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Molecular phylogeny of Chloropseidae and Irenidae – Cryptic species and biogeography

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ABSTRACT

Chloropseidae (Leafbirds) and Irenidae (Fairy-bluebirds) are colourful Oriental birds, which have been placed as a deep (old) branch in the radiation of passeroid songbirds. We present a densely sampled molecular phylogeny of the two families based on two nuclear introns (GAPDH and ODC) and two mitochondrial genes (ND3 and cyt-*b*) largely stemming from old museum specimens. Our results show that several subspecies within both Chloropseidae and Irenidae are genetically distinct and separated in the Miocene some 10–11 Million years ago (Mya), indicating a substantial underestimation of species numbers within the two families. Based on our molecular findings, plumage distinctiveness and contemporary distributions we propose that several subspecies be recognised at the species level. Furthermore, we use the molecular data to examine biogeographical patterns of the two families in the light of historical geological re-arrangements in the region. The results indicate that the Philippines were colonised in the Pliocene and that colonisation probably progressed via the Sulu islands from Borneo and not via Palawan, which was first colonised in the Pleistocene.

1. Introduction

Leafbirds (Chloropseidae) and Fairy-bluebirds (Irenidae) are colourful passerine birds inhabiting the tropical forest canopies of the Oriental Region. Their phylogenetic relationships within the songbirds (Oscines) have been subject to long controversy (Wells, 2005a,b). Because of the plastic morphology in the songbird radiation, the traditional classification was based on a practical subdivision of some major eco-morphological groups such as Old World insect-eaters and their relatives, New World nine-primaried oscines, including various groups of seed-eaters, and crows and their allies (Mayr and Greenway, 1956). Few attempts to undertake a phylogenetic analysis have been made, other than that of Beecher (1952) who interpreted the feeding apparatus of *Chloropsis* and *Irena* as being derived from that of *Pycnonotus* in the greatly expanded assemblage of warbler-like birds. Delacour (1960), in "Peters' checklist", included *Aegithina*, *Chloropsis* and *Irena* in one family, Irenidae. This view may reflect the overall similarity in body shape, short legs and colourful plumage of birds with mainly frugivorous diet.

DNA–DNA hybridization studies (Sibley and Ahlquist, 1990) linked *Chloropsis* and *Irena* as sister clades near the base of the parvorder Corvida. However, more recent findings based on nuclear DNA sequence data (Barker et al., 2004; Cracraft et al., 2003; Johansson et al., 2008) moved Chloropseidae and Irenidae into Sibley and Ahlquist's 'parvorder' Passerida, with a basal position in the large Passeroidea radiation (sparrow-like birds), near the Nectarinidae (sunbirds). While this placement is well supported, no molecular data are available with respect to relationships within the group or rates and modes of speciation.

The 11 species of *Chloropsis*, and numerous subspecies (Wells, 2005a), are morphologically rather uniform, viridian-green and yellowish, often with a black or blue facial mask in males. Although most species are sexually dimorphic, some species stand out by being sexually monomorphic, with no facial mask in males of the Philippine *C. flavipennis* and *C. palawanensis*, and mask developed in both sexes of *C. kinabaluensis* of the mountains of northern Borneo, in the widespread *C. aurifrons*, and to a lesser extent in *C. venusta* of Sumatra. *Irena* currently comprises two species, which show significant geographical differentiation. *I. puella*, inhabiting the Asian mainland and Sundaland, is strongly sexually dimorphic and males in some populations stand out by having unusually long blue upper tail-coverts more or less encasing the tail. *I. cyanogastra* from the Philippines exhibits weaker sexual dimorphism with females more male-like but with duller plumage.

Chloropseidae and Irenidae are distributed in Southeast Asia, from India in the west to the Philippines in the east, and from the Himalayas in the north to Java in the south (Fig. 1). One

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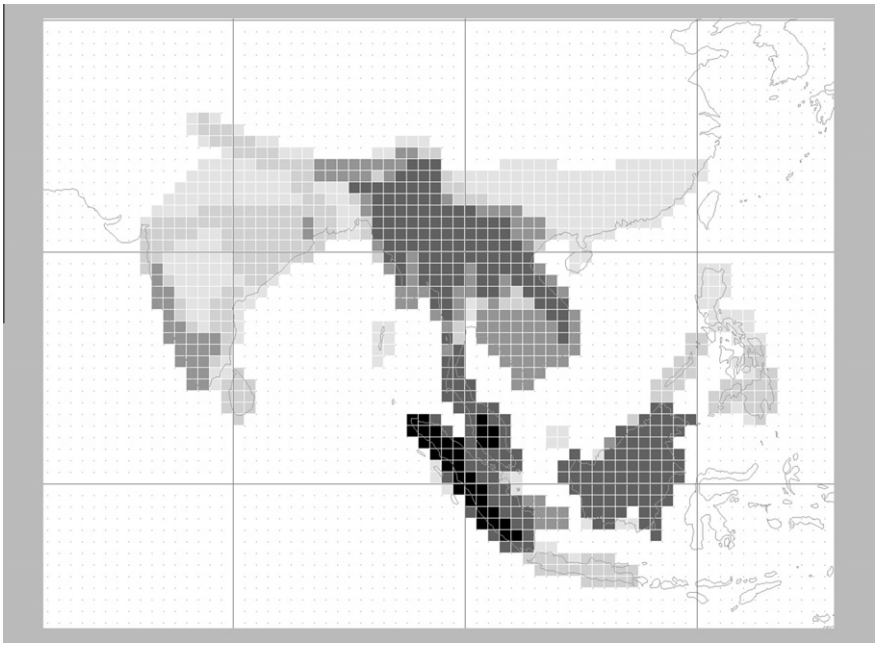

Fig. 1. The distribution of 11 presently recognised species of Chloropseidae and two presently recognised species of Irenidae, per grid cell corresponding to 1 × 1 geographical degrees in the Oriental Region, with the black gridcell representing most species of six.

member of *Chloropsis* (*C. flavipennis*) occurs in the central and southern Philippine islands and one species (*C. palawanensis*) is endemic to Palawan and its satellite islands. Several endemic subspecies are represented in the Indonesian archipelago and five species of *Chloropsis* co-occur in Sumatra, where two of them are endemic. For *Irena cyanogastra* of the Philippines, one subspecies is endemic to Basilan in the Sulu Sea, whereas the other three subspecies are distributed in the northern, central, and southern Philippine regions, respectively. However, the island of Palawan is inhabited by *Irena puella tweeddalei*.

Both families live in the canopy in evergreen forests or gardens and are generally considered to be sedentary. However, *Chloropsis hardwickei* and *C. aurifrons* are known to undertake seasonal altitudinal migratory movements in the Himalayan foothills (Wells, 2005a), and *Irena puella* is able to cross gaps of unsuitable habitat in response to seasonal changes in the fruit supply (Wells, 2005b). However, no crossings of marine water barriers have been confirmed.

In the present paper we provide the first molecular assessment of relationships within the Chloropseidae and Irenidae. We use this phylogenetic framework to assess whether the current classification, which was mainly based on plumage characters, reflects the evolutionary relationships within the groups. Additionally, to illuminate biogeographical dispersal patterns, we compare evolutionary history and geological history; the latter is known in considerable detail in terms of plate tectonics (notably Hall, 1998) and changes in connectivity of land in the Sundaland area (Bintanja et al., 2005; Voris, 2000; Hall, 2002),

2. Materials and methods

2.1. Taxon sampling, amplification and sequencing

We obtained samples from all 11 species and 24 out of 27 subspecies for Chloropseidae and two species and nine out of ten subspecies for Irenidae. Our taxonomy follows Wells (2005a,b). Samples from as many island populations as possible were included. We used another member of the superfamily Passeroidea, *Passer montanus*, as outgroup. All except seven of the samples are vouchered, and all DNA sequences were deposited on GenBank (Table 1).

We isolated and purified DNA from tissues using QIAamp Mini Kits (Qiagen Inc., 2003) following the manufacturer's recommendations. The nuclear loci glyceraldehyde-3-phosphodehydrogenase (GAPDH) intron 11 and ornithine decarboxylase (ODC) introns 6–7, and the mitochondrial loci NADH dehydrogenase subunit 3 (ND3) and cytochrome *b* (cyt-*b*), were amplified and sequenced. Procedures for study skins are detailed in Irestedt et al. (2006). Because nuclear DNA evolves at a slower rate than mitochondrial DNA (i.e., nuclear DNA is useful for resolving basal relationships), the nuclear markers were only sequenced at the species level. We sequenced more than one individual of almost all species (except *C. venusta* and *C. kinabaluensis*) and for most subspecies. For fresh tissue the target markers were amplified in one fragment but for museum samples, markers were amplified in shorter overlapping fragments (see Table 2 for primers used in this study). All sequences were aligned in MegAlign™ (DNA STAR Inc., Madison, Wisconsin) and gaps were treated as missing data. All coding sequences were manually checked for stop codons and indels that may have disrupted the reading frame.

2.2. Model selection and phylogenetic inference

We used Bayesian inference and Maximum Likelihood to estimate the phylogenetic relationships. The models for nucleotide substitution used in the analyses were selected for each gene individually and for mtDNA codon positions by applying the Akaike information criterion as implemented in ModelTest 3.7 (Posada and Crandall, 2005). Posterior probabilities of trees and parameters in the substitution models were approximated with Metropolis coupled Markov Chain Monte Carlo (MC^3) using the program MrBayes 3.1.1. (Huelsenbeck and Ronquist, 2003; Ronquist and Huelsenbeck, 2003). Analyses were performed for each gene partition and for mtDNA codon positions as well as for the concatenated data set. Three heated and one cold chain of MCMC were run for

Table 1
Taxonomic sampling and DNA sources. All samples but seven are vouchered. Unvouchered samples are marked by *. Acronyms are: LSU, Louisiana State University, MNHN, Muséum National d'Histoire Naturelle, Paris, France, NRM, Swedish Museum of Natural History, Stockholm, Sweden, ZMUC, Zoological Museum, University of Copenhagen, Natural History Museum of Denmark.

Taxa	Voucher number	Locality	GAPDH	ODC	ND3	Cyt-b	DNA source
Chloropsis aurifrons ssp?	ZMUC130542	Captivity	JX445261	JX445378	JX445297	JX445178	Blood
Chloropsis aurifrons aurifrons	ZMUC93822	Nepal			JX445285	JX445171	Skin
Chloropsis aurifrons aurifrons	ZMUC105561	NE India			JX445286	JX445172	Skin
Chloropsis aurifrons incomta	NRM570543	C Vietnam			JX445290	JX445176	Skin
Chloropsis aurifrons incomta	NRM570544	C Vietnam			JX445289	JX445175	Skin
Chloropsis aurifrons inornata	ZMUC105554	Thailand			JX445291	JX445177	Skin
Chloropsis aurifrons inornata	NRM570542	SW Thailand			JX445292	JX445183	Skin
Chloropsis aurifrons insularis	ZMUC105556	Sri Lanka		JX445374	JX445287	JX445173	Skin
Chloropsis aurifrons insularis	ZMUC105555	Sri Lanka			JX445288	JX445174	Skin
Chloropsis aurifrons insularis	MNHN1970947	SW India		JX445376	JX445293	JX445179	Skin
Chloropsis aurifrons insularis	MNHN1970948	SW India	JX445260	JX445377	JX445294	JX445180	Skin
Chloropsis aurifrons pridii	NRM570539	NW Thailand			JX445296	JX445182	Skin
Chloropsis aurifrons pridii	NRM570538	N Thailand		JX445375	JX445295	JX445181	Skin
Chloropsis cochinchinensis chlorocephala	ZMUC105560	SE Thailand			JX445298	JX445184	Skin
Chloropsis cochinchinensis cochinchinensis	NRM570527	Java			JX445307	JX445193	Skin
Chloropsis cochinchinensis cochinchinensis	NRM570526	Java			JX445309	JX445195	Skin
Chloropsis cochinchinensis cochinchinensis	NRM570525	Java		JX445381	JX445308	JX445194	Skin
Chloropsis cochinchinensis kinneari	NRM570529	Myanmar			JX445301	JX445187	Skin
Chloropsis cochinchinensis kinneari	NRM570528	SE Vietnam			JX445299	JX445185	Skin
Chloropsis cochinchinensis kinneari	NRM570532	E Thailand			JX445300	JX445186	Skin
Chloropsis cochinchinensis kinneari	NRM570533	N Thailand			JX445303	JX445189	Skin
Chloropsis cochinchinensis kinneari	NRM570537	S Vietnam	JX445264	JX445379	JX445302	JX445188	Skin
Chloropsis cochinchinensis kinneari	NRM570536	C Vietnam			JX445304	JX445190	Skin
*Chloropsis cochinchinensis moluccensis**	ZMUC137976	Sumatra	JX445262	JX445380	JX445306	JX445192	Feather
Chloropsis cochinchinensis moluccensis	NRM570534	Malay Peninsula			JX445305	JX445191	Skin
*Chloropsis cochinchinensis serithai**	ZMUC137975	SE Thailand	JX445263	JX445382	JX445310	JX445196	Feather
Chloropsis cochinchinensis viridinucha	NRM570523	Borneo			JX445311	JX445197	Skin
Chloropsis cyanopogon ssp?	ZMUC130784	Captivity	JX445266	JX445385	JX445317	JX445203	Blood
Chloropsis cyanopogon cyanopogon	NRM570531	Malay Peninsula			JX445315	JX445201	Skin
Chloropsis cyanopogon cyanopogon	ZMUC105562	SW Thailand	JX445265	JX445384	JX445314	JX445200	Skin
Chloropsis cyanopogon cyanopogon	ZMUC137973	Sumatra			JX445313	JX445199	Skin
Chloropsis cyanopogon cyanopogon	NRM570545	Borneo		JX445383	JX445312	JX445198	Skin
Chloropsis cyanopogon septentrionalis	NRM570530	Malay Peninsula			JX445316	JX445202	Skin
Chloropsis flavipennis	ZMUC105551	Mindanao	JX445267	JX445387	JX445320	JX445206	Skin
Chloropsis flavipennis	ZMUC105553	Mindanao			JX445318	JX445204	Skin
Chloropsis flavipennis	ZMUC105552	Mindanao		JX445386	JX445319	JX445205	Skin
Chloropsis hardwickii hardwickii	NRM568339	E India			JX445322	JX445210	Skin
Chloropsis hardwickii hardwickii	NRM570521	N Thailand			JX445324	JX445209	Skin
Chloropsis hardwickii hardwickii	ZMUC93826	Nepal	JX445268	JX445388	JX445321	JX445208	Skin
Chloropsis hardwickii hardwickii	ZMUC93825	Nepal			JX445323	JX445207	Skin
Chloropsis hardwickii hardwickii	NRM568342	N Vietnam			JX445333	JX445218	Skin
Chloropsis hardwickii hardwickii	NRM570519	N Vietnam			JX445331	JX445216	Skin
Chloropsis hardwickii malayana	NRM570546	Malay Peninsula			JX445330		Skin
Chloropsis hardwickii malayana	NRM568340	Malay Peninsula			JX445329	JX445215	Skin
Chloropsis hardwickii melliana	NRM570520	S Vietnam			JX445325	JX445211	Skin
Chloropsis hardwickii melliana	NRM568343	C Vietnam	JX445269	JX445389	JX445327	JX445213	Skin
Chloropsis hardwickii melliana	NRM568345	C Vietnam			JX445328	JX445214	Skin
Chloropsis hardwickii melliana	NRM568348	C Vietnam			JX445326	JX445212	Skin
Chloropsis hardwickii melliana	NRM568341	China	JX445270	JX445390	JX445334	JX445219	Skin
Chloropsis hardwickii melliana	NRM570547	N Vietnam			JX445332	JX445217	Skin
Chloropsis jerdoni	MNHN1270	SW India			JX445335	JX445220	Skin
Chloropsis jerdoni	MNHN1271	SW India			JX445336	JX445221	Skin
Chloropsis jerdoni	MNHN1273	SW India			JX445337	JX445222	Skin
Chloropsis kinabaluensis	LSU0052	Borneo	JX445271	JX445391	JX445338	JX445223	Blood
*Chloropsis media**	ZMUC137978	Sumatra	JX445272	JX445393	JX445340	JX445225	Feather
*Chloropsis media**	ZMUC137977	Sumatra	JX445273	JX445392	JX445339	JX445224	Feather
Chloropsis palawanensis	ZMUC105548	Palawan			JX445341	JX445228	Skin
Chloropsis palawanensis	ZMUC105550	Palawan	JX445274	JX445394	JX445342	JX445226	Skin
Chloropsis palawanensis	ZMUC105549	Palawan	JX445275	JX445395	JX445343	JX445227	Skin
Chloropsis sonnerati sonnerati	NRM568891	Java			JX445344	JX445229	Skin
Chloropsis sonnerati sonnerati	NRM570524	Java			JX445349	JX445230	Skin
Chloropsis sonnerati zosterops	ZMUC105557	Thailand			JX445348	JX445234	Skin
Chloropsis sonnerati zosterops	ZMUC105558	Sumatra			JX445351	JX445236	Skin
Chloropsis sonnerati zosterops	NRM570535	Borneo			JX445347	JX445233	Skin
Chloropsis sonnerati zosterops	MNHN1960856	Borneo	JX445277	JX445397	JX445346	JX445232	Skin
Chloropsis sonnerati zosterops	NRM570522	Malay Peninsula	JX445276	JX445396	JX445345	JX445231	Skin
Chloropsis sonnerati zosterops	ZMUC105559	SW Thailand			JX445350	JX445235	Skin
Chloropsis venusta	LSU0051	Sumatra	JX445278	JX445398	JX445352	JX445237	Blood
*Irena cyanogastra cyanogastra**	ZMUC116747	Luzon	JX445280	JX445400	JX445356	JX445242	Blood
*Irena cyanogastra cyanogastra**	ZMUC116748	Luzon	JX445281	JX445401	JX445357	JX445243	Blood
*Irena cyanogastra cyanogastra**	ZMUC119544	Luzon		JX445402	JX445358	JX445244	Blood
Irena cyanogastra ellae	ZMUC105592	Bohol	JX445279	JX445399	JX445354	JX445240	Skin

(*continued on next page*)

Table 1 (*continued*)

Taxa	Voucher number	Locality	GAPDH	ODC	ND3	Cyt-b	DNA source
Irena cyanogastra ellae	ZMUC105602	Dinagat			JX445355	JX445241	Skin
Irena cyanogastra hoogstraali	ZMUC105599	Mindanao				JX445239	Skin
Irena cyanogastra hoogstraali	ZMUC105600	Mindanao			JX445353	JX445238	Skin
Irena puella andamanica	ZMUC105881	Andaman			JX445363	JX445254	Skin
Irena puella andamanica	ZMUC105582	Andaman			JX445362	JX445253	Skin
Irena puella cinigera	NRM570548	Borneo			JX445359	JX445245	Skin
Irena puella malayensis	NRM570549	Malay Peninsula			JX445360	JX445246	Skin
Irena puella puella	NRM570551	Myanmar			JX445369	JX445248	Skin
Irena puella puella	NRM570552	N Thailand			JX445364	JX445256	Skin
Irena puella puella	NRM570554	S Thailand			JX445371	JX445250	Skin
Irena puella puella	NRM570555	S Vietnam			JX445373	JX445255	Skin
Irena puella puella	NRM570556	C Vietnam			JX445361	JX445252	Skin
Irena puella puella	ZMUC105583	Thailand			JX445370	JX445249	Skin
Irena puella ssp?	ZMUC124501	Captivity	JX445284	JX445405	JX445372	JX445251	Blood
Irena puella ssp?	ZMUC140789	Captivity	JX445283	JX445404	JX445368	JX445247	Blood
Irena puella turcosa	NRM570557	Java			JX445365	JX445257	Skin
Irena puella tweeddalei	ZMUC105588	Palawan			JX445367	JX445259	Skin
Irena puella tweeddalei	ZMUC105589	Palawan	JX445282	JX445403	JX445366	JX445258	Skin
Outgroup							
Passer montanus			AY336586	DQ785937	AY030164	EU325789	

Table 2
Primers used in this study.

Primer name	Locus	Primer sequence	References
Cytb-IreF1	Cytochrome-*b*	CCATACACTATACAGCAGACAC	This study
Cytb-IreF2	Cytochrome-*b*	CCCTAATAGCAACCGCATTCGT	This study
Cytb-IreF3	Cytochrome-*b*	CTCTACATTTCCTCCTCCCATT	This study
Cytb-RemizR1c	Cytochrome-*b*	TCAGAATGATATTTGTCCTCAGG	This study
Cytb-IreR2	Cytochrome-*b*	GGTTGTTTGATCCTGTTTCGTG	This study
Cytb-IreR3	Cytochrome-*b*	GGTTGGCTGGTGTGAAGTTTTC	This study
Cytb-IreR1b	Cytochrome-*b*	CATTTGGCCTCATGGTAGTACGT	This study
L14841	Cytochrome-*b*	CCATCCAACATCTCAGCATGATGAAA	Kocher et al. (1989)
H15915	Cytochrome-*b*	AACTGCAGTCATCTCCGGTTTACAAGAC	Edwards et al. (1991)
ND3-H11151	ND3	GACTGCGACAAAATCCCATTCCA	Chesser (1999)
ND3-L10755	ND3	GACTTCCAATCTTTAAAATCTGG	Chesser (1999)
ND3-ChlintF1	ND3	CCATTTTCAATCCGCTTCTTCCTAGT	This study
ND3-ChlintR1	ND3	AGGAGTAGGGCGATTTCTAGGTC	This study
ND3-ChlintF1b	ND3	CTAAACCCAGAGAAGAGTAATGAA	This study
ND3-Chl-coR1	ND3	TAGGTCGAACAGGAGAAATAAGAT	This study
ND3-Chl-fl-mR1	ND3	TCTAGGTCAAATAATAGGAATAAGAT	This study
ODintF2	ODC	CACTTAAGACTAGCAGGCTTCTTCTGGA	Irestedt et al. (2006)
ODintR3	ODC	CAAACACACAGCGGGCATCAGA	Irestedt et al. (2006)
ODintF1	ODC	ATGCCCGCTGTGTGTTTG	Irestedt et al. (2006)
ODintR4	ODC	CATATTGAAGCCAAGTTCAGCCTA	Irestedt et al. (2006)
OD6	ODC	GACTCCAAAGCAGTTTGTCGTCTCAGTGT	Allen and Omland (2003)
OD8r	ODC	TCTTCAGAGCCAGGGAAGCCACCACCAAT	Allen and Omland (2003)
G3P14b	GAPDH	AAGTCCACAACACGGTTGCTGTA	Fjeldså et al. (2003)
G3PintL1	GAPDH	GAACGACCATTTTGTCAAGCTGGTT	Fjeldså et al. (2003)

30 million generations for the individual gene partitions, and for 50 million generations for the combined data set, with trees sampled every 500th generation. The first one million trees were discarded as burn-in after checking for convergence. We used AWTY (Are We There Yet) (Nylander et al., 2008) to graphically assess convergence diagnostics.

Maximum Likelihood analyses were performed for 50 million generations for both the individual gene alignments and the concatenated alignment (with one global GTR+I+G) using GARLI 0.95 (Zwickl, 2006). Nodal support was evaluated with 100 non-parametric bootstrap pseudoreplicates (Felsenstein, 1985).

All phylogenetic analyses were replicated multiple times to ensure that we obtained the same topologies.

2.3. Molecular dating

To estimate the divergence times within Chloropseidae and Irenidae, we used BEAST v.1.5 (Drummond et al., 2002, 2006; Drummond and Rambaut, 2007). We assigned the best fitting model, as estimated by ModelTest 3.7 (Posada and Crandall, 2005) to each of the partitions. We assumed a Yule Speciation Process for the tree prior and an uncorrelated lognormal distribution for the molecular model (Drummond et al., 2006; Ho, 2007). We used default prior distributions for all other parameters and ran MCMC chains for 50 million generations. We used the program Tracer (Rambaut and Drummond, 2007) to assess convergence diagnostics. To obtain absolute divergence time estimates, we used the "2% rule" (Weir and Schluter, 2008) corresponding to 1% sequence divergence of the mitochondrial gene cyt-*b* per lineage per million years.

3. Results

We obtained GAPDH sequences for 25 individuals, ODC sequences for 32 individuals, and ND3 sequences and cyt-*b* sequences for 89 individuals. For some individuals, short gene

regions at the ends are lacking; with those missing base pairs taken into account, sequences varied between 353–373 bp for GAPDH and 590–666 bp for ODC. Additionally, we sequenced the entire ND3 and part of the tRNA flanking regions (395 bp) and part of cytochrome-*b* (583 bp). The concatenated alignment of all four gene fragments consisted of 2017 aligned nucleotide positions. We found no stop codons or indels in the coding gene sequences that would suggest the presence of pseudogenes. The *a priori* selection of nucleotide substitution models suggested the best models to be TVM+I+G for cyt-*b*, TRN+I+G for ND3, TVM+G for ODC, and HKY+G for G3P.

Bayesian analyses of the individual genes (Figs. 2–5) were overall in good agreement with no conflicting relationships for well-supported nodes. The nuclear introns, however, provided little resolution and thus the species tree is largely driven by the mitochondrial data. The Bayesian and Maximum Likelihood analyses of the concatenated dataset (Fig. 6) resulted in congruent and highly supported trees (presented as a 50% majority rule consensus obtained from the Bayesian analysis, Fig. 6) where nearly all clades at the species level received bootstrap values higher than 70 and posterior probabilities higher than 0.95.

Applying the 2% rule (Weir and Schluter, 2008) to our mitochondrial dataset (ND3 and cyt-*b*) produced a chronogram (Fig. 7) that suggests that Chloropseidae and Irenidae diverged in the late Miocene some 10 Ma and that diversification leading to extant Chloropseidae and Irenidae species started in the late Miocene (6 Ma) and in the Pliocene (3 Ma), respectively. At the species level, for *Chloropsis* there are eight deep branches that separated in the early Pliocene and *C. venusta* represents the oldest lineage that diverged in the late Miocene.

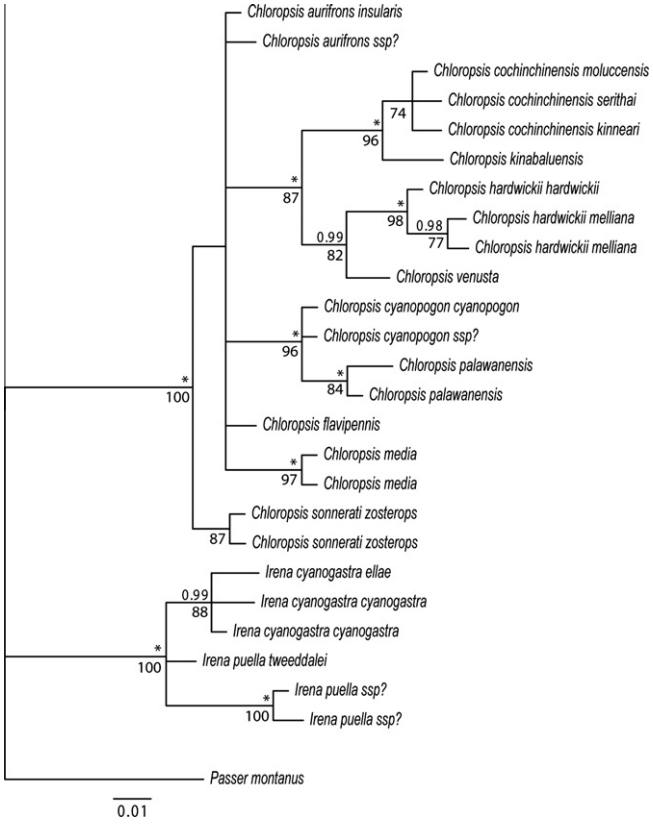

Fig. 2. The 50% majority rule consensus tree of Chloropseidae and Irenidae obtained from the Bayesian analysis of GAPDH. Posterior probabilities ⩾0.95 (*denotes a posterior probability = 1.00) and bootstrap values (from the ML analysis) ⩾70 are shown.

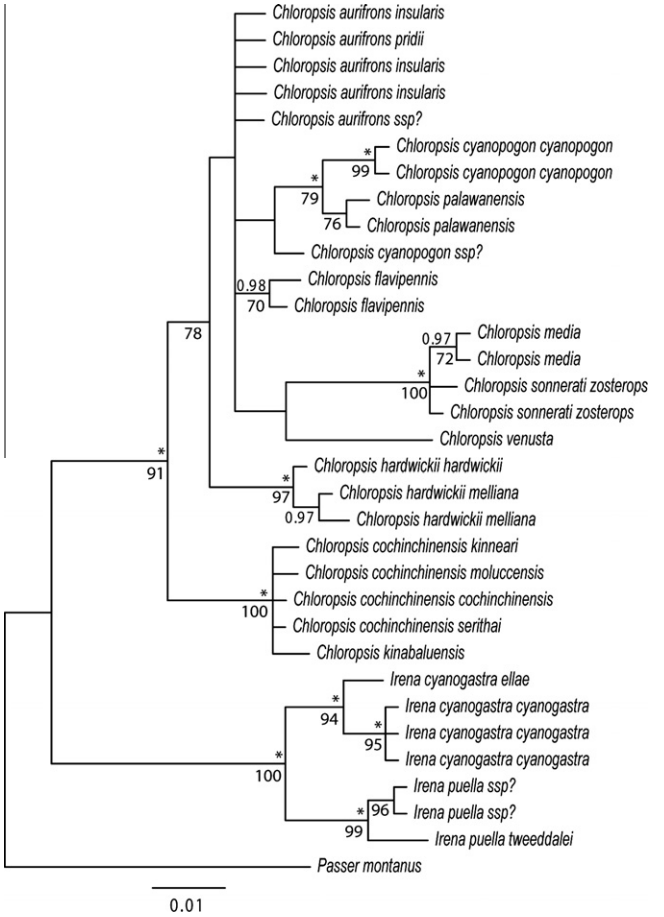

Fig. 3. The 50% majority rule consensus tree of Chloropseidae and Irenidae obtained from the Bayesian analysis of ODC. Posterior probabilities ⩾0.95 (*denotes a posterior probability = 1.00) and bootstrap values (from the ML analysis) ⩾70 are shown.

The classification of species and subspecies, which has hitherto been based only on measurements and plumage characters, is overall in good agreement with the molecular phylogeny, although we found several taxa ranked as subspecies by Wells (2005a,b) to be genetically very distinct (Table 3) from the nominate subspecies. This applies to *Chloropsis cochinchinensis cochinchinensis* and *Chloropsis cyanopogon*. The latter is paraphyletic with *Chloropsis palawanensis*, and comprises two distinct clades (*C. cyanopogon cyanopogon* and *C. cyanopogon septentrionalis*), which are also diagnostically different by plumage traits. *Chloropsis hardwickii* forms two clades, which are also phenotypically distinct. Unfortunately, we lack molecular data from *C. h. lazulina* endemic to Hainan. Also *C. aurifrons* forms two clades, which are well defined phenotypically, but here we lack molecular data from *C. a. frontalis* from India. Three species recognised by Wells (2005a) (*C. jerdoni, C. flavocinta* and *C. aurifrons media*), are all phenotypically diagnosable, in good agreement with the molecular phylogeny. Furthermore, *C. palawanensis*, *C. venusta* and *C. sonnerati* form distinct clades, but the two described subspecies of the latter are not reciprocally monophyletic.

The molecular phylogeny further divides *I. cyanogastra* in three clades (*I. c. cyanogastra, I. c. ellae* and *I. c. hoogstraali*), which are clearly phenotypically diagnosable. However, we lack molecular data from *I. c. melanochlamys* from the island of Basilan. There are three distinct clades within *I. puella* (*I. p. crinigera, I. p. andamanica*, and *I. p. tweeddalei*), morphologically diagnosable. The rest of the *I. puella* complex forms a well-supported clade, but unfortunately we lack samples from southern India.

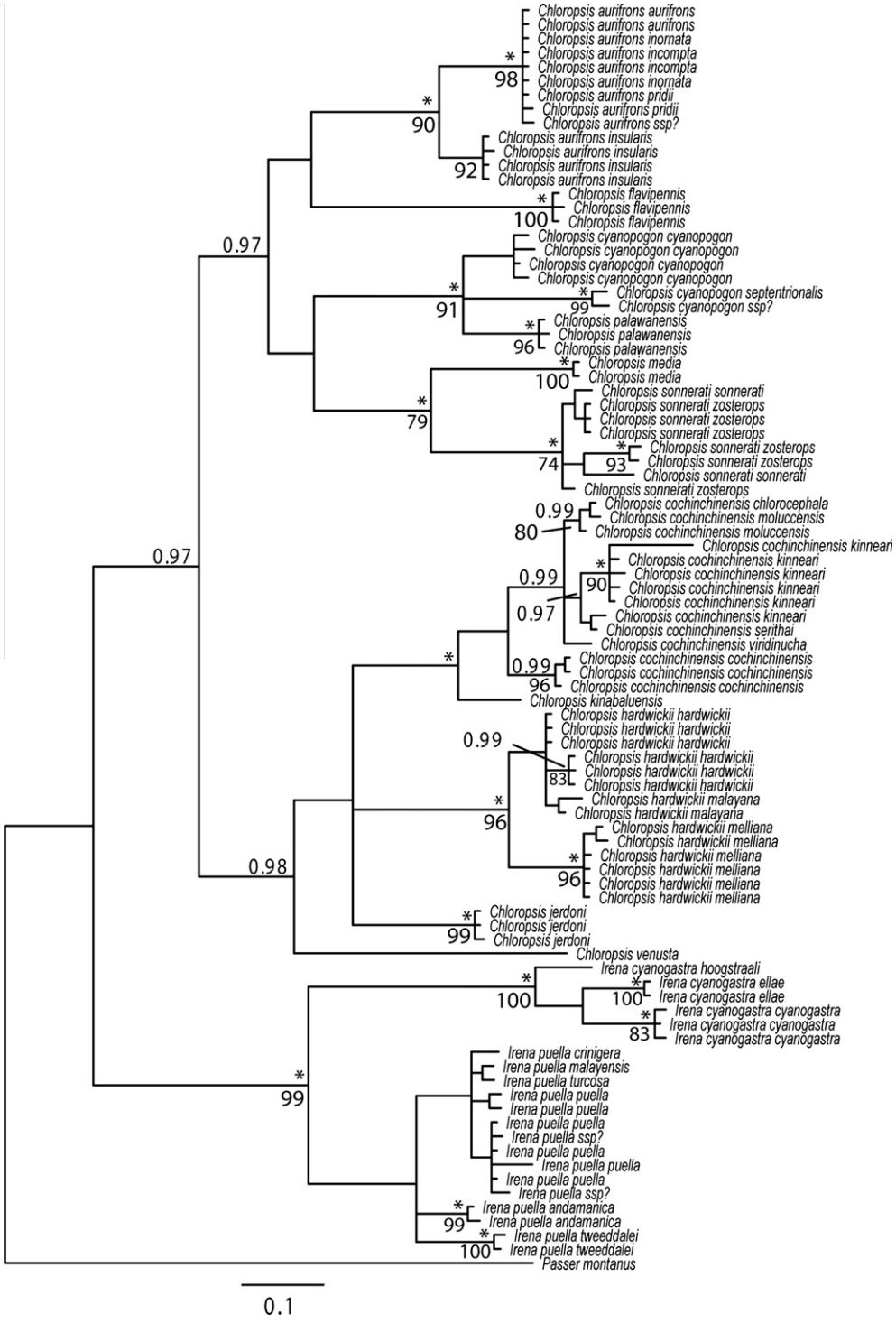

Fig. 4. The 50% majority rule consensus tree of Chloropseidae and Irenidae obtained from the Bayesian analysis of ND3. Posterior probabilities ⩾0.95 (*denotes a posterior probability = 1.00) and bootstrap values (from the ML analysis) ⩾70 are shown.

Based on morphology, Wells (2005a) suggested that *C. jerdoni* and *C. kinabaluensis* (previously referred to as *C. cochinchinensis flavocincta*) should be recognised as separate species, forming a superspecies together with *C. palawanensis* and *C. cochinchinensis*. Wells (2005a) also suggested species rank for *C. aurifrons media*. Our phylogeny supports recognising *C. kinabaluensis*, *C. media* and *C. jerdoni* as distinct species (Wells 2005a). The superspecies classification by Wells (2005a) is generally rejected by the molecular data. Instead our analyses suggest a clade consisting of *C. aurifrons*, *C. sonnerati* and *C. media*, and another clade for *C. cyanopogon* and *C. palawanensis*. These two monophyletic "superspecies" together form a highly supported clade (PP = 1 and bootstrap = 100), which also includes *C. flavipennis*, although the relationships between the three clades are unresolved. Also, the well-supported *C. cochinchinensis* complex and *C. kinabaluensis* and *C. jerdoni* form a clade, though again poorly supported. The *C. hardwickii* complex forms two clades, which are highly supported, and together form a clade with *C. venusta*.

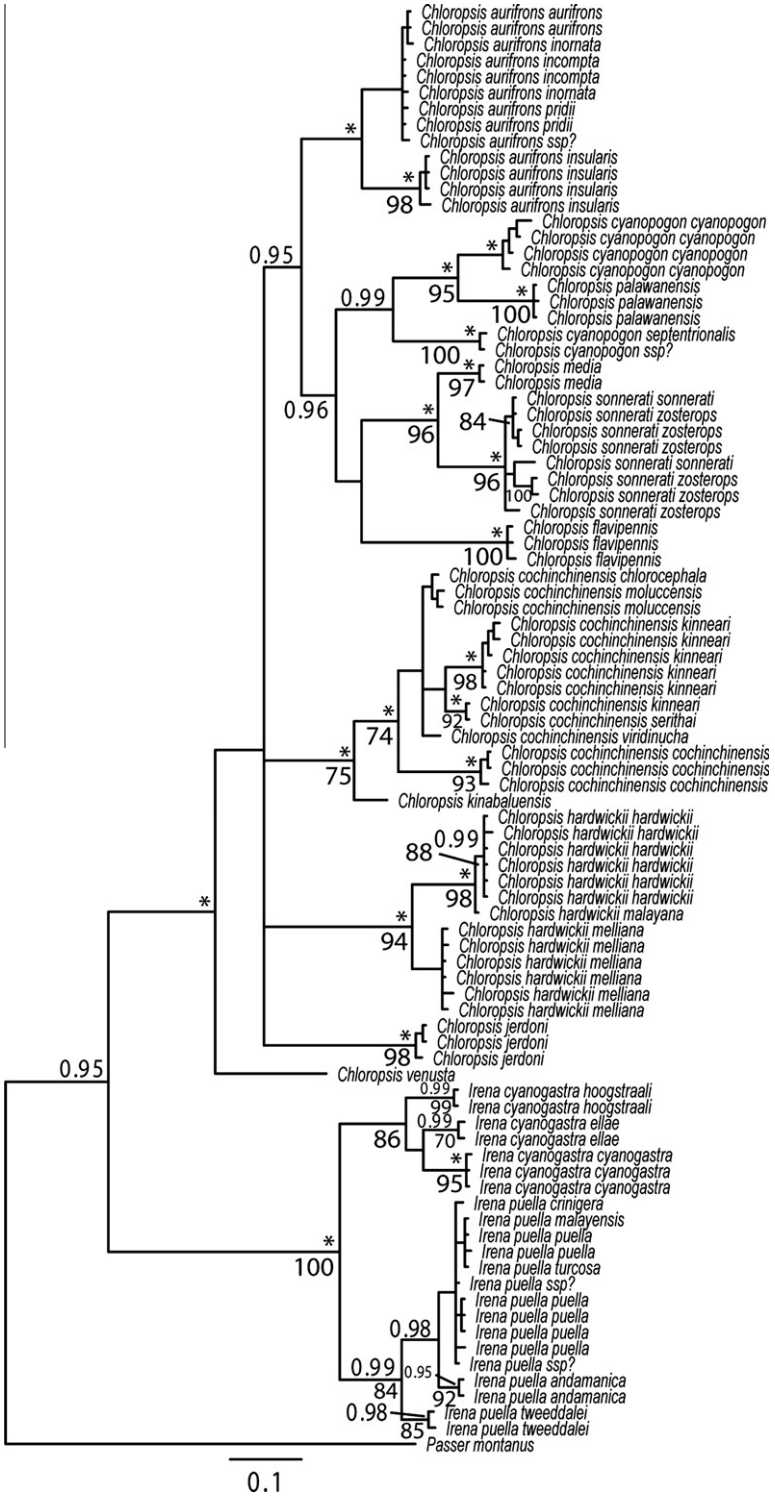

Fig. 5. The 50% majority rule consensus tree obtained of Chloropseidae and Irenidae from the Bayesian analysis of cyt-*b*. Posterior probabilities ⩾0.95 (*denotes a posterior probability = 1.00) and bootstrap values (from the ML analysis) ⩾70 are shown.

In *Chloropsis*, plumages, where males lack the facial masks, are most likely a result of convergent evolution, as *C. palawanensis* and *C. kinabaluensis* are in separate clades. Likewise, the plumage pattern where females have masks also seems to reflect convergent evolution because *C. kinabaluensis, C. aurifrons and C. venusta*, are in separate clades. Populations of *Irena* with long upper tail coverts are paraphyletic, nested among eastern and western subspecies with short upper tail coverts.

4. Discussion

4.1. Systematics and taxonomy

The topology as well as marked sequence divergences between populations suggests that some taxa currently ranked as subspecies may represent distinct lineages that are better ranked as species. We propose a taxonomic revision of Chloropseidae and

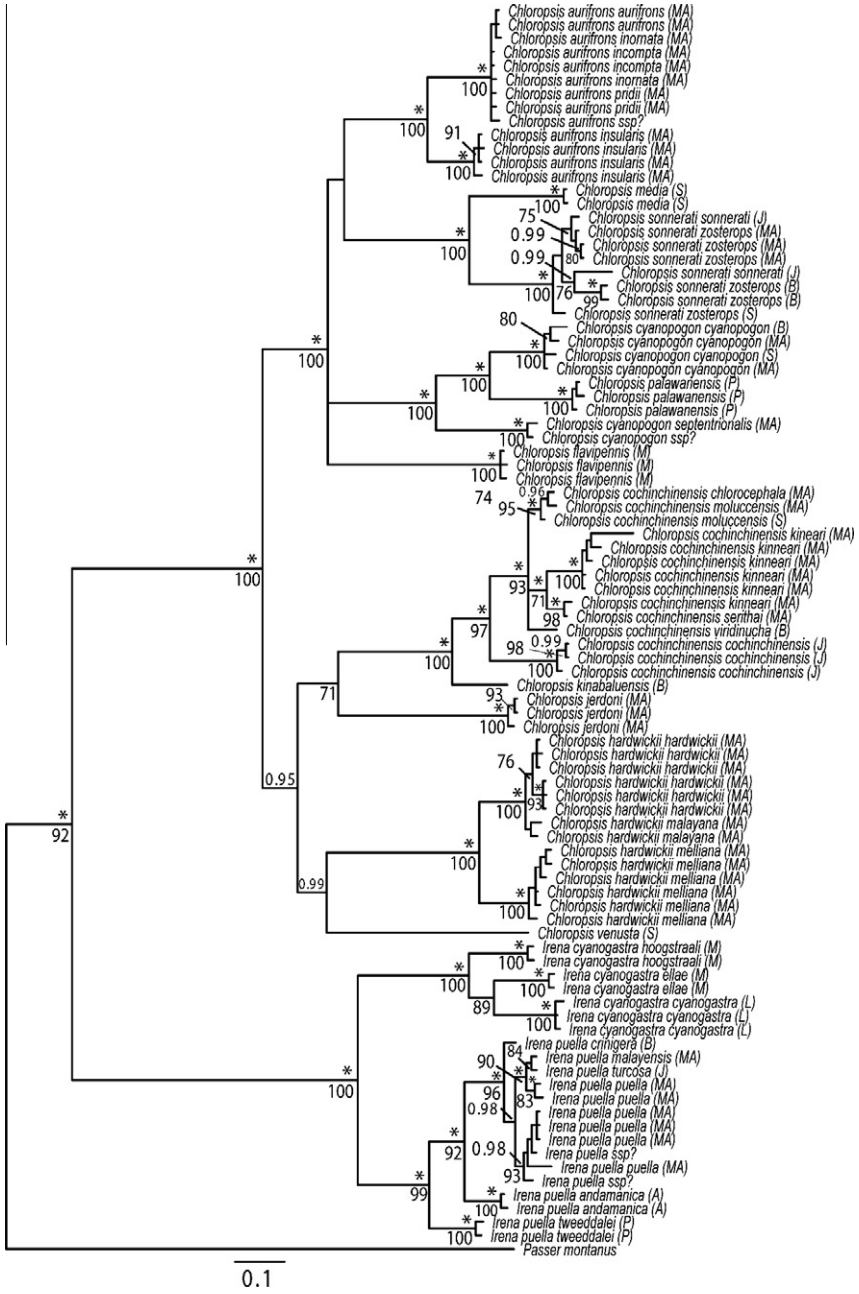

Fig. 6. The 50% majority rule consensus tree of Chloropseidae and Irenidae obtained from the Bayesian analysis of two nuclear introns (ODC and GAPDH) and two mitochondrial (cyt-*b* and ND3) genes. Posterior probabilities $\geqslant 0.95$ (*denotes a posterior probability = 1.00) and bootstrap values (from the ML analysis) $\geqslant 70$ are shown. The present distribution according to seven recognised geographical regions is indicated after the taxon name: MA: mainland Asia, S: Sumatra, J: Jawa, A: Andaman islands, B: Borneo, P: Palawan, L: Luzon Shelf, M: Mindanao Shelf.

Irenidae raising the species numbers of the two families from 11 to 15 and from two to six, respectively (Fig. 7 and Table 3). We acknowledge that these species level recommendations rely on a result that is largely driven by the mitochondrial data.

Chloropsis aurifrons forms two distinct clades that differ by 4.23% in mtDNA (uncorrected pairwise distances). *C. a. insularis* occurs in southwest India and Sri Lanka and the other members of *C. aurifrons* occur in northern India and Indochina. Plumage characters of violet-blue within the mask and lack of yellow bordering the bib, and variation in body size also support recognising *C. a. insularis* as a distinct species.

Chloropsis cyanopogon septentrionalis from southern Myanmar, southwest Thailand and the north Malay Penninsula and *C. c. cyanopogon* from Borneo, Sumatra and the south Malay Peninsula are paraphyletic with *C. palawanensis*, from which they differ by 6.90% mtDNA and 7.18% mtDNA, respectively. *C. c. cyanopogon* and *C. c. septentrionalis* differ by 7.43% in mtDNA and they are clearly diagnosable by size and by the clear yellow border of the black mask in *C. c. septentionalis* males (Wells 2005a). Thus, we propose that *C. c. cyanopogon* and *C. c. septentrionalis* should be treated as separate species.

We also suggest species rank for *Chloropsis cochinchinensis cochinchinensis* endemic to Java and the only form of the *C. cochinchinensis* complex on that island. It differs by 5.56% mtDNA from other members of the *C. cochinchinensis* complex and females have distinct turquoise-green chin and throat.

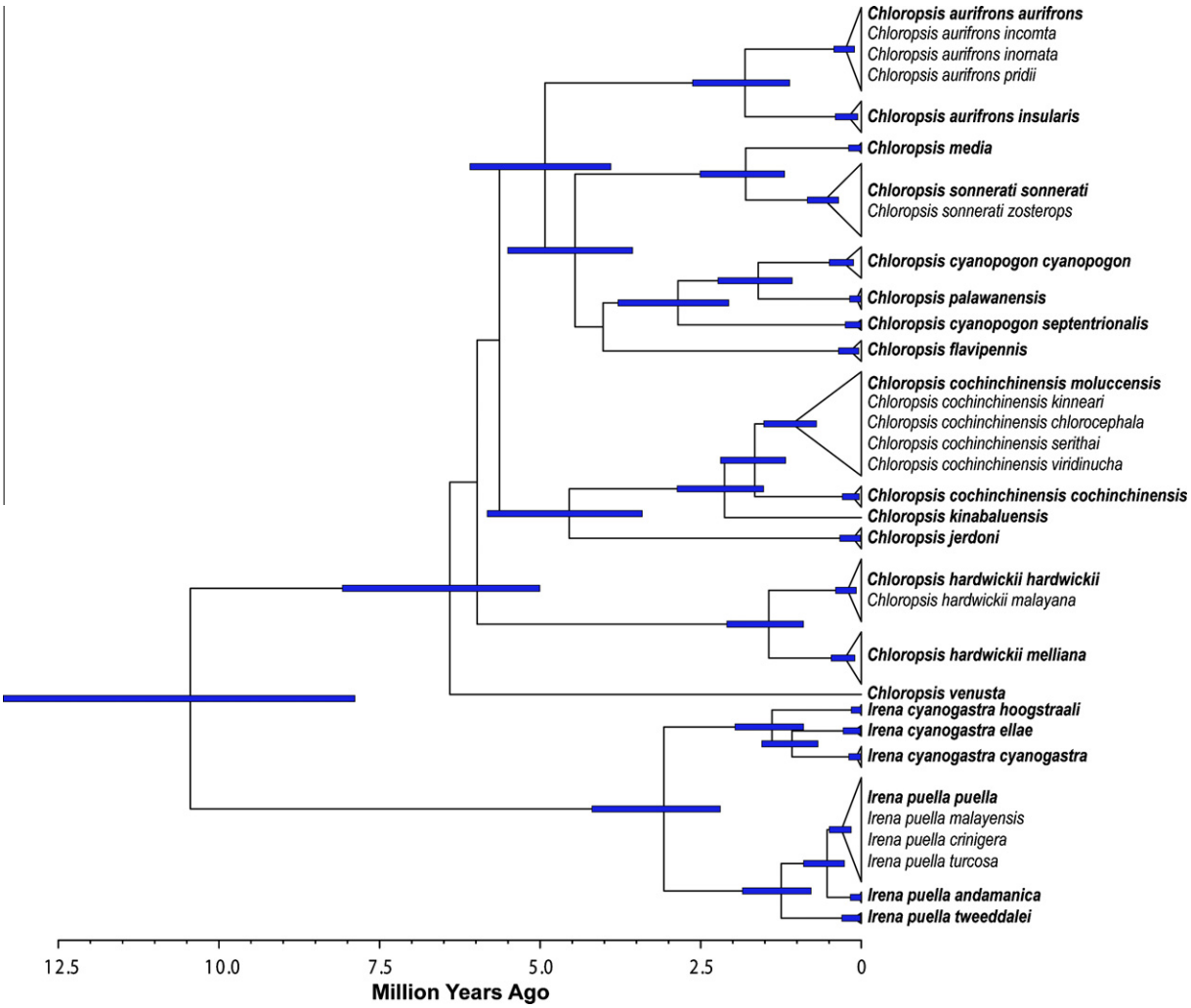

Fig. 7. Chronogram based on the BEAST analysis of Chloropseidae and Irenidae indicating the proposed number of species (with the species names and subspecies names that have priority in bold) for Chloropseidae (15) and Irenidae (six) based on the present study. A rate of 1% sequence divergence per lineage per million years (2% rule) for the mitochondrial DNA was used to obtain a rough estimate of absolute divergence times (see main text for details). Node bars indicate the 95% highest posterior density (HPD) intervals.

Chloropsis hardwickii forms two distinct clades that are partially sympatric in Asia and differ by 4.01% mtDNA. Plumage characters also support this division because *C. h. melliana* represents one plumage type with dark blue breast and dark blue shoulders while *C. h. hardwickii* and *C. h. malayana* represent a different plumage type with black breast and 'shoulders' in brilliant turquoise, and with blue-grey cap in *C. h. malayana* instead of bronzy (Wells 2005a).

The molecular phylogeny as well as plumage characters support species rank (as already proposed by Wells 2005a) for *Chloropsis media*, which was considered a subspecies of *C. aurifrons*, although we found it to be most closely related to *C. sonnerati*. We also suggest species rank for *C. kinabaluensis* and *C. jerdoni*, which were historically treated as subspecies of *C. cochinchinensis* (Dickinson, 2003). The divergence of *C. jerdoni* from the *C. cochinchinensis* complex including *C. kinabaluensis* is 9.93% mtDNA. The divergence of *C. kinabaluensis* from *C. cochinchinensis* is 4.94% mtDNA, and the divergence of *C. media* from *C. sonnerati* is 6.54% mtDNA.

It is noteworthy that *Chloropsis venusta* diverged in the late Miocene some 6.4 Mya. It is monotypic and the smallest species in the family with a distinct plumage pattern having a unique blue face and throat, and it occurs in the mountains 600–1500 m above sea level (Wells 2005a). Another Sumatra endemic, *C. media*, which lives in the submontane zone of the same geographical range, was long considered conspecific with *C. aurifrons*, but differs in having yellow (not golden) forehead and a more narrow violet jawline. Furthermore, it is dichromatic and our molecular phylogeny places it as sister to *C. sonnerati*, which also lives in Sumatra but prefers lower montane forest up to 1100 m. Together with *C. cyanopogon* and *C. cochinchinensis*, these five co-occurring Sumatran species represent different clades in the phylogeny.

For Irenidae, the molecular phylogeny supports three distinct clades within *Irena cyanogastra*, (*I. c. cyanogastra*, *I. c. ellae* and *I. c. hoogstraali*), which differ by 3.88–4.44% mtDNA. As they are segregated in three different regions of the Philippines, and vary in the extent of black versus indigo plumage on upperparts and underparts (Wells 2005a), we propose species status for these three subspecies. Within *I. puella* there are three distinct clades, which also differ in plumage, and we suggest elevation to species rank also for these. *I. p. tweeddalei* from Palawan differs from other members of Irena puella by 4.33% mtDNA and is distinct in having brilliant turquoise-blue plumage colours rather than violet-tinted royal blue. The Andaman islands subspecies *andamanica* differs from other populations by 3.11% mtDNA and in having a broader and heavier bill (Wells, 2005). The divergence between *I. p. crinigera* and a rather tight-knit group of *I. p. puella*, *I. p. malayensis* and *I. p. turcosa*,

Table 3
Overview of proposed elevation from subspecies to species rank including information on genetic divergence and diagnostic plumage characters.

Proposed split	Split from	% uncorrected pairwise distances (mtDNA)	Distribution	Diagnosable characters
Chloropsis aurifrons insularis	All other members of *Chloropsis aurifrons.*	4.23 % between *insularis* and other members of *C. aurifrons*	SW India, Sri Lanka	Similar in plumage to *Chloropsis aurifrons frontalis* with no yellow band around the black mask and fully black chin and throat and orange on forhead only to mideye level, but differ in smaller size
Chloropsis cyanopogon septentrionalis	*Chloropsis cyanopogon cyanopogon*, paraphyletic	7.18 % between *septentrionalis* and *cyanopogon*, also paraphyletic	S Myanmar, SW Thailand and N Malay Penninsula	Diagnosable from *Chloropsis cyanopogon cyanopogon* by smaller size and by the clear yellow border of the black mask in males
Chloropsis cyanopogon septentrionalis	All other members of *Chloropsis cochinchinensis*, the name for this group should be *moluccensis*	5.56 % between *cochinchinensis* and other members of *cochinchinensis*	Java	Females have turquoise-green chin and throat
Chloropsis hardwickii melliana	All other members of *Chloropsis hardwickii*	4.01 % between *melliana* and other members of *hardwickii*	S China, N and C Vietnam	Males have dark blue breast and dark blue "shoulders", females have entirely green underparts
Irena cyanogastra cyanogastra	All subspecies of *Irena cyanogastra* would become separate species but we miss *Irena cyanogastra melanochlamys*	3.88 % between *cyanogastra* and *ellae*	Luzon, Polillo and Cantanduanes	Neck, scapulars and whole upper body deep indigo-blue and colour petering out on upper neck
Irena cyanogastra ellae	All subspecies of *Irena cyanogastra* would become separate species but we miss *Irena cyanogastra melanochlamys*	3.88 % between *ellae* and *cyanogastra*	Bohol, Leyte and Samar	Upper neck, mantle and scapulars black
Irena cyanogastra hoogstraali	All subspecies of *Irena cyanogastra* would become separate species but we miss *Irena cyanogastra melanochlamys*	4.44 % between *hoogstaali* and *ellae*/*cyanogastra*	Mindanao and Dinagat	Smaller, black below only down to breast
Irena puella andamanica	All other members of *Irena puella*	3.11 % between *andamanica* and *puella*	Andaman and Nicobar Islands	Heavy bill, broader and marginally deeper than in any other subspecies
Irena puella tweeddalei	All other members of *Irena puella*	4.33 % between *tweeddalei* and *andamanica/puella*	Palawan and nearby islands	Males have blue areas cold azure to turquoise-blue (rather than violet-tinted royal blue)

is minimal and took place in the late Pleistocene. *I. p. crinigera* is endemic to Sumatra and represents the smallest of the fairy-bluebirds, having the tail-coverts completely encasing its tail.

Our data demonstrate that *Choropsis* consists of 15 species with somewhat overlapping distributions, indicating that speciation within Chloropseidae has allowed for sufficient time after speciation for full compatibility to evolve. It is remarkable that Sumatra hosts five species of *Chloropsis*, of which the endemic *C. venusta* diverged in the late Miocene some 6.4 Mya. These five species are not each others closest relatives, so this is not a local radiation but rather a case of high persistence of ancient lineages.

Our data suggest that the Irenidae comprises six distinct species that are genetically and morphologically less differentiated than those in Chloropseidae, perhaps reflecting their greater ability to disperse over disturbed land. Studies of small fruit bats (*Chiroptera*, Pteropodidae) also indicate that species associated with disturbed habitats show more genetic variation within populations than species associated with primary rain forest (Heaney et al., 2005). It is possible that members of Irenidae that often fly over open habitats maintain a higher gene flow connectivity between populations and therefore show less differentiation than members of Chloropseidae, which generally avoid flying out from the forest canopy.

4.2. Plumage variation

The two monochromatic species, *Chloropsis palawanensis* and *C. flavipennis*, in which males have female-like plumages with no mask, do not form a monophyletic clade and have probably lost dichromatism independently after their isolation on the Philippine islands and Palawan. This also applies to *Irena cyanogastra cyanogastra*, suggesting that monochromatism may be related to geographic isolation, as seen in many island birds (see, e.g., Mayr, 1942, for *Petroica multicolour*). We may assume that the black mask tends to be reinforced wherever there is sympatry and there may be a tendency for interspecific differences in the amount of yellow contrasting with the mask. Monochromatic species in which both sexes have facial masks are *Chloropsis kinabaluensis*, *Chloropsis aurifrons* and to a lesser degree also *Chloropsis venusta*, which are unrelated and therefore represent independent cases. Also many other studies now suggest a high incidence of parallelism in plumage evolution (e.g., Jønsson et al., 2010, for *Pericrocotus* minivets; Jones and Kennedy, 2008, for *Turdus poliocephalus*; Martens et al., 2006, for *Periparus ater*; García-Moreno and Fjeldså, 1999, for *Atlapetes*; Ödeen and Björklund, 2003, for *Motacilla flava*). At the same time, however, plumage characters like dimorphism are prone to high levels of homoplasy (Omland and Lanyon, 2000).

We suggest that dimorphism is primitive for Irenidae because ancestral monochromatism in Philippine taxa would require independent loss of the trait in both *Chloropsis* and *Irena puella*.

Long tail-coverts are a morphological character of *Irena puella turcosa* from Java, *I. p. crinigera* from Sumatra and Borneo, and *I. p. malayensis* from the southern Malay Peninsula. Other subspecies of *Irena puella* with normal (short) tail-coverts occur to the west (*I. p. puella* and *I. p. andamanica*) and to the north (*I. p. tweedalei* from Palawan). This morphological leapfrog pattern further emphasizes the complexity of this group.

4.3. Biogeography

Most taxa of Chloropseidae and Irenidae are distributed in tropical Asia and the adjacent Sundaland (Fig. 1). Based on this distribution and our divergence time estimates, it is most likely that the origin of Irenidae and Chloropseidae was on the Asian mainland at the time (late Miocene 10–11 Mya), when this included much of the present Sunda Shelf (see Hall, 1998). No species have been able to cross Wallace's line and colonise islands east of Java, where deep sea trenches separate Bali from Lombok, and Borneo and the Philippines from Sulawesi (Bintanja et al., 2005; Hall, 1998, 2002).

The colonisation of the Philippine archipelago is particularly interesting, since it arose from oceanic crust in the volcanic island arcs out in the Pacific, and slowly moved west to its present position where finally the northern and southern island groups were pieced together (Hall, 1998). These islands have been isolated by deep sea from the Sunda Shelf and from other island systems throughout their history.

Palawan Island has a different history, as this microplate broke from the Asian mainland and drifted south until it collided with the Philippine mobile belt in the early Miocene (20–16 Ma), resulting in uplift of some parts of the microplate (Hall, 2002; Yumul et al., 2005). In the late Miocene (10 Mya) Palawan came into close proximity with Borneo (Hall, 2002), and southern Palawan may have been uplifted above sea level around that time. Palawan was also periodically connected to Borneo during low sea levels in the Pleistocene, and recent studies indicate that Palawan is best viewed as having had a young and an old connection with the Sunda Shelf (Hall, 2002).

The oceanic Philippine archipelago was colonised by *Irena cyanogastra* in the Pleistocene and by *Chloropsis flavipennis* in the Pliocene. It is possible that these two taxa colonised the Philippines from Borneo across the Sulu Sea because *I. c. melanochlamys* (not included in our study but expected to belong within the *Irena cyanogastra* complex) occurs on the island of Basilan in the Sulu archipelago, and because no members of *I. cyanogastra* are part of the present fauna of Palawan. This is in line with a recent study on Philippine Bulbuls (Oliveros and Moyle, 2010).

Although many terrestrial vertebrate taxa are shared between Palawan and the Sunda Shelf, an increasing number of species and populations that occur on Palawan are now recognised as close relatives of lineages from the oceanic Philippines (*Cyrtodactylus* geckos, Siler et al., 2010 and *Crocidura* shrews, Esselstyn et al., 2009, 2010), which may indicate that Palawan has acted as a stepping-stone for colonisation of the oceanic Philippines (Esselstyn et al., 2009, 2010). In our study, however, we find that Palawan endemics *Chloropsis palawanensis* and *Irena puella tweeddalei* are closely related to taxa that occur on the Greater Sunda islands and on the Asian mainland. *C. palawanensis* and *I. p. tweeddalei* colonised Palawan in the early Pleistocene (1.3–1.6 Mya), during periods of low sea levels when the Sunda Shelf, including Palawan, was exposed repeatedly as dry land (Esselstyn et al., 2009, 2010).

Irena cyanogastra cyanogastra occurs in the northern Philippines and diverged from its southern Philippine sister species *I. c. ellae* about 1 Mya, and *I. c. hoogstralii* about 1.4 Mya, indicative of a south to north dispersal. During low sea levels in the late Pleistocene, Luzon and the nearby islands Cantanduanes and Polillo coalesced into Greater Luzon and Leyte, Bohol and Mindanao coalesced into Greater Mindanao (Fairbanks, 1989; Siddall et al., 2003). *I. c. cyanogastra* probably dispersed onwards to nearby smaller islands. The other two subspecies of *I. c.* (data missing on the fourth subspecies *I. c. melanochlamys*, endemic to Basilan) that occur in the southern islands are not co-occurring on any islands. Today *I. c. ellae* occurs on Samar, Leyte and Bohol and *I. c. hoogstraali* occurs on Dinagat and Mindanao islands.

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