Influences of oceanic islands and the Pleistocene on the biogeography and evolution of two groups of Australasian parrots (Aves: Psittaciformes: *Eclectus roratus, Trichoglossus haematodus* complex). Rapid evolution and implications for taxonomy and conservation

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ABSTRACT

The Australasian region is a centre of biodiversity and endemism, mainly based on the tropical climate in combination with the large amount of islands. During the Pleistocene, islands of the Sahul Shelf (Australia, New Guinea, Aru Islands) had been part of the same land mass, while islands within the Wallacea (Lesser Sunda Islands, Moluccas, Sulawesi etc.) remained isolated. We investigated biogeographical avian diversification patterns of two species complexes across the Wallacea and the Sahul Shelf: the Eclectus Parrot *Eclectus roratus* Wagler, 1832, and the Rainbow Lorikeet *Trichoglossus haematodus* Linnaeus, 1771. Both species are represented by a large number of described geographical subspecies. We used mitochondrial cytochrome *b* (cyt *b*) sequences for phylogenetic and network analysis to detect biogeographic roles of islands and avian diversification patterns. The number of threatened taxa in this region is increasing rapidly and there is an urgent need for (sub-)species conservation in this region. Our study provides first genetic evidence for treating several island taxa as distinct species.

In both species complexes similar genetic patterns were detected. Genetic diversification was higher across the islands of the Wallacea than across the islands of the Sahul Shelf. Divergence in *E. roratus* can be dated back about 1.38 million years ago, whereas in the younger *T. haematodus* it was 0.80 million years ago. Long distance dispersal was the most likely event for distribution patterns across the Wallacea and Sahul Shelf. The geographic origin of the species-complex *Eclectus roratus* spp. is supposed to be Wallacean, but for the species-complex *Trichoglossus haematodus* spp. it is supposed to be non-Wallacean. *Trichoglossus euteles*, so far considered a distinct species, clearly belongs to the *Trichoglossus-haematodus*-complex. The only case of sympatry in the complex is the distribution of *T. (h.) euteles* and *T. h. capistratus* on Timor, which means a rapid evolution from one ancestor into two distinct species within only 800,000 years. For all other taxa a Checkerboard distribution pattern is present. In this complex, 8 taxa are already treated as separate species (del Hoyo et al. 2014). Based on genetic evidence, the following populations are supported to represent phylogenetic units: (1) N New Guinea (*haematodus*) incl. Biak (*rosenbergii*), Bismarck Archipelago (*massena*), and New Caledonia (*deplanchii*); (2) Flores (*weberi*); (3) E Australia (*moluccanus*) incl. Aru Islands (*nigrogularis*) and S New Guinea (*caeruleiceps*); (4) N Australia (*rubritorquis*); (5) Timor 1st lineage (*capistratus*) incl. Sumba (*fortis*); (6) Bali and Lombok (*mitchellii*); (7) Sumbawa (*forsteni*); (8) Timor 2nd lineage (*euteles*). Those 8 phylogenetic units are not identical to the 8 species listed by del Hoyo et al. (2014). Several populations on smaller islands are under decline, a separate species status may lead to a higher conservation status in both species complexes, which are currently listed as "Least Concern". *Eclectus roratus* is currently treated as monospecific. Based on genetic evidence, the following populations are suggested being treated as valid species: (1) Sumba (*Eclectus cornelia*), (2) Tanimbar Islands (*E. riedeli*), (3) Moluccas (*E. roratus*), and (4) New Guinea (*E. polychloros* incl. Aru Islands (*E. aruensis*), and Solomon Island (*E. solomonensis*).

KEYWORDS

avifauna; Checkerboard distribution; vicariance; dispersal; island biogeography; geographic isolation; Indonesia; Loriidae; population genetics; Psittacidae

INTRODUCTION

Geological background and Pleistocene influence on Australasia

The Indo-Malayan or Australasian region underwent several major geological periods, a good overview is given in Hall (2002). New Guinea collided with the East Philippines-Halmahera system 25 Ma, resulting in a rotation of the Philippine Sea Plate. Since 25 Ma the Pacific Plate and Australia are moving, causing rotations and sending microcontinental fragments to SE Asia. About 5 Ma boundaries and plate motions changed again. The region was and still is changing at a rapid rate based on plate tectonics and volcanic activity. A complex geological pattern is observed in Sulawesi. While West Sulawesi originates from the Sunda Shelf in SE Asia, East Sulawesi originates from the Australian plate; both merged

in the late Miocene. Moreover, the Lesser Sunda Islands are of different origin and its current formation became part of the Wallacea during the past 0-15 million years (Hall 2002).

The Australasian region includes Australia, New Zealand, New Guinea and the Wallacea, see Figure 1. The region is a hotspot of biodiversity and endemism (Marsden & Fielding 1999; Carstensen et al. 2012). The Wallacea is a biogeographic region including the Lesser Sunda Islands, Sulawesi, and the Moluccas, it is located between the Orientalis (S Asia) and the Australis (Australia, New Guinea, and New Zealand). The Wallacea is defined as a transition zone between the Indomalayan and the Australian fauna using Wallace's line (birds) as the western border and Lydekker's line (mammals) as the eastern border (Lydekker 1896; Newton 2003; Wallace 1876), see

Figure 1. Pleistocene sea level changes had a strong influence on the shoreline of Australasia (Figure 1). When glaciations occurred in the northern hemisphere, sea levels were usually low, whereas a rise in sea levels occurred during warm periods. During the last glacial maximum (18,000 years BP), with a sea level of 120 to 130 m below the current shoreline, Australia, New Guinea and the Aru archipelago were part of the same land mass of the Sahul Shelf (Lavering 1993; Voris 2000). The climate of N Australia was drier than today, leading to an increase of grassland replacing eucalypt forests (Van der Kaars 1991).

Avifauna of the Wallacea

In general, 17% of all land bird species occur on islands, but the land birds of Australasia hold the highest proportion of island
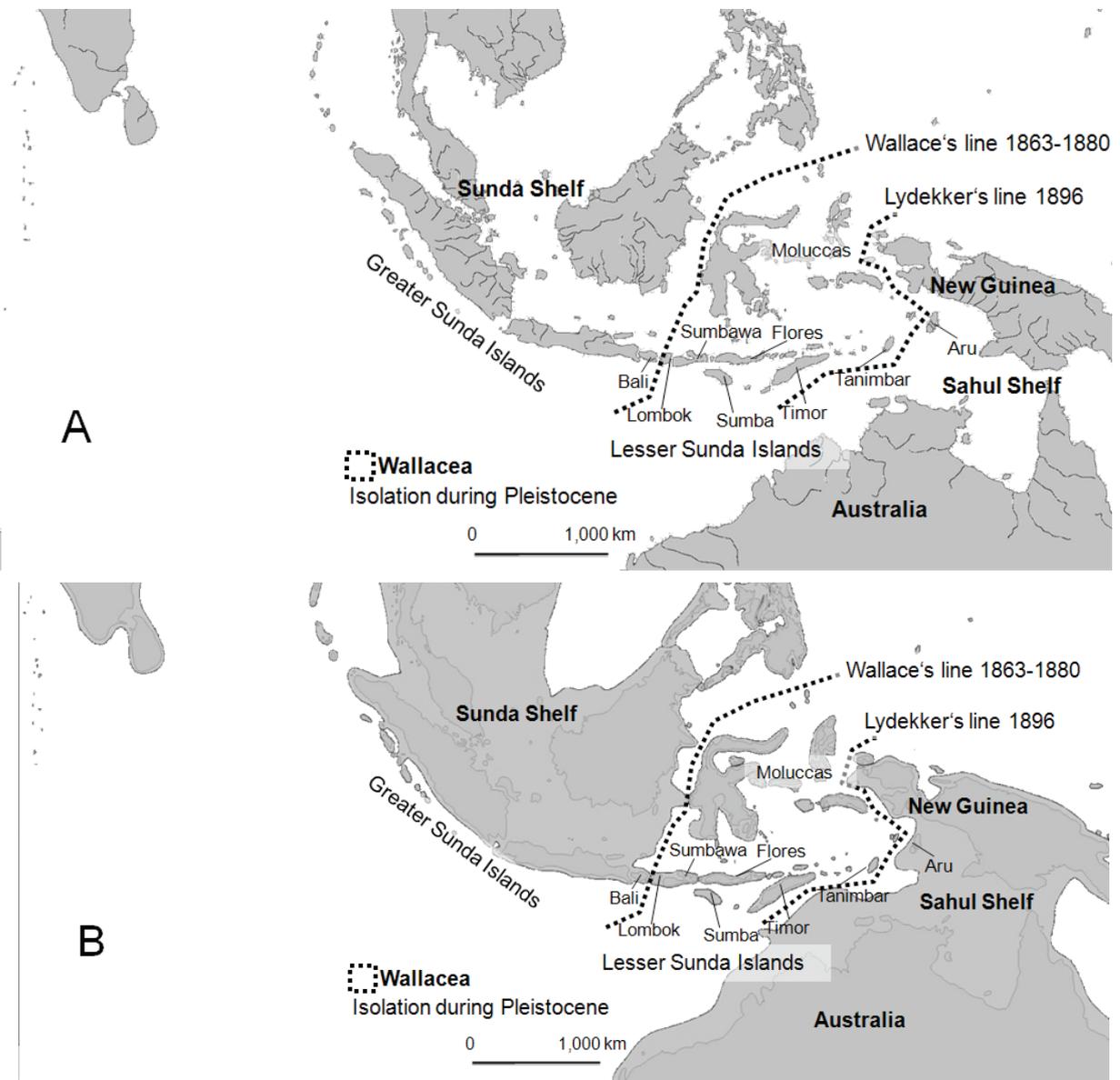
Figure 1. Australasian region including the Wallacea. Regions shaded in grey represent land mass, white regions represent sea. A: current sea level; B: sea level of 120 m below the current shoreline (18,000 years BP). The islands of the Wallacea (shape) remained isolated both from the Sunda and Sahul Shelf during the Pleistocene (Voris 2000). During the last Pleistocene, Australia, New Guinea and the Aru Islands were part of the same land mass (Sahul Shelf). Map by courtesy of H. Voris, Fieldmuseum Chicago.

taxa with a total of 36% (Newton 2003). Endemism is high in the Wallacean avifauna, with 64% of endemic bird species both in the Moluccas and Lesser Sunda Islands (Carstensen et al. 2012). The avifauna of the Wallacea has been a research object for ornithologists and evolutionary biologists since the time of Alfred Russel Wallace and Ernst Mayr (Wallace 1869; Mayr 1941). Parrots are abundant in the Wallacea and are still an object of current research (Marsden & Fielding 1999). 111 parrot species are threatened with extinction worldwide, representing 28% of all parrot species (Olah et al. 2016). It should be recalled that Australasia is one of the regions with the highest number of threatened parrot taxa (Collar 2000).

Dispersal, colonization, and island evolution

Dispersal is regarded as a fragmentation process that can lead to speciation (Newton 2003). The ability to colonize new islands is a key feature of organisms in island biogeography. The 'species-area' relationship describes the theory that species numbers increase with island size and with proximity to a colonization source (MacArthur & Wilson 1967; Newton 2003). Given that relationship, the number of native species is approximately doubling with every ten-fold increase in the land surface area (Newton 2003).

Colonization is dependent on the abundance within a species' range, which is a mixture between source and sink areas. Highest densities (source areas) are mostly found in the centre of the range (Newton 2003). Source areas enable a species to produce a surplus of offspring, which are able to colonize other areas. Sink areas, on the other hand, are most likely to occur in range boundaries, where conditions become less suitable and populations often depend on immigration (Newton 2003). While some bird families like herons, rails, parrots, pigeons, or kingfishers are generally successful colonizers of oceanic islands, others like pelicans, storks, larks, pheasants, or birds of paradise are less successful colonizers (Begon et al. 1998). The colonization of islands may lead to rapid evolution in morphology and behaviour through founder events. As an example, flightlessness and considerably modified skeleton in Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*) may be attained in less than 80,000 years (Newton 2003). The evolution of four to five distinct bird taxa in Northern Melanesia occurred within only 300 years (Mayr & Diamond 2001). A rapid morphological evolution within only 10 generations was detected in introduced 'habitat island' bird populations: introduced Asian Ring-necked Parakeets (*Psittacula krameri*) in cities of Europe have broader beaks, longer skulls and longer wings than in their native range (Le Gros et al. 2016).

Wallacea vs. Sahul Shelf: Is there a biogeographical pattern which can be explained by the two parrot species complexes?

The Islands of the Wallacea have been geographically isolated over several millions of years, while the land mass of the Sahul Shelf connected Australia and New Guinea until 18,000 years BP (Voris 2000). Two main questions arise from this setting.

1) Do bird populations on shelf islands, that were connected by land bridges during the Pleistocene, show similar genetic distances when compared to populations within several million year old oceanic islands?

2) Is the Wallacea an origin of endemism or are source populations (ancestral origins) located outside the Wallacea? Can we assign ancestral lineages to the Wallacea or Sahul Shelf?

In order to investigate these questions, two groups of parrots native to the Australasian region were chosen: the *Eclectus-roratus*- and the *Trichoglossus-haematodus*-complex. Their distribution patterns are located both inside and outside the Wallacea. For *Trichoglossus haematodus*, the origin was suggested to be located in New Guinea with several colonization events to the Wallacea and Australia (see Forshaw 1977). No colonization scenario has been suggested so far for the species *Eclectus roratus*. In order to understand the effects of geographical isolation on these bird populations, a haplotype network and phylogenetic analysis were performed.

Study species

Study species 1: Eclectus Parrot Eclectus roratus *Wagler, 1832*
The Eclectus Parrot, a rain forest dweller (deciduous forest on Sumba), is known for its well-defined reverse sexual dichromatism: males are greenish and females are red and blue (Forshaw 2006). Furthermore the polyandrous mating system (up to seven males for one female) in this species is unusual in parrots and some females are known to produce consecutive chicks of the same sex (Heinsohn et al. 1997). Breeding success in wild birds is low in this species, only 18% of eggs and 27% of clutches produced a fledgling (Heinsohn & Legge 2003). The greenish males fly long distances to feed the female and brood, and need to camouflage themselves from predators while the red-and-bluish females compete for rare nest holes (Heinsohn et al. 2005). Although the sex ratio of nestlings is equal, the adult sex ratio in the population is skewed towards males (Heinsohn & Legge 2003). Currently there are nine recognized subspecies: *E. roratus roratus*, *vosmaeri*, *cornelia*, *riedeli*, *polychloros*, *solomonensis*, *aruensis*, *biaki*, and *macgillivrayi* (*westermani* not included) (Forshaw 2010). For distributions see Figure 2. There is no current discussion about the elevation of subspecies to full species within the *Eclectus-roratus*-complex (see Ekstrom & Butchart 2014).

Study species 2: Rainbow Lorikeet Trichoglossus haematodus *Linnaeus, 1771*
In contrast, the colourful Rainbow Lorikeet, which does not exhibit a pronounced sexual dichromatism, is an abundant, social, nectarivorous parrot (Forshaw 2010). It is found in open woodland in the tropical lowlands, and commonly occurs in urban areas of Australia. It competes with similarly sized birds for nest holes (Franklin 1997; Waterhouse 1997; Shukuroglou &

Table 1. Sample information of the current study. Origin: LPF: Loro Parque Fundación, Tenerife, Spain; CMH: C. Mettke-Hofmann. Some sequences were retrieved from GenBank.

Scientific Name	IPMB ID.	Accession number	Origin	Distribution	Wild/Captive
Charmosyna papou	49578	KM372511	LPF	New Guinea	c
Psitteuteles goldiei	31315	KM372512	LPF	New Guinea	c
Melopsittacus undulatus	–	EF450826		Australia	c
Psittacula alexandri abbotti	34985	KM372495	LPF	Nicobar Islands	c
Eclectus roratus aruensis	34683	KM372496	LPF	Aru Islands	c
Eclectus roratus aruensis	34684	KM372497	LPF	Aru Islands	c
Eclectus roratus cornelia	34685	KM372498	LPF	Sumba	c
Eclectus roratus cornelia	34686	KM372499	LPF	Sumba	c
Eclectus roratus polychloros	34687	KM372500	LPF	New Guinea	c
Eclectus roratus riedeli	34688	KM372501	LPF	Tanimbar Island	c
Eclectus roratus riedeli	34689	KM372502	LPF	Tanimbar Island	c
Eclectus roratus riedeli	34692	KM372503	LPF	Tanimbar Island	c
Eclectus roratus	–	AB177948	Astuti et al. (2006)	Moluccas	w?
Eclectus roratus roratus	34693	KM372504	LPF	Buru, Seram	c
Eclectus roratus solomonensis	34680	KM372506	LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c
Eclectus roratus solomonensis	34682	KM372507	LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c
Eclectus roratus solomonensis	34697	KM372508	LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c
Eclectus roratus solomonensis	34698	KM372509	LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c
Eclectus roratus roratus	34701	KM372505	LPF	Moluccas	c
Eclectus ssp. unknown origin	34702	MG429727	LPF	presumably New Guinea	c
Trichoglossus euteles	–	AB177963	Astuti et al. (2006)	Timor, Lomblen to Nila & Babar	w?
Trichoglossus euteles	–	AB177943	Astuti et al. (2006)	Timor, Lomblen to Nila & Babar	w?
Trichoglossus haematodus nigrogularis	9353	KM372513	CMH	Aru Islands	c
Trichoglossus haematodus caeruleiceps	35195	KM372514	LPF	S New Guinea	c
Trichoglossus haematodus caeruleiceps	35196	KM372515	LPF	S New Guinea	c
Trichoglossus haematodus caeruleiceps	35197	MG429705	LPF	S New Guinea	c

Table 1 continued. Sample information of the current study. Origin: LPF: Loro Parque Fundación, Tenerife, Spain; CMH: C. Mettke-Hofmann. Some sequences were retrieved from GenBank.

Scientific Name	IPMB ID.	Accession number	Origin	Distribution	Wild/Captive
Trichoglossus haematodus caeruleiceps	35198	MG429706	LPF	S New Guinea	C
Trichoglossus haematodus capistratus	35199	MG429709	LPF	Timor	C
Trichoglossus haematodus capistratus	35200	KM372516	LPF	Timor	C
Trichoglossus haematodus capistratus	35201	KM372517	LPF	Timor	C
Trichoglossus haematodus capistratus	35202	MG429707	LPF	Timor	C
Trichoglossus haematodus capistratus	31259	MG429708	LPF	Timor	C
Trichoglossus haematodus capistratus	9346	MG429724	CMH	Timor	C
Trichoglossus haematodus deplanchii	35205	MG429710	LPF	New Caledonia & Loyalty Islands	C
Trichoglossus haematodus deplanchii	35206	KM372519	LPF	New Caledonia & Loyalty Islands	C
Trichoglossus haematodus deplanchii	35207	MG429711	LPF	New Caledonia & Loyalty Islands	C
Trichoglossus haematodus forsteni	35209	KM372520	LPF	Sumbawa Island	C
Trichoglossus haematodus forsteni	35210	MG429713	LPF	Sumbawa Island	C
Trichoglossus haematodus forsteni	35211	MG429712	LPF	Sumbawa Island	C
Trichoglossus haematodus forsteni	35212	KM372521	LPF	Sumbawa Island	C
Trichoglossus haematodus fortis	9354	MG429726	CMH	Sumba Island	C
Trichoglossus haematodus massena	35213	MG429714	LPF	Karkar, Bismarck Archipelago & Solomon Islands	C
Trichoglossus haematodus massena	35214	MG429715	LPF	Karkar, Bismarck Archipelago & Solomon Islands	C
Trichoglossus haematodus mitchellii	35215	KM372525	LPF	Bali & Lombok	C
Trichoglossus haematodus mitchellii	35216	KM372526	LPF	Bali & Lombok	C
Trichoglossus haematodus mitchellii	35217	MG429716	LPF	Bali & Lombok	C
Trichoglossus haematodus mitchellii	35218	MG429717	LPF	Bali & Lombok	C
Trichoglossus haematodus moluccanus	35221	MG429718	LPF	eastern Australia to Tasmania	C
Trichoglossus haematodus moluccanus	35222	KM372527	LPF	eastern Australia to Tasmania	C
Trichoglossus haematodus moluccanus	35223	KM372528	LPF	eastern Australia to Tasmania	C
Trichoglossus haematodus moluccanus	9312	MG429722	CMH	eastern Australia to Tasmania	C

Table 1 continued. Sample information of the current study. Origin: LPF: Loro Parque Fundación, Tenerife, Spain; CMH: C. Mettke-Hofmann. Some sequences were retrieved from GenBank.

Scientific Name	IPMB ID.	Accession number	Origin	Distribution	Wild/Captive
Trichoglossus haematodus moluccanus	9323	MG429723	CMH	eastern Australia to Tasmania	C
Trichoglossus haematodus rosenbergii	35224	MG429719	LPF	Biak Island	C
Trichoglossus haematodus rosenbergii	35226	KM372529	LPF	Biak Island	C
Trichoglossus haematodus rosenbergii	35227	KM372530	LPF	Biak Island	C
Trichoglossus haematodus rosenbergii	9347	MG429725	CMH	Biak Island	C
Trichoglossus haematodus rubritorquis	35225	KM372531	LPF	N Australia	C
Trichoglossus haematodus rubritorquis	35228	KM372532	LPF	N Australia	C
Trichoglossus haematodus rubritorquis	35229	MG429720	LPF	N Australia	C
Trichoglossus haematodus weberi	35231	KM372533	LPF	Flores Island	C
Trichoglossus haematodus weberi	35232	KM372534	LPF	Flores Island	C
Trichoglossus haematodus weberi	35233	MG429721	LPF	Flores Island	C

McCarthy 2006; Legault et al. 2011). *T. haematodus* is strikingly diverse, the number of taxa differs – according to authors – between 20 (Forshaw 2010) and 22 subspecies (Arndt 2012), see Figure 4.

The taxonomy of the *Trichoglossus-haematodus*-complex is currently under discussion. Del Hoyo et al. (2014) distinguish the following taxa, using criteria of Tobias et al. (2010): (1) *T. rosenbergii* (monotypic), (2) *T. forsteni* (incl. *mitchellii*, *djampeanus* and *stresemanni*), (3) *T. weberi* (monotypic), (4) *T. haematodus* (all taxa from New Guinea North and South including satellite islands and Solomons), (5) *T. moluccanus* (incl. *septentrionalis*), (6) *T. capistratus* (incl. *fortis* and *flavotectus*), and (7) *T. rubritorquis* (monotypic). (8) *T. euteles* is treated as a separate species. Molecular evidence is still insufficient for this group and was not a basis for the arrangement of del Hoyo et al. (2014). The taxon *T. h. brooki* Ogilvie-Grant, 1907 (Aru Islands) is regarded taxonomically invalid, as the two known museum specimen are of captive origin, most likely to be juveniles of *T. h. nigrogularis* (T. A.).

1.   MATERIALS AND METHODS

1.1. Sampling

Nucleotide sequences of the mitochondrial cytochrome b (cyt *b*) gene from two species complexes were analyzed: *Eclectus roratus* is represented by six out of nine taxa (Forshaw 2006), and the *Trichoglossus-haematodus*-complex by 12 out of 20-22 taxa (see Forshaw 2010; Arndt 2012) plus *T. euteles*. This allowed us to reconstruct a phylogenetic and phylogeographic scenario. The samples were derived from captive individuals of *E. roratus* ssp. and *T. haematodus* ssp. (see Table 1).

1.2. DNA isolation, PCR, sequencing

DNA was obtained from blood and tissue samples and stored in EDTA buffer (Carl Roth, Karlsruhe). Total DNA was isolated using standard proteinase K (Merck, Darmstadt) and phenol/chloroform protocols (Sambrook et al. 1989). Fragments of the mitochondrial cytochrome *b* gene (cyt *b*) were amplified using specific primers, see Table 2. The PCR amplifications were performed in 50 µl reaction volumes containing 1 × PCR buffer (Bioron, Ludwigshafen), 100 µM dNTPs, 0.2 units of *Taq* DNA polymerase (Bioron, Ludwigshafen), 200 ng of DNA and 5 pmol of primers. PCR was carried out under the following conditions: 5 min at 94°C, followed by 35 cycles of 45 s at 94°C, 1 min at 52.0°C, 2 min at 72°C and a final extension at 72°C for 5 min. PCR products were precipitated with 4 M NH4Ac and ethanol (1:1:12) followed by a centrifugation for 15 min (13,000 rpm).

Sequencing was performed by capillary electrophoresis using a MegaBACE™ 1000 sequencer (Molecular Dynamics, Amersham Pharmacia). DNA length of cyt *b* sequences were 1,140 nucleotides (Braun 2014).
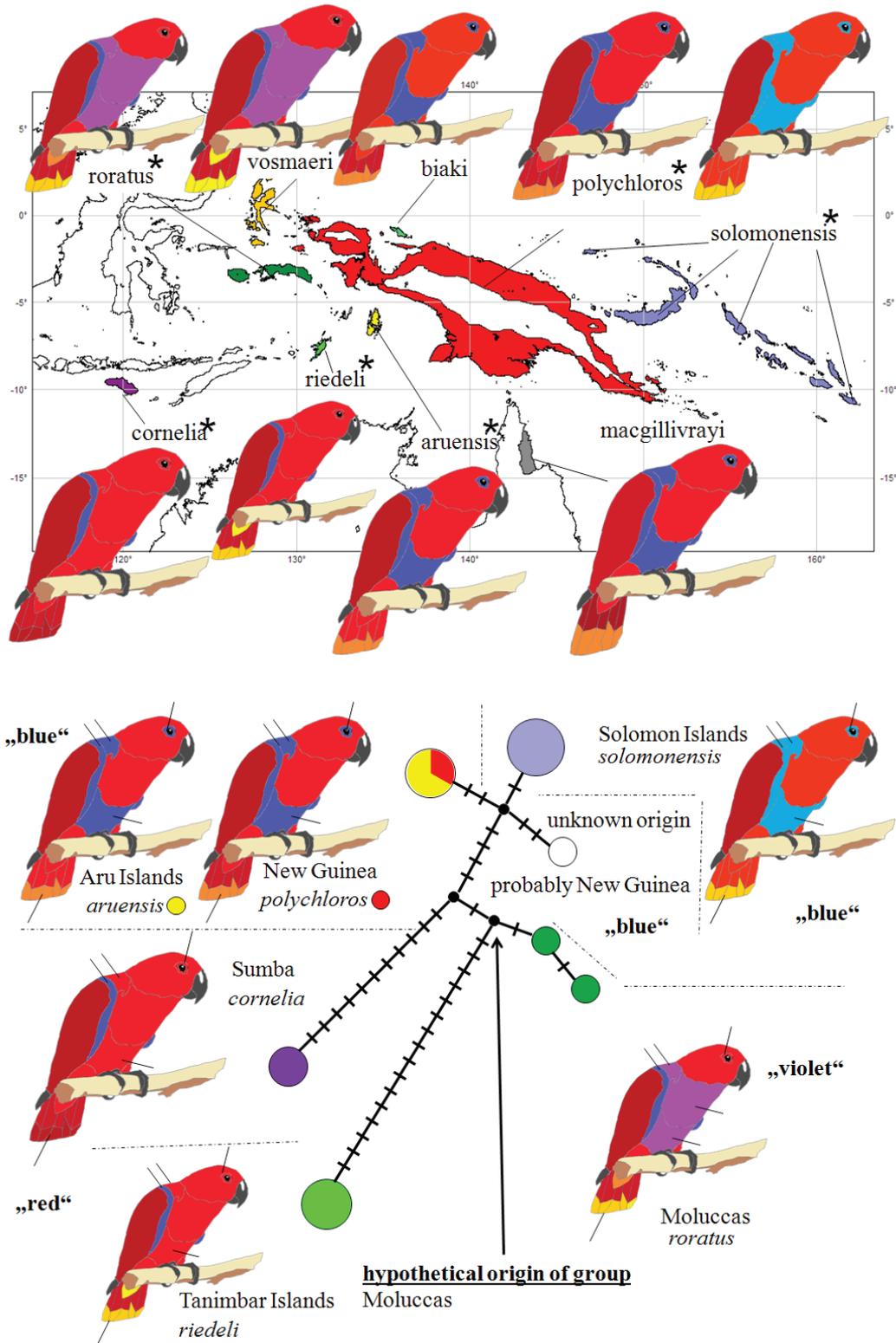
Figure 2. (a) above: Distribution of all subspecies of Eclectus roratus. Asterisks indicate all available taxa included in the analysis. Each population is represented by a separate colour code, which is also used in the network analysis. Only females are illustrated, males of different taxa are similar and have a bright greenish plumage. Bird of unknown origin clusters within the blue-bellied New Guinea group.
(b) below: Median-joining network of Eclectus Parrots (Eclectus roratus ssp.) in Australasia based on 1,005 nucleotides of cytochrome b (cyt b) (ε=0). The hypothetical ancestral node (geographical origin) is underlined. Circles indicate different populations/islands. Circle colours correspond to population colour code in distribution maps. Circle size is proportional to haplotype frequency in the dataset. Solid lines on the branches within the network indicate mutation events. Belly colour of females is indicated as "colour", characteristical differences between taxa are marked with lines. Only females are illustrated. An individual with unknown origin clusters within the blue-bellied New Guinea group.

Table 2. Primers used for PCR amplification (amp) and DNA sequencing (seq) of cytochrome b gene (cyt b), being 1,140 nt in Psittaciformes. f= forward, r = reverse; L = light strand, H = heavy strand; Sequencing: X=CY5 fluorescent label;

Cyt b – primer	sequence (5'-3')	Direction	Use	reference
MT-A1	CAACATCTCAGCATGATGAAACTTCG	f	amp/seq (L)	Wink & Sauer-Gürth (2000)
MT-C2-CY	XGAGGACAAATATCATTCTGAGG	f	amp/seq (L)	Clouet & Wink (2000)
HThr 16082	TCTTTTGGTTTACAAGACCAATG	r	amp/seq (H)	Kornegay et al. (1993)
Mte	GCAAATAGGAAGTATCATTCTGG	r	amp/seq (H)	Fritz et al. (2006)
Mtfr	CATAGAAGGGTGGAGTCTTCAGTTTTTGGTTTACAA	r	amp/seq (H)	modified from Wink et al. (2002)
ND5L 14754	GGACCAGAAGGACTTGCCGACCTA	f	amp/seq (L)	Ribas (2004)
L15311	GTCCTACCATGAGGTCAAATATC	f	amp/seq (L)	Braun (2014)
L15558	TGTGAYAAAATCCCATTCCACCC	f	amp/seq (L)	Braun (2014)
H15400	AAGAATCGGGTTAGGGTGGGG	r	amp/seq (H)	Braun (2014)
H15494	CCTAGGGGRTTRTTTGACC	r	amp/seq (H)	Braun (2014)
L14764_MW	TGATACAAAAAAATAGGMCCMGAAGG	f	amp/seq (L)	modified from Sorenson et al. (1999)
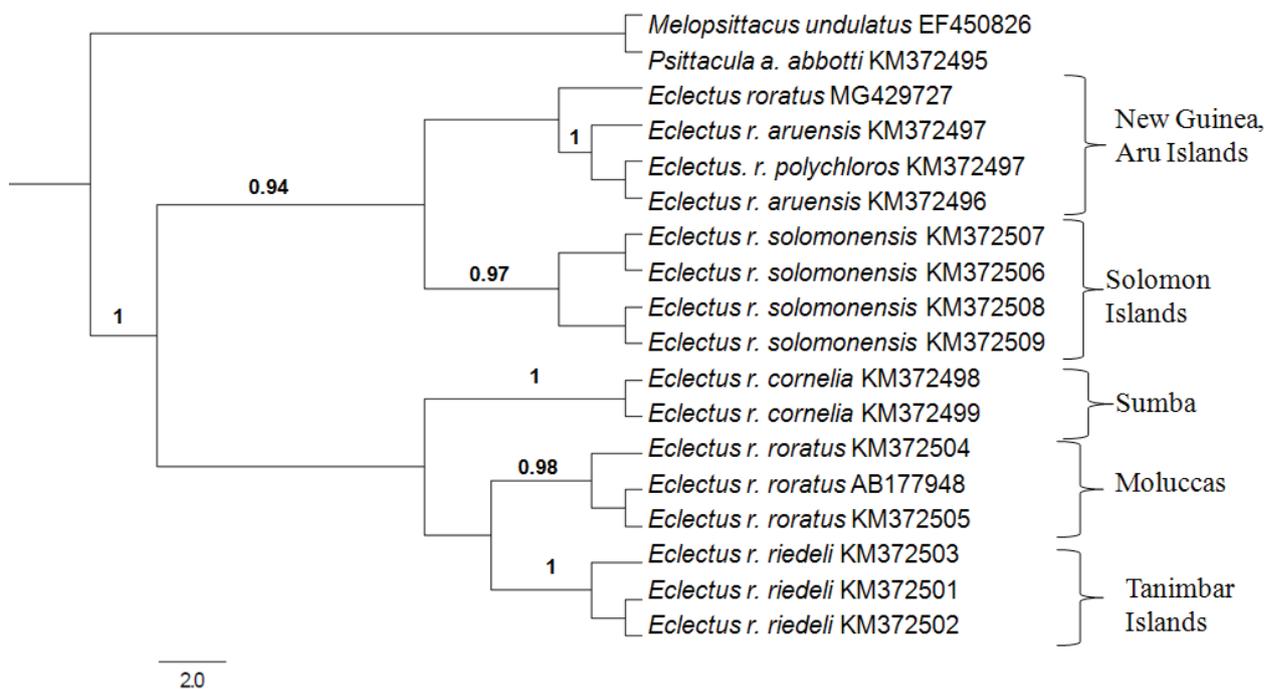
Figure 3. Bayesian analysis using BEAST v.1.4.8: maximum clade credibility tree of Eclectus (cyt b, 1,140 nt). Clades corresponding to different islands, also reported in the network analysis are well supported. Support values (posterior probabilities) above 0.9 are displayed.

1.3. Alignment

The nucleotide sequences were aligned using the Clustal W algorithm (Thompson et al. 1994) with BioEdit version 7.0.9.0 (Hall 1999). DNA sequences were checked for their quality manually, and for their vertebrate mitochondrial origin by translating them into amino acids. No internal stop codons or frame-shifts were observed in the sequences. Basic statistics,

Neighbor-joining trees and average uncorrected *p*-distances were calculated with MEGA 5.2.2 (Tamura et al. 2011).

1.4. Model selection

For the best fitting evolutionary model, jModelTest (Guindon & Gascuel 2003; Posada 2008; Darriba et al. 2012) was used. The model Hasegawa, Kishino and Yano plus invariant sites (HKY+I)
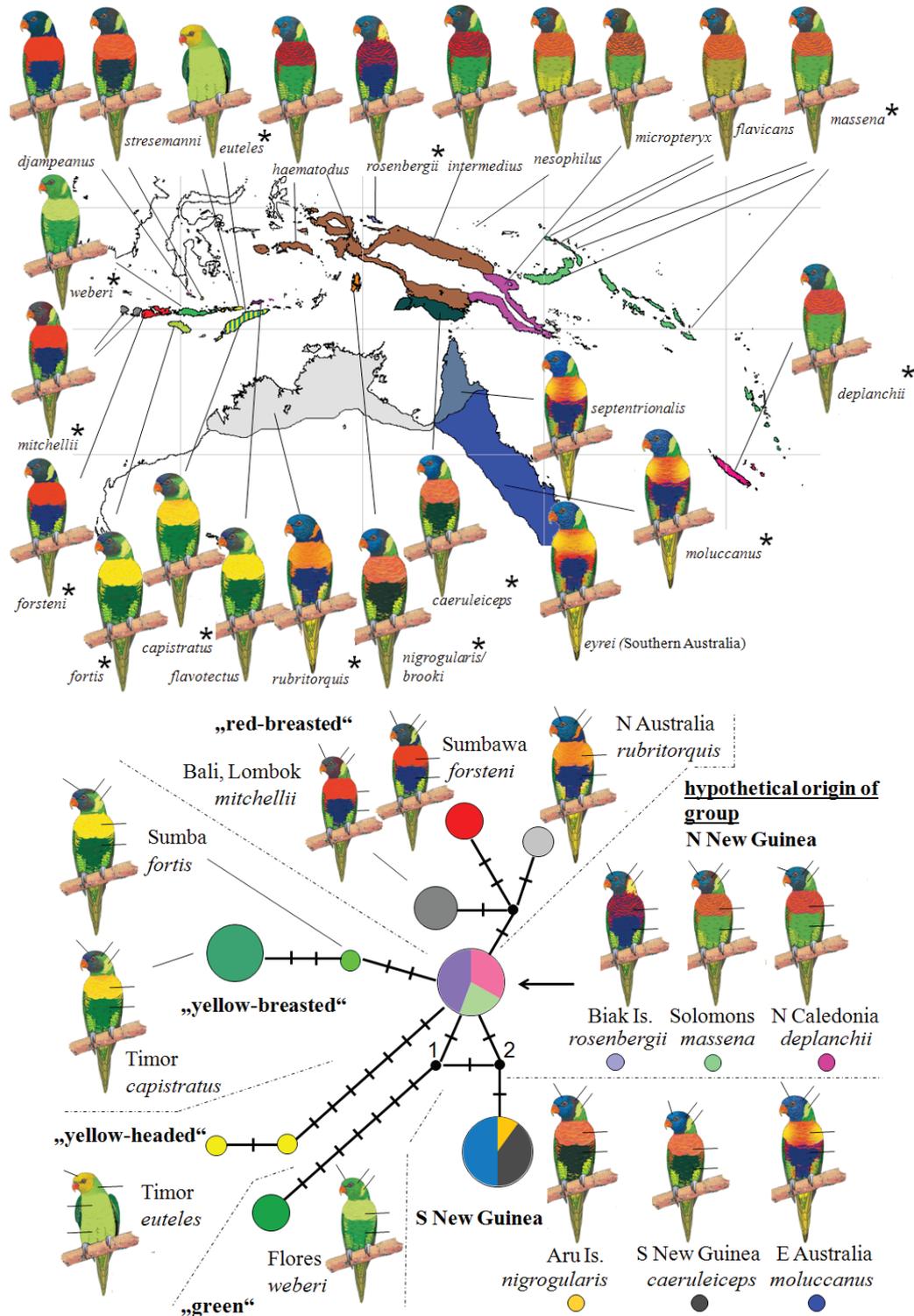
Figure 4. (a) above: Distribution of the subspecies of the Trichoglossus-haematodus-complex (T. haematodus 22 ssp. & Trichoglossus euteles, see Arndt (2012)). Asterisks indicate all available taxa included in the analysis. Each population is represented by a separate colour code, which is also used in the network analysis. The taxon T. h. nigrogularis includes T. h. brooki (Aru Islands, see text). Sympatric distribution occurs on Timor with T. euteles and T. h. capistratus.

(b) below: Medium-joining network of the Trichoglossus-haematodus-complex (T. haematodus ssp. & Trichoglossus euteles) in Australasia based on 562 nucleotides of cytochrome b (cyt b) (ε=0). The hypothetical ancestral node (geographical origin) is underlined. Numbers 1 and 2 show median vectors (presumed ancestral sequence). Names of groups are indicated as "yellow-breasted" etc., characteristical differences between taxa are marked with lines. Circles indicate different populations/islands. Circle colours correspond to population colour code in distribution maps. Circle size is proportional to haplotype frequency in the dataset. Solid lines on the branches within the network indicate mutation events. The taxon T. h. brooki is included in T. h. nigrogularis (see text). Sympatric distribution occurs on Timor with T. euteles and T. h. capistratus. The two Australian taxa T. h. moluccanus and T. h. rubritorquis represent two independent genetic lineages. Drawings are with courtesy of Thomas Arndt.

Table 3. Variable sites of the network dataset of Eclectus-roratus-complex. *Taxon names and haplotype names given. Sites as numbers top down. abbreviation of haplotypes: NG= New Guinea clade incl. Aru Islands, Solomon Islands; SUM= Sumba clade; TAN = Tabimbar clade; MOL= Moluccas clade;*

Taxon + IPMB ID	haplotype/site	1	1	1	1	1	1	1	1	2	2	3	3	3	3	3	3	3	4	4	4	4	5	5	6
		1	2	3	3	3	6	7	9	5	7	0	1	6	7	9	9	9	1	1	2	5	2	9	1
		1	7	2	4	6	8	6	8	8	0	6	5	7	2	0	6	9	1	4	9	9	2	7	2
aruensis 34683	NG	-	-	-	-	-	T	A	T	C	C	C	C	A	T	T	C	C	C	A	A	C	T	T	A
aruensis 34684	NG	-	-	-	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
solomonensis 34680	NG	-	-	-	-	-	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	C	.	.
solomonensis 34682	NG	-	-	-	-	-	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	C	.	.
solomonensis 34697	NG	-	-	-	-	-	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	C	.	.
solomonensis 34698	NG	-	-	-	-	-	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	C	.	.
polychloros 34687	NG	-	-	-	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
unknown origin 34702	NG	-	-	-	-	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	.	.
cornelia 34685	SUM	-	-	-	-	-	.	.	.	T	.	.	.	.	A	.	.	.	.	.	.	.	C	C	.
cornelia 34686	SUM	-	-	-	-	-	.	.	.	T	.	.	.	.	A	.	.	.	.	.	.	.	C	C	.
riedeli 34688	TAN	C	A	C	A	A	C	.	.	.	T	.	T	.	C	.	T	.	.	.	.	.	C	.	G
riedeli 34689	TAN	C	A	C	A	A	C	.	.	.	T	.	T	.	C	.	T	.	.	.	.	.	C	.	G
riedeli 34692	TAN	C	A	C	A	A	C	.	.	.	T	.	T	.	C	.	T	.	.	.	.	.	C	.	G
roratus AB177948	MOL	-	G	A	G	G	.	G	C	.	.	T	.	.	.	G	.	A	A	G	C	.	C	.	.
roratus 34693	MOL	T	A	T	A	A	.	.	C	.	.	T	.	.	.	.	.	.	.	G	.	.	C	.	.
roratus 34701	MOL	T	A	T	A	A	.	.	C	.	.	T	.	.	.	.	.	.	.	G	.	.	C	.	.

taxon	haplotype/site	6	6	7	7	7	7	7	8	8	8	8	8	9	9	9	9	9	9	1 0	1 0	1 0	1 0	1 0	1 0
		8	9	0	1	4	5	7	2	6	7	7	8	0	1	6	6	8	9	0	5	6	8	8	8
		4	6	2	5	4	1	4	2	7	0	7	8	3	0	1	2	5	0	2	6	8	3	5	9
aruensis 34683	NG	G	A	T	C	C	T	T	C	T	A	C	T	T	T	G	T	C	T	C	A	A	T	T	T
aruensis 34684	NG	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
solomonensis 34680	NG	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
solomonensis 34682	NG	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
solomonensis 34697	NG	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
solomonensis 34698	NG	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.
polychloros 34687	NG	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
unknown origin 34702	NG	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	C	.	.	.
cornelia 34685	SUM	A	G	C	.	.	.	C	T	.	G	T	.	C	.	T	.	.	C	.	G	G	C	.	.
cornelia 34686	SUM	A	G	C	.	.	.	C	T	.	G	T	.	C	.	T	.	.	C	.	G	G	C	.	.
riedeli 34688	TAN	A	G	C	T	T	C	.	.	C	G	T	C	.	C	.	C	T	.	T	.	.	.	C	C
riedeli 34689	TAN	A	G	C	T	T	C	.	.	C	G	T	C	.	C	.	C	T	.	T	.	.	.	C	C
riedeli 34692	TAN	A	G	C	T	T	C	.	.	C	G	T	C	.	C	.	C	T	.	T	.	.	.	C	C
roratus AB177948	MOL	A	G	C	.	.	.	.	.	.	G	T	.	.	C	.	.	.	.	.	-	-	-	-	-
roratus 34693	MOL	A	G	C	.	.	.	.	.	.	G	T	.	.	C	.	.	.	.	.	.	.	.	.	.
roratus 34701	MOL	A	G	C	.	.	.	.	.	.	G	T	.	.	C	.	.	.	.	.	.	.	.	.	.

Figure 5. Bayesian Analysis using BEAST v.1.4.8: maximum clade credibility tree of Trichoglossus (cyt b, 1,140 nt). Clades defined in Network 4.6.1.1 are well supported as distinct lineages while the clades "N New Guinea" (rosenbergii, massena, deplanchii) and "S New Guinea" (nigrogularis, caeruleiceps, moluccanus) remain unresolved. Support values (posterior probabilities) above 0.9 are displayed.
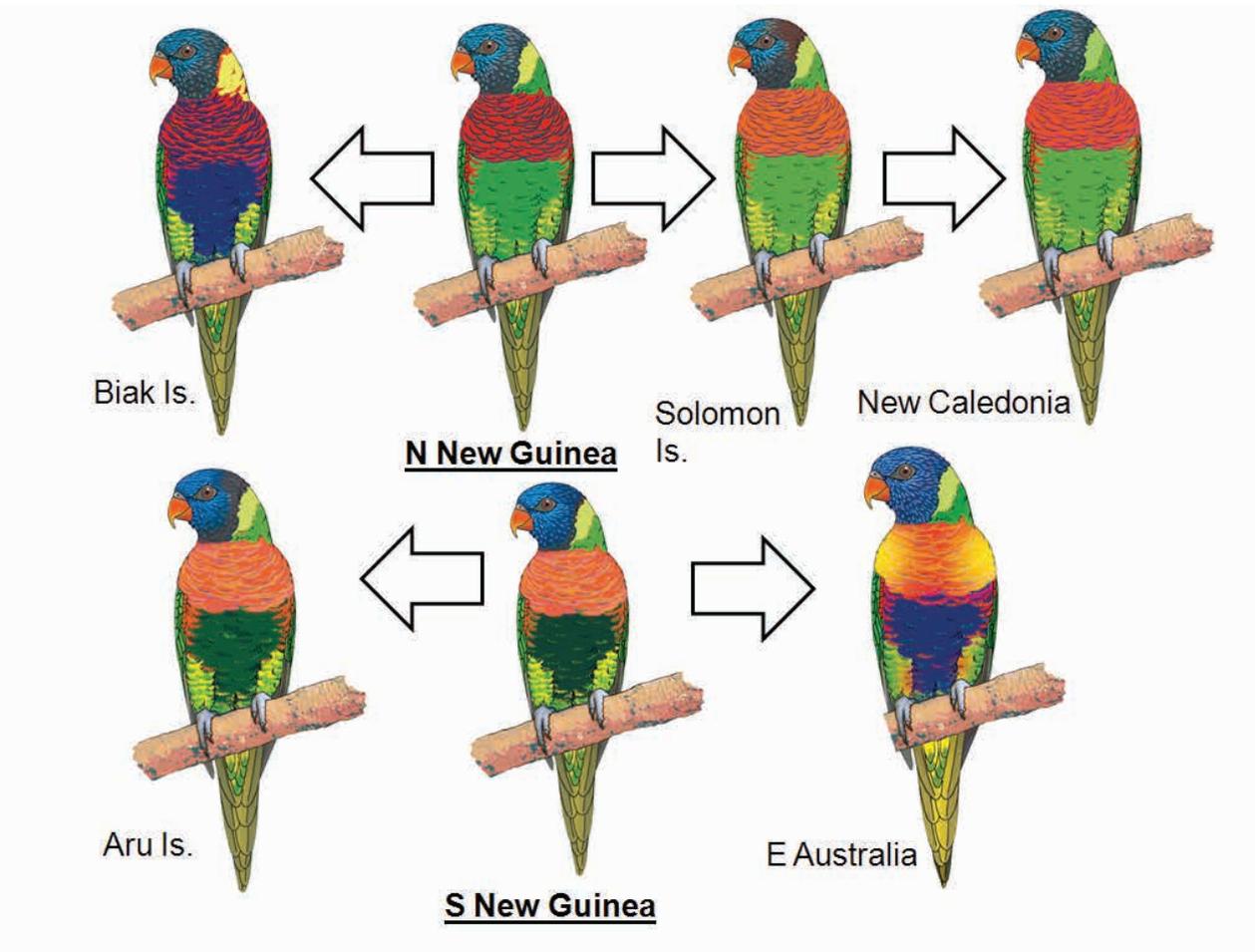
Figure 6. Divergence in T. haematodus can occur very quickly. The youngest lineages (N New Guinea vs. S New Guinea) evolved by dispersal and/or isolation (arrows) from New Guinea during the Pleistocene, less than 50,000 years ago, probably as young as 18,000 years ago (last glacial maximum). Drawings are with courtesy of Thomas Arndt.

Table 4. Variable sites of the network dataset of Trichoglossus-haematodus-complex. Taxon names and haplotype names given. Sites as numbers top down. abbreviation of haplotypes: TIM= Timor I clade; FLOR = Flores clade; NNG = N New Guinea; SNG = S New Guinea; SUM = Sumba and Timor II clade; SMBW = Sumbawa clade; BAL = Bali & Lombok clade; AUS = N Australia clade;

Taxon + IPMB ID	haplotype/site																							
							1	1	1	1	2	2	2	2	3	3	3	3	3	3	4	4	5
		2	2	3	3	6	8	2	2	5	9	2	2	3	5	3	3	4	5	6	9	1	7	1
		5	6	3	9	6	1	7	9	5	5	5	6	7	8	3	9	8	1	6	6	7	1	0
euteles AB177943	TIM	-	-	-	-	-	-	G	A	G	A	A	T	A	C	G	C	T	G	C	T	G	T	T
euteles AB177963	TIM	-	-	-	-	-	-	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.
weberi 35231	FLOR	C	A	A	G	A	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	C
weberi 35232	FLOR	C	A	A	G	A	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	C
deplanchii 35205	NNG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.	.
deplanchii 35206	NNG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.	.
massena 35213	NNG	C	A	G	A	G	C	.	.	T	.	.	.	.	.	A	.	C	.	.	C	A	.	.
massena 35214	NNG	C	A	G	A	G	C	.	.	T	.	.	.	.	.	A	.	C	.	.	C	A	.	.
rosenbergii 35226	NNG	-	-	-	-	-	-	-	-	T	.	.	.	.	.	A	.	C	.	.	C	A	.	.
rosenbergii 35227	NNG	C	A	G	A	G	C	.	.	T	.	.	.	.	.	A	.	C	.	.	C	A	.	.
nigrogularis 9353	SNG	-	-	-	-	-	-	-	-	.	.	.	.	.	.	.	.	.	.	.	T	C	A	.	.
caeruleiceps 35195	SNG	C	A	G	G	G	T	.	.	T	.	.	.	.	.	.	.	.	.	.	T	C	A	.	.
caeruleiceps 35196	SNG	C	A	G	G	G	T	.	.	T	.	.	.	.	.	.	.	.	.	.	T	C	A	.	.
moluccanus 35222	SNG	C	A	G	G	G	T	.	.	T	.	.	.	.	.	.	.	.	.	.	T	C	A	.	.
moluccanus 35223	SNG	C	A	G	G	G	T	.	.	T	.	.	.	.	.	.	.	.	.	.	T	C	A	.	.
capistratus 35200	SUM	C	A	G	G	A	C	.	.	T	.	.	.	C	.	T	.	T	.	.	.	A	C	.
capistratus 35201	SUM	C	A	G	G	A	C	.	.	T	.	.	.	C	.	T	.	T	.	.	.	A	C	.
fortis 9354	SUM	-	-	-	-	-	-	.	G	T	.	.	.	C	.	T	.	T	.	.	.	A	C	.
forsteni 35209	SMBW	-	-	-	-	-	-	-	-	-	G	.	.	.	.	.	.	T	.	.	.	A	.	.
forsteni 35212	SMBW	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.	.
mitchellii 35215	BAL	A	C	G	G	A	C	A	.	T	.	G	.	.	.	.	.	T	.	.	.	A	.	.
mitchellii 35216	BAL	C	A	G	G	A	C	A	.	T	.	G	.	.	.	.	.	T	.	.	.	A	.	.
rubritorquis 35225	AUS	-	-	-	-	-	-	-	-	-	-	-	-	-	.	.	.	.	A	.	.	A	.	.
rubritorquis 35228	AUS	C	A	G	G	A	C	.	.	T	.	.	.	C	.	.	.	.	A	.	.	A	.	.

taxon	haplotype/site																			1	1	1	1
		5	5	6	6	6	7	7	7	7	8	8	8	8	8	9	9	9	9	9	0	0	0	0
		4	8	2	9	9	0	2	2	5	2	4	6	7	9	1	2	5	5	7	0	1	6	8
		3	2	1	6	9	0	2	6	3	2	3	4	0	4	2	7	0	4	2	2	7	9	6
euteles AB177943	TIM	C	C	C	A	T	A	C	T	G	C	T	G	A	T	G	T	A	C	T	T	T	C	T
euteles AB177963	TIM	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
weberi 35231	FLOR	T	T	T	G	.	G	.	C	A	.	.	.	.	C	.	.	C	T	.	C	.	.	.
weberi 35232	FLOR	T	T	T	G	.	G	.	C	A	.	.	.	.	C	.	.	C	T	.	C	.	.	.
deplanchii 35205	NNG	.	.	T	.	.	G	.	C	A	.	C	.	.	.	C	C	T	.	.	.	.	.	.
deplanchii 35206	NNG	.	.	T	.	.	G	.	C	A	.	C	.	.	.	C	C	T	.	.	.	.	.	.
massena 35213	NNG	.	.	T	.	.	G	.	C	A	.	C	.	.	.	C	C	T	.	.	.	.	.	.
massena 35214	NNG	.	.	T	.	.	G	.	C	A	.	C	.	.	.	C	C	T	.	.	.	.	.	.
rosenbergii 35226	NNG	.	.	T	.	.	G	.	C	A	.	C	.	.	.	C	C	T	.	.	.	.	.	.
rosenbergii 35227	NNG	.	.	T	.	.	G	.	C	A	.	C	.	.	.	C	C	T	.	.	.	.	.	.
nigrogularis 9353	SNG	.	A	T	.	.	G	.	C	A	.	C	A	.	.	.	C	C	T	.	.	.	T	.
caeruleiceps 35195	SNG	.	A	T	.	.	G	.	C	A	.	C	A	.	.	.	C	C	T	.	.	.	T	.

Table 4. Variable sites of the network dataset of Trichoglossus-haematodus-*complex. Taxon names and haplotype names given. Sites as numbers top down. abbreviation of haplotypes: TIM= Timor I clade; FLOR = Flores clade; NNG = N New Guinea; SNG = S New Guinea; SUM = Sumba and Timor II clade; SMBW = Sumbawa clade; BAL = Bali & Lombok clade; AUS = N Australia clade;*

Taxon	Clade																							
caeruleiceps 35196	SNG	.	A	T	.	.	G	.	C	A	.	C	A	.	.	.	C	C	T	.	.	.	T	.
moluccanus 35222	SNG	.	A	T	.	.	G	.	C	A	.	C	A	.	.	.	C	C	T	.	.	.	T	.
moluccanus 35223	SNG	.	A	T	.	.	G	.	C	A	.	C	A	.	.	.	C	C	T	.	.	.	T	.
capistratus 35200	SUM	.	.	T	G	.	G	.	C	A	.	C	.	.	.	.	C	C	T	C	.	C	.	.
capistratus 35201	SUM	.	.	T	G	.	G	.	C	A	.	C	.	.	.	.	C	C	T	C	.	C	.	.
fortis 9354	SUM	.	.	T	G	.	G	.	C	A	.	C	.	.	.	.	C	C	T	C	.	.	.	.
forsteni 35209	SMBW	.	.	T	.	.	G	G	C	A	T	C	.	.	.	.	C	C	T	.	.	C	.	.
forsteni 35212	SMBW	.	.	T	.	.	G	G	C	A	.	C	.	G	.	.	C	C	T	.	.	C	.	.
mitchellii 35215	BAL	.	.	T	.	.	G	.	C	A	.	C	.	.	.	A	C	C	T	.	.	C	.	.
mitchellii 35216	BAL	.	.	T	.	.	G	.	C	A	.	C	.	.	.	A	C	C	T	.	.	C	.	.
rubritorquis 35225	AUS	.	.	T	.	C	G	.	C	A	.	C	.	.	.	.	C	C	T	.	.	C	.	C
rubritorquis 35228	AUS	.	.	T	.	C	G	.	C	A	.	C	.	.	.	.	C	C	T	.	.	C	.	C

(Hasegawa et al. 1985) was proposed to be the best fitting evolutionary model for both *Trichoglossus* and *Eclectus* mtDNA according to Bayesian information criterion (BIC).

1.5. Maximum-Likelihood analysis

Starting Maximum-likelihood (ML) trees were obtained using PhyML 3.0 (Guindon et al. 2010) on Phylogeny.fr (Dereeper et al. 2008). More sophisticated ML calculations were performed using RAxML 7.0.4 (Stamatakis 2006) and RAxML-HPC2 7.6.3 (Stamatakis et al. 2008) on XSEDE (Miller et al. 2010). ML searches were conducted with the rapid hill-climbing algorithm under the GTR (General Time Reversible), which is the most common and general model for DNA (see Tavaré 1986).

1.6. Bayesian analysis, tree editing

Bayesian inferences were performed with BEAST v.1.4.8 (Drummond & Rambaut 2008) and BEAST on XSEDE (Miller et al. 2010). The searches were conducted under HKY model with four rate (gamma) categories as model of evolution. The MCMC chain length was set to 10,000,000, logging parameters every 1,000 steps, resulting in 10,000 trees. The burnin was set to 1,000 (cut off the first 10% of trees). Results of the log files have been statistically evaluated using the program Tracer v.1.4 (Rambaut & Drummond 2007). Additional Bayesian analysis was performed using MrBayes 3.2.2 (Ronquist et al. 2012) on XSEDE (Miller et al. 2010) with HKY and equal rates. Phylogenetic trees were arranged and edited using FigTree v1.4.0 (Rambaut 2012).

1.7. Network

Mitochondrial haplotype alignments (cyt *b*) were analyzed using Network v. 4.6.1.1 (Polzin & Daneshmand 2012). The network was calculated using the Median Joining method (MJ) (Bandelt et al. 1999) with epsilon=0 in order to keep the shortest tree. The dataset was formatted in Network 4.6.1.1 and redrawn for publication.

1.8. Molecular clock

For *Trichoglossus*, and *Eclectus* no appropriate fossil data were known which could be used for a molecular dating. However, a calibration for cyt *b* was assumed based on a molecular rate of 2.1% (see Weir & Schluter 2008). This rate has been used in parrots (Groombridge et al. 2004; Eberhard & Bermingham 2005; Tavares et al. 2006; Ribas & Miyaki 2007; Ribas et al. 2009) and other birds for a period of c. 12 million years (Shields & Wilson 1987; Tarr & Fleischer 1993; Fleischer et al. 1998; Weir & Schluter 2008).

2. RESULTS

In *Eclectus roratus* and the *Trichogossus-haematodus*-complex similar genetic patterns were discovered. In both species complexes, a lower genetic distance was observed across populations of the Sahul Shelf (including New Guinea, Aru Islands and Australia), Bismarck Archipelago, and Solomon Islands, while a higher genetic distance (speciation) was found in populations inside the Wallacea. An overview over variable sites in the mitochondrial dataset of the *Eclectus-roratus*-complex is given in Table 3. The overview of the *Trichoglossus-haematodus*-complex is found in Figure 4.

2.1. Eclectus-roratus-complex: haplotype network, Wallacean origin and molecular clock

The haplotype network for *Eclectus* is illustrated in Figure 2. Based on the haplotype network data, the evolutionary origin (ancestral node) of the *Eclectus-roratus*-complex might be in the Moluccas, so a Wallacean origin is proposed for this group. In *Eclectus* three distinct lineages occur within the Wallacea (Sumba, Tanimbar Is., Moluccas), while the New Guinea lineages (Aru Is., New Guinea, Solomon Is.) show little genetic distance. In the *Eclectus-roratus*-complex, populations from Tanimbar Islands (*E. r. riedeli*), Sumba (*E. r. cornelia*) and the Moluccas (*E. r. roratus*) are genetically distinct from the populations in New Guinea (*E. r. polychloros*), the Solomon Islands/

Bismarck Archipelago (*E. r. solomonensis*), and the Aru Islands (*E. r. aruensis*).

The Bayesian analysis is documented in Figure 3. Based on a molecular rate of 2.1% divergence per one million years for cyt *b* in birds (Weir & Schluter 2008), divergence in the stem clades in *Eclectus* is set to a maximum of 1.38 million years ago (p-distance=0.029, see Table 5). The population on the Tanimbar Islands (*E. r. riedeli*) became isolated at around 1.38 Ma and the Sumba population (*E. r. cornelia*) at around 0.67-0.90 Ma. The populations of New Guinea, the adjacent land mass (today e.g. represented by Aru Islands), and the Solomon Islands diverged within the past 0.43-0.81 Ma.

2.2. *Trichoglossus-haematodus*-complex: haplotype network, non-Wallacean origin and molecular clock

The haplotype network for the *Trichoglossus-haematodus*-complex is illustrated in Figure 4, the Bayesian analysis is given in Figure 5. Based on the network data, the evolutionary origin of the *Trichoglossus*-complex might be situated in N New Guinea, so a non-Wallacean origin is proposed for this group. Based on the molecular rate of 2.1%-rule (Weir & Schluter 2008) and the maximum divergence time within the group (N New Guinea lineage as source population to oldest lineages), the evolutionary time frame for the examined taxa of *Trichoglossus haematodus* is set to 0.80 million years ago (p-distance = 0.017, see Figure 4).

The most likely origin of the *Trichoglossus-haematodus*-group is northern New Guinea, as shown in Figure 4. Several genetic lineages may be distinguished: (1) *T. euteles* on Timor, (2) *T. h. weberi* on Flores, (3) *T. h. fortis* on Sumba and *T. h. capistratus* on Timor, (4) *T. h. mitchellii* on Bali and Lombok; (5) *T. h. forsteni* on Sumbawa (6) *T. h. rubritorquis* in N Austra-

lia. The two main lineages of New Guinea split at around 0.33 Ma between (7) N New Guinea clade (*T. h. rosenbergii*, *T. h. massena*, *T. h. deplanchii*) and (8) S New Guinea/Aru Islands/E Australia clade (*T. h. caeruleiceps*, *T. h. nigrogularis*, *T. h. moluccanus*). The most recent divergence events took place in the late Pleistocene, within the lineages N New Guinea and S Guinea/Australia. The genetic distance (p-distance <0.001) suggests a rapid evolution within less than 50,000 years BP, probably younger than 18,000 years BP (last glacial maximum), see Figure 6.

3. DISCUSSION

3.1. Vicariance and dispersal

Geological and climatic events like Pleistocene sea level changes resulted in land area dissection and severing islands. Populations with previously continuous distributions became fragmented. This process is known as vicariance (concept see Newton 2003). Subsequently, mutations and genetic drift led to divergence of populations in different areas from each other, depending on local selection pressures and differences in environmental conditions. These conditions favour a rapid evolution of closely related allospecies under the same superspecies (concept see Newton 2003). Furthermore, dispersal is a second fragmentation process that can lead to speciation. Individuals may disperse across pre-existing barriers to found new populations. Those populations may subsequently become genetically and ecologically isolated from the founder population (Newton 2003). Parrots are among the land bird families with relatively good dispersal and colonization abilities on oceanic islands (Begon et al. 1998).

Table 5. Pairwise p-distance values for 16 taxa of Eclectus roratus *used in the phylogenetic analysis, based on 1,140 mtDNA nucleotides of cytochrome b (cyt b). The analysis was calculated in MEGA 5.2.2 (Tamura et al. 2011).*

No	Taxon + IPMB ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	*E. r. aruensis* 34683															
2	*E. r. aruensis* 34684	0.000														
3	*E. r. cornelia* 34685	0.017	0.017													
4	*E. r. cornelia* 34686	0.017	0.017	0.000												
5	*E. r. polychloros* 34687	0.000	0.000	0.017	0.017											
6	*E. r. riedeli* 34688	0.023	0.023	0.027	0.027	0.023										
7	*E. r. riedeli* 34689	0.023	0.023	0.027	0.027	0.023	0.000									
8	*E. r. riedeli* 34692	0.023	0.023	0.027	0.027	0.023	0.000	0.000								
9	*E. r. roratus* AB177948	0.017	0.017	0.019	0.019	0.017	0.029	0.029	0.029							
10	*E. r. roratus* 34693	0.009	0.009	0.014	0.014	0.009	0.017	0.017	0.019	0.011						
11	*E. r. roratus* 34701	0.010	0.010	0.015	0.015	0.010	0.018	0.018	0.020	0.010	0.001					
12	*E. r. solomonensis* 34680	0.003	0.003	0.016	0.016	0.003	0.022	0.022	0.022	0.016	0.008	0.009				
13	*E. r. solomonensis* 34682	0.003	0.003	0.016	0.016	0.003	0.022	0.022	0.022	0.016	0.008	0.009	0.000			
14	*E. r. solomonensis* 34697	0.003	0.003	0.016	0.016	0.003	0.022	0.022	0.022	0.016	0.008	0.009	0.000	0.000		
15	*E. r. solomonensis* 34698	0.003	0.003	0.016	0.016	0.003	0.022	0.022	0.022	0.016	0.008	0.009	0.000	0.000	0.000	
16	*E. r.* unknown origin 34702	0.004	0.004	0.015	0.015	0.004	0.023	0.023	0.023	0.016	0.009	0.010	0.003	0.003	0.003	0.003

Table 6. Pairwise p-distance values for 24 taxa of Trichoglossus used in the phylogenetic analysis, based on mitochondrial 1,140 nucleotides of cyt b. The analysis was calculated in MEGA 5.2.2 (Tamura et al. 2011).

No	Taxon + IPMB ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	T. euteles AB177943																							
2	T. euteles AB177963	0.002																						
3	T. h. nigrogularis 9353	0.014	0.013																					
4	T. h. caeruleiceps 35195	0.015	0.013	0.000																				
5	T. h. caeruleiceps 35196	0.015	0.013	0.000	0.000																			
6	T. h. capistratus 35200	0.017	0.015	0.012	0.012	0.012																		
7	T. h. capistratus 35201	0.017	0.015	0.012	0.012	0.012	0.000																	
8	T. h. deplanchii 35205	0.012	0.010	0.004	0.004	0.004	0.006	0.006																
9	T. h. deplanchii 35206	0.012	0.010	0.004	0.004	0.004	0.006	0.006	0.000															
10	T. h. forsteni 35209	0.014	0.013	0.010	0.010	0.010	0.008	0.008	0.004	0.004														
11	T. h. forsteni 35212	0.016	0.014	0.008	0.008	0.008	0.007	0.007	0.004	0.004	0.003													
12	T. h. fortis 9354	0.017	0.015	0.011	0.012	0.012	0.002	0.002	0.004	0.004	0.009	0.008												
13	T. h. massena 35213	0.013	0.011	0.006	0.007	0.007	0.010	0.010	0.000	0.000	0.008	0.004	0.010											
14	T. h. massena 35214	0.013	0.011	0.006	0.007	0.007	0.010	0.010	0.000	0.000	0.008	0.004	0.010	0.000										
15	T. h. mitchellii 35215	0.015	0.013	0.009	0.012	0.012	0.009	0.009	0.003	0.003	0.005	0.004	0.010	0.010	0.010									
16	T. h. mitchellii 35216	0.015	0.013	0.009	0.010	0.010	0.007	0.007	0.003	0.003	0.005	0.004	0.010	0.009	0.009	0.002								
17	T. h. moluccanus 35222	0.015	0.013	0.000	0.000	0.000	0.012	0.012	0.004	0.004	0.010	0.008	0.012	0.007	0.007	0.012	0.010							
18	T. h. moluccanus 35223	0.015	0.013	0.000	0.000	0.000	0.012	0.012	0.004	0.004	0.010	0.008	0.012	0.007	0.007	0.012	0.010	0.000						
19	T. h. rosenbergii 35226	0.013	0.011	0.006	0.006	0.006	0.010	0.010	0.000	0.000	0.008	0.004	0.009	0.000	0.000	0.007	0.007	0.006	0.006					
20	T. h. rosenbergii 35227	0.013	0.011	0.006	0.007	0.007	0.010	0.010	0.000	0.000	0.008	0.004	0.010	0.000	0.000	0.010	0.009	0.007	0.007	0.000				
21	T. h. rubritorquis 35225	0.014	0.013	0.010	0.010	0.010	0.009	0.009	0.004	0.004	0.007	0.006	0.010	0.008	0.008	0.006	0.006	0.010	0.010	0.008	0.008			
22	T. h. rubritorquis 35228	0.015	0.013	0.010	0.010	0.010	0.009	0.009	0.004	0.004	0.008	0.006	0.012	0.009	0.009	0.009	0.007	0.010	0.010	0.008	0.009	0.000		
23	T. h. weberi 35231	0.013	0.011	0.013	0.014	0.014	0.013	0.013	0.012	0.012	0.014	0.016	0.013	0.013	0.013	0.015	0.013	0.014	0.014	0.012	0.013	0.014	0.013	
24	T. h. weberi 35232	0.013	0.011	0.013	0.014	0.014	0.013	0.013	0.012	0.012	0.014	0.016	0.013	0.013	0.013	0.015	0.013	0.014	0.014	0.012	0.013	0.014	0.013	0

3.2. Speciation events in Australasia

Both vicariance and dispersal may be of importance for speciation processes in the two examined parrot species complexes. Populations may diverge quite quickly in morphological terms, especially in the *Trichoglossus-haematodus* complex. Genetic differentiation was lower for shelf populations connected by land bridges during the Pleistocene and Holocene than for older populations on isolated islands across the Wallacea. The higher genetic diversity in the Wallacea may be a consequence of several independent colonization events from source islands (*Eclectus*: Moluccas, *Trichoglossus*: New Guinea) to sink islands (e.g. Lesser Sunda Islands), where some populations may have become extinct and were later replaced by new invasions.

The distribution patterns of land birds in the Wallacea which are younger than 5 million years are apparently due to long distance dispersal and not due to tectonic activity (concept see Carstensen et al. 2012). Based on the finding that speciation in the two examined parrot complexes is much younger, it is clear that tectonic activity can neither explain speciation in *Eclectus*, nor in *Trichoglossus*. Their occurrence on oceanic islands should be attributed to long distance dispersal or vicariance during the Pleistocene and Holocene.

3.3. Genetic origin inside or outside the Wallacea

Two separate scenarios for *Eclectus* and *Trichoglossus* can be inferred from both phylogenetic analysis and molecular dating.

Eclectus scenario: out-of-Moluccas-hypothesis

As shown in Figure 2, the most likely origin of *Eclectus* spp. is in the Moluccas (*roratus*). The Lesser Sunda Islands with Sumba (*cornelia*), the Tanimbar islands (*riedeli*) and New Guinea (*polychloros*, *solomonensis*, *aruensis*) had presumably been colonized from there, very likely also N Australia (*macgillivrayi*) which was not included in the dataset. *Eclectus* is capable of long-distance dispersal: Pleistocene and Holocene fossils were found on Tonga, c. 2,700 km SE of the current distribution, probably also on Rota (Mariana Is.) (Steadman 1993). An explanation for the low genetic distance across the Sahul Shelf may be land bridges during the Pleistocene (Voris 2000) or recent dispersal.

Trichoglossus scenario: out-of-New-Guinea-hypothesis

In the *T.-haematodus*-complex at least four different lineages occur on the Lesser Sunda Islands (*euteles*, *weberi*, *capistratus/fortis*, *mitchellii/forsteni*), Australia was colonized by two different lineages (*rubritorquis* and *moluccanus*). A similar colonization pattern of the Rainbow Lorikeet was proposed by Forshaw (1977) without given the genetic background. He stated that Australia had been colonized twice, through S New Guinea and through the Lesser Sunda islands. This conjecture is supported by this study.

The finding of the populations in N Australia and the Lesser Sunda Islands being closely related is puzzling because the taxa are found more than 1,000 km from each other. A similar biogeographic pattern as in *mitchellii/forsteni/rubritorquis*

(Lesser Sunda Islands and N Australia) can be found in fruit doves. *Ptilinopus alligator* lives in N Australia, *P. cinctus* on the Lesser Sunda Islands except Sumba, and *P. dohertyi* on Sumba (Cox 1997). This finding may be explained by the smaller geographic distance between Lesser Sunda Islands and the Sahul Shelf during the Pleistocene.

3.4. *Eclectus* and *Trichoglossus*: rapid evolution and implications for taxonomy

In the *Eclectus-roratus*-complex four morphologically and biogeographically distinct lineages are clearly defined genetically. A separate species status based on genetic distance is supported for the following populations: (1) Sumba (*cornelia*), (2) Tanimbar Is. (*riedeli*), (3) Moluccas (*roratus*)*,* and (4) New Guinea (including *aruensis, polychloros, solomonensis*, and probably other blue-bellied taxa in and around New Guinea and N Australia). A taxonomic revision for *Eclectus roratus* is suggested in Table 7, but further studies including more material of wild populations are needed.

In case of the cryptic Western Ground Parrot (*Pezoporus wallicus flaviventris*) p-distance values of 4.4–5.1% between western and eastern populations of Australia were equal to a divergence time of 2 Ma, suggesting a separate species status for the western population *P. wallicus* (Murphy et al. 2011). In the *Trichoglossus-haematodus*-complex, the situation is more complicated. The distribution of the *T. haematodus* taxa reflects the Checkerboard distribution pattern (Diamond 1975), meaning that two closely related species never occur on the same islands, based on the presence of competitors (Newton 2003). The case of *T.* (*h.*) *euteles* and *T. h. capistratus* is puzzling as both are occurring on the island of Timor, which is contradictory to the Checkerboard distribution for closely related species. The sympatry of *euteles* and *capistratus* suggests that both taxa are evolutionary sufficiently distinct from each other to form two distinct species. Given the p-distance of 1.7% and the time frame of 800,000 years, a rapid evolution into two distinct species took place. This is the highest p-distance value within the *T. haematodus* complex. The smaller *T.* (*h.*) *euteles* lives at altitudes from sea level to 2,400 m and seems to be commoner than the larger *T. h. capistratus* on Timor, replacing *capistratus* at higher altitudes and on several nearby islands (Juniper & Parr 2003). *T. h. rosenbergii* is considered a full species by del Hoyo et al. (2014) based on its different colour pattern and the isolated population on the island of Biak. Our data shows an identical haplotype of *rosenbergii* together with other taxa from the islands north of New Guinea (*massena, deplanchii*). It is a case of dramatically rapid evolution within less than 50,000 years, probably less than 18.000 years BP, see Figure 6. The same situation is present in the Australia-S New Guinea clade. *T. h. moluccanus* (E Australia), *T. h. nigrogularis* (Aru Is.) and *T. h. caeurleiceps* (S New Guinea) share a common haplotype. A similar case of very recent speciation is known from the swift complex *Apus apus/A. pallidus*, which are considered distinct species, but share a common haplotype. The same is true for the complex *A. affinis/A. nipalensis*, see Päck-

Table 7. Suggested taxonomic revision of Eclectus roratus *based on phylogenetic units. Only taxa used in the study are displayed.*

Species	includes
Eclectus roratus	*E. r. roratus*
Eclectus cornelia	*E. r. cornelia*
Eclectus riedeli	*E. r. riedeli*
Eclectus polychloros	*E. r. polychloros*
	E. r. aruensis
	E. r. solomonensis

Table 8. Suggested taxonomic revision of Trichoglossus haematodus *based on phylogenetic units. Only taxa used in the study are displayed.*

Species	includes
Trichoglossus haematodus	*T. h. rosenbergii*
	T. h. massena
	T. h. deplanchii
Trichoglossus weberi	*T. h. weberi*
Trichoglossus moluccanus	*T. h. moluccanus*
	T. h. nigrogularis
	T. h. caeruleiceps
Trichoglossus rubritorquis	*T. h. rubritorquis*
Trichoglossus capistratus	*T. h. capistratus*
	T. h. fortis
Trichoglossus mitchellii	*T. h. mitchellii*
Trichoglossus forsteni	*T. h. forsteni*
Trichoglossus euteles	*T. (h.) euteles*

ert et al. (2012). Other examples of rapid radiation within the parrot family is the genus *Psittacula* (Braun et al. 2016) with the South Asian Ring-necked Parakeet showing a new breeding behavior or rapid morphological changes in a different climate such as in temperate Europe (Braun 2007, 2014; Le Gros et al. 2016).

In summary, our study largely follows the suggestions of del Hoyo et al. (2014), but additionally provides molecular data for a majority of taxa as a supplementary criterion. The following 8 different lineages are proposed for recognition in taxonomy based on mitochondrial haplotypes: (1) haplotype N New Guinea (*rosenbergii*, *massena*, *deplanchii*), (2) haplotype S New Guinea (*nigrogularis*, *caeruleiceps*, *moluccanus*), (3) Flores (*weberi*), (4) Timor (*euteles*), (5) Timor and Sumba (*capistratus*, *fortis*), (6) Bali/Lombok (*mitchellii*), (7) Sumbawa (*forsteni*), and (8) N Australia (*rubritorquis*). A taxonomic revision for *T. haematodus* is suggested in Table 8.

3.5. Implications for conservation and further research

Studies in several groups of organisms increase the importance of Australasia for global biodiversity (Springer et al. 1998; Aplin 2006; Sanders et al. 2008). While morphological or ecological change is low in some groups of non-migratory songbirds, leading to a so-called 'cryptic diversity' (Lohman et al. 2010; Fernandes et al. 2013), the investigated parrots were found to diverge to a greater extent.

The study shows that speciation is underway in Australasia. Diversification took place in both *Eclectus* and *Trichoglossus*. This highlights the importance of areas of endemism, in which the Wallacea clearly belongs. For conservation reason, several taxa are suggested being elevated to species level under the criteria of Tobias et al. (2010). Although *T. haematodus* has been regarded as a common species with a conservation status of "Least Concern" (Stattersfield et al. 2014), the elevation of several populations to species level will lead to a different situation (see Taylor 2013). Several populations are now under decline, especially due to the trapping pressure, especially on Biak (*T. h. rosenbergii*) with a population < 10,000 birds, but also on

Flores (*T. h. weberi*), on Bali/Lombok (*T. h. mitchellii*), on Sumbawa (*T. h. forsteni*) and other populations on smaller islands (Taylor 2013). The taxon *mitchellii* currently is in the situation of being 'extinct in the wild' from both Bali and Lombok (T.A., R. Wüst, pers. comm., 2015), the status of many other taxa is still insufficiently known.

In the *Eclectus-roratus*-complex, the elevation of several populations to species level will lead to a different situation regarding the current conservation status of "Least Concern" (Ekstrom & Butchart 2014). Populations on Sumba (*E. r. cornelia*) and Tanimbar Islands (*E. r. riedeli*) are endangered through trapping pressure, while *E. r. roratus* became extinct on Ambon, Saparua and Haruku for the same reason (Arndt 2008).

Further investigations are recommended. As only captive individuals were sampled, a taxon sampling of all wild populations and supplemental methods may reveal further information on the speciation processes of these and other Australasian birds.

For conservation policy of parrots in Australasia and Indonesia it is strongly recommended to (1) conserve the smaller island populations, (2) ban trapping of wild birds for the pet trade, and (3) ban the release of traded non-native populations into new areas in order to avoid genetic mixture between different populations.

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