Taxonomy of species not included in this study

Several species currently placed in various genera in Estrildidae were not included in this study. Most were placed in their current taxonomic position based on both previous molecular analyses and various morphological evidence, and in most cases we see no arguments against upholding this taxonomy. However, in our judgement five species missing from our analyses should be treated differently than by Payne (2010) and del Hoyo and Collar (2016) (Table 2). In clade A, we would place *Estrilda thomensis* in *Glaucestrilda* and *E. charmosyna* in *Brunhilda.* In both these cases, morphological similarities make it unlikely that they would be part of other clades. We propose that *Lonchura nigriceps* in clade E is placed in *Spermestes.* This species is often treated as conspecific with *Spermestes bicolor*. The other two are *Lonchura fuscata* and *L. tristissima,* in clade E, proposed to be placed in the genera *Padda* and *Mayrimunia,* respectively, as discussed above.

Table 2
Comparison between taxonomy proposed here and taxonomy of Gill and Donsker (2019: v 9.1) and del Hoyo and Collar (2016). Species belonging in any of the genera proposed to be reinstated in the present study are listed under the appropriate name. Species not included in our analyses assumed to belong in these genera are marked with an asterisk (*). For species not included in this table, we propose no taxonomic action compared to Gill and Donsker (2019: v 9.1) and del Hoyo and Collar (2016). See Discussion for details and rationale.

Proposed revised taxonomy	Gill and Donsker (2019)	del Hoyo and Collar (2016)
Glaucestrilda caerulescens	*Estrilda caerulescens*	*Estrilda caerulescens*
Glaucestrilda perreini	*Estrilda perreini*	*Estrilda perreini*
*Glaucestrilda thomensis**	*Estrilda thomensis*	*Estrilda thomensis*
Brunhilda erythronotos	*Estrilda erythronotos*	*Estrilda erythronotos*
*Brunhilda charmosyna**	*Estrilda charmosyna*	*Estrilda charmosyna*
Delacourella capistrata	*Nesocharis capistrata*	*Nesocharis capistrata*
Granatina ianthinogaster	*Uraeginthus ianthinogaster*	*Granatina ianthinogaster*
Granatina granatinus	*Uraeginthus granatinus*	*Granatina granatinus*
Spermestes bicolor	*Lonchura bicolor*	*Spermestes bicolor*
*Spermestes nigriceps**	*Lonchura nigriceps*	*Spermestes bicolor nigriceps*
Spermestes fringilloides	*Lonchura fringilloides*	*Spermestes fringilloides*
Spermestes cucullata	*Lonchura cucullata*	*Spermestes cucullata*
Spermestes griseicapilla	*Odontospiza caniceps*	*Odontospiza griseicapilla*
Mayrimunia leucosticta	*Lonchura leucosticta*	*Lonchura leucosticta*
*Mayrimunia tristissima**	*Lonchura tristissima*	*Lonchura tristissima*
Padda oryzivora	*Lonchura oryzivora*	*Lonchura oryzivora*
*Padda fuscata**	*Lonchura fuscata*	*Lonchura fuscata*
Bathilda ruficauda	*Neochmia ruficauda*	*Neochmia ruficauda*
Aidemosyne modesta	*Neochmia modesta*	*Neochmia modesta*
Taeniopygia castanotis	*Taeniopygia guttata castanotis*	*Taeniopygia castanotis*
Stizoptera bichenovii	*Taeniopygia bichenovii*	*Taeniopygia bichenovii*
Chloebia gouldiae	*Erythrura gouldiae*	*Chloebia gouldiae*

5. Conclusions

The generally well resolved and well supported time calibrated phylogeny is a major step forward compared to earlier studies that were based on a smaller number of species and loci. Estrildidae is demonstrated to be a well-defined and strongly supported clade, with six well supported subclades, to a large part consistent with previous taxonomy that was also informed by behavioral and morphological criteria. This study can provide a basis for future studies of other aspects of the evolution of this ecologically important group of birds.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.106757.

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