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

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32 SUMMARY

33 Background

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

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

62 listed as "Least Concern". *Eclectus roratus* is currently treated as monospecific. Based on genetic evidence, the
63 following populations are suggested being treated as valid species: (1) Sumba (*Eclectus cornelia*), (2) Tanimbar
64 Islands (*E. riedeli*), (3) Moluccas (*E. roratus*), and (4) New Guinea (*E. polychloros* incl. Aru Islands (*E. aruensis*),
65 and Solomon Island (*E. solomonensis*).

66 **Keywords** avifauna; Checkerboard distribution; vicariance; dispersal; island biogeography; geographic
67 isolation; Indonesia; Loriidae; population genetics; Psittacidae

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69 INTRODUCTION

70 **Geological background and Pleistocene influence on Australasia**

71 The Indo-Malayan or Australasian region underwent several major geological periods, a good overview is given
72 in Hall (2002). New Guinea collided with the East Philippines-Halmahera system 25 Ma, resulting in a rotation of
73 the Philippine Sea Plate. Since 25 Ma the Pacific Plate and Australia are moving, causing rotations and sending
74 microcontinental fragments to SE Asia. About 5 Ma boundaries and plate motions changed again. The region was
75 and still is changing at a rapid rate based on plate tectonics and volcanic activity. A complex geological pattern is
76 observed in Sulawesi. While West Sulawesi originates from the Sunda Shelf in SE Asia, East Sulawesi originates
77 from the Australian plate; both merged in the late Miocene. Moreover, the Lesser Sunda Islands are of different
78 origin and its current formation became part of the Wallacea during the past 0-15 million years (Hall 2002).

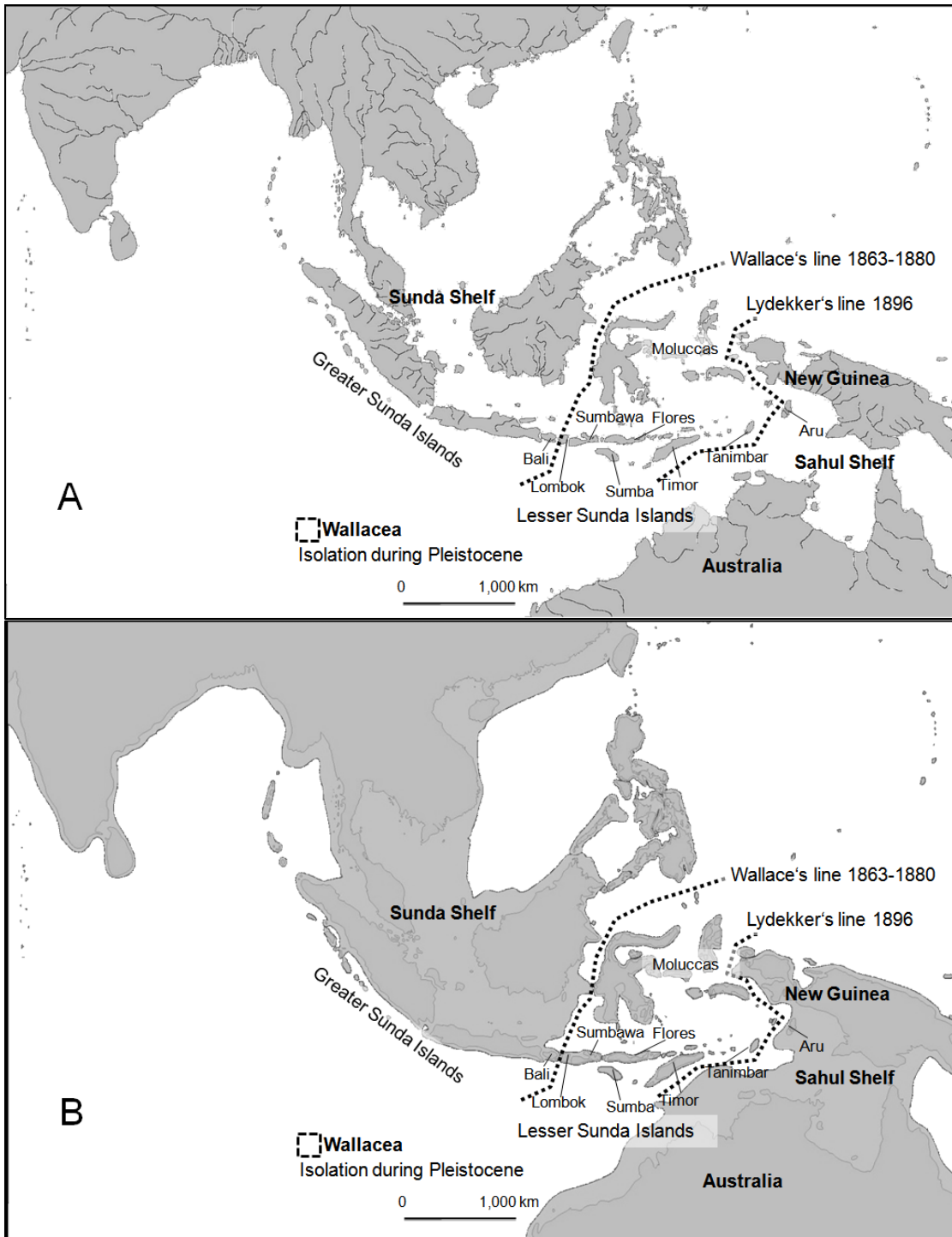
79 The Australasian region includes Australia, New Zealand, New Guinea and the Wallacea, see Figure 1. The region
80 is a hotspot of biodiversity and endemism (Marsden & Fielding 1999; Carstensen et al. 2012). The Wallacea is a
81 biogeographic region including the Lesser Sunda Islands, Sulawesi, and the Moluccas, it is located between the
82 Orientalis (S Asia) and the Australis (Australia, New Guinea, and New Zealand). The Wallacea is defined as a
83 transition zone between the Indomalayan and the Australian fauna using Wallace's line (birds) as the western
84 border and Lydekker's line (mammals) as the eastern border (Lydekker, 1896; Newton, 2003; Wallace, 1876), see
85 Figure 1. Pleistocene sea level changes had a strong influence on the shoreline of Australasia (Figure 1). When
86 glaciations occurred in the northern hemisphere, sea levels were usually low, whereas a rise in sea levels occurred
87 during warm periods. During the last glacial maximum (18,000 years BP), with a sea level of 120 to 130 m below
88 the current shoreline, Australia, New Guinea and the Aru archipelago were part of the same land mass of the Sahul
89 Shelf (Lavering, 1993; Voris, 2000). The climate of N Australia was drier than today, leading to an increase of
90 grassland replacing eucalypt forests (Van der Kaars, 1991).

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97 Figure 1 – Australasian region including the Wallacea. Regions shaded in grey represent land mass, white regions
 98 represent sea. A: current sea level; B: sea level of 120 m below the current shoreline (18,000 years BP). The islands
 99 of the Wallacea (shape) remained isolated both from the Sunda and Sahul Shelf during the Pleistocene (Voris
 100 2000). During the last Pleistocene, Australia, New Guinea and the Aru Islands were part of the same land mass
 101 (Sahul Shelf). Map by courtesy of H. Voris, Fieldmuseum Chicago.

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105 **Avifauna of the Wallacea**

106 In general, 17% of all land bird species occur on islands, but the land birds of Australasia hold the highest
107 proportion of island taxa with a total of 36% (Newton, 2003). Endemism is high in the Wallacean avifauna, with
108 64% of endemic bird species both in the Moluccas and Lesser Sunda Islands (Carstensen et al. 2012). The avifauna
109 of the Wallacea has been a research object for ornithologists and evolutionary biologists since the time of Alfred
110 Russel Wallace and Ernst Mayr (Wallace 1869; Mayr 1941). Parrots are abundant in the Wallacea and are still an
111 object of current research (Marsden & Fielding 1999). 111 parrot species are threatened with extinction worldwide,
112 representing 28% of all parrot species, (Olah et al., 2016). It should be recalled that Australasia is one of the
113 regions with the highest number of threatened parrot taxa (Collar 2000).

114 **Dispersal, colonization, and island evolution**

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

120 Colonization is dependent on the abundance within a species' range, which is a mixture between source and sink
121 areas. Highest densities (source areas) are mostly found in the centre of the range (Newton 2003). Source areas
122 enable a species to produce a surplus of offspring, which are able to colonize other areas. Sink areas, on the other
123 hand, are most likely to occur in range boundaries, where conditions become less suitable and populations often
124 depend on immigration (Newton 2003). While some bird families like herons, rails, parrots, pigeons, or kingfishers
125 are generally successful colonizers of oceanic islands, others like pelicans, storks, larks, pheasants, or birds of
126 paradise are less successful colonizers (Begon et al. 1998). The colonization of islands may lead to rapid evolution
127 in morphology and behaviour through founder events. As an example, flightlessness and considerably modified
128 skeleton in Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*) may be attained in less than 80,000
129 years (Newton 2003). The evolution of four to five distinct bird taxa in Northern Melanesia occurred within only
130 300 years (Mayr & Diamond 2001). A rapid morphological evolution within only 10 generations was detected in
131 introduced 'habitat island' bird populations: introduced Asian Ring-necked Parakeets (*Psittacula krameri*) in
132 cities of Europe have broader beaks, longer skulls and longer wings than in their native range (Le Gros et al.,
133 2016).

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

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

- 139 1. Do bird populations on shelf islands that were connected by land bridges during the Pleistocene,
140 show similar genetic distances when compared to populations within several million year old oceanic
141 islands?
- 142 2. Is the Wallacea an origin of endemism or are source populations (ancestral origins) located outside
143 the Wallacea? Can we assign ancestral lineages to the Wallacea or Sahul Shelf?

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

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151 **Study species**

152 Study species 1: Eclectus Parrot *Eclectus roratus* Wagler, 1832

153 The Eclectus Parrot, a rain forest dweller (deciduous forest on Sumba), is known for its well-defined reverse sexual
154 dichromatism: males are greenish and females are red and blue (Forshaw 2006). Furthermore the polyandrous
155 mating system (up to seven males for one female) in this species is unusual in parrots and some females are known
156 to produce consecutive chicks of the same sex (Heinsohn et al., 1997). Breeding success in wild birds is low in
157 this species, only 18% of eggs and 27% of clutches produced a fledgling (Heinsohn & Legge, 2003). The greenish
158 males fly long distances to feed the female and brood, and need to camouflage themselves from predators while
159 the red-and-bluish females compete for rare nest holes (Heinsohn et al. 2005). Although the sex ratio of nestlings
160 is equal, the adult sex ratio in the population is skewed towards males (Heinsohn & Legge 2003). Currently there
161 are nine recognized subspecies: *E. roratus*, *vosmaeri*, *cornelia*, *riedeli*, *polychloros*, *solomonensis*, *aruensis*, *biaki*,

162 and *macgillivrayi* (*westermani* not included) (Forshaw 2010). For distributions see Figure 2. There is no current
 163 discussion about the elevation of subspecies to full species within the *Eclectus-roratus*-complex (see Ekstrom &
 164 Butchart 2014).

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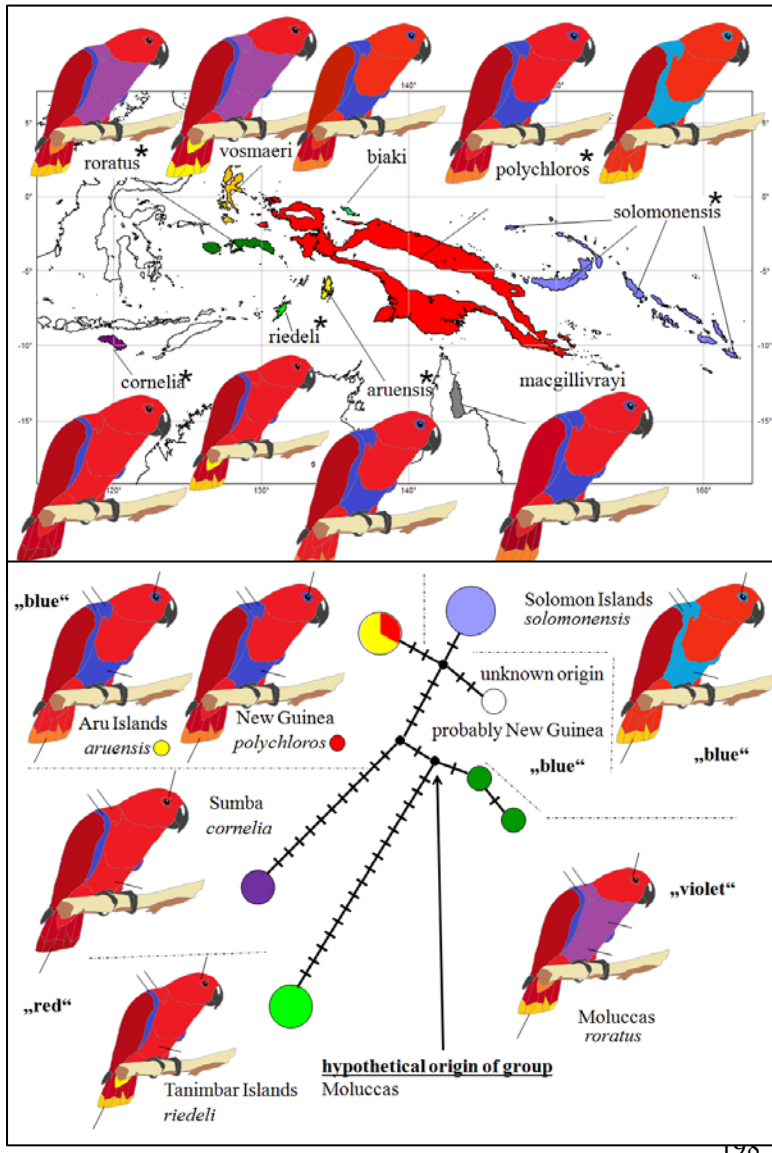


Figure 2 – (a) above: Distribution of all subspecies of *Eclectus roratus*. Asterisks indicate all available taxa included in the analysis. Each population is represented by a separate colour code, which is also used in the network analysis. Only females are illustrated, males of different taxa are similar 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*) ($\epsilon=0$). 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", characteristic differences between taxa are marked with lines. Only females are illustrated. An individual with unknown origin clusters within the blue-bellied New Guinea group.

Study species 2: Rainbow lorikeet

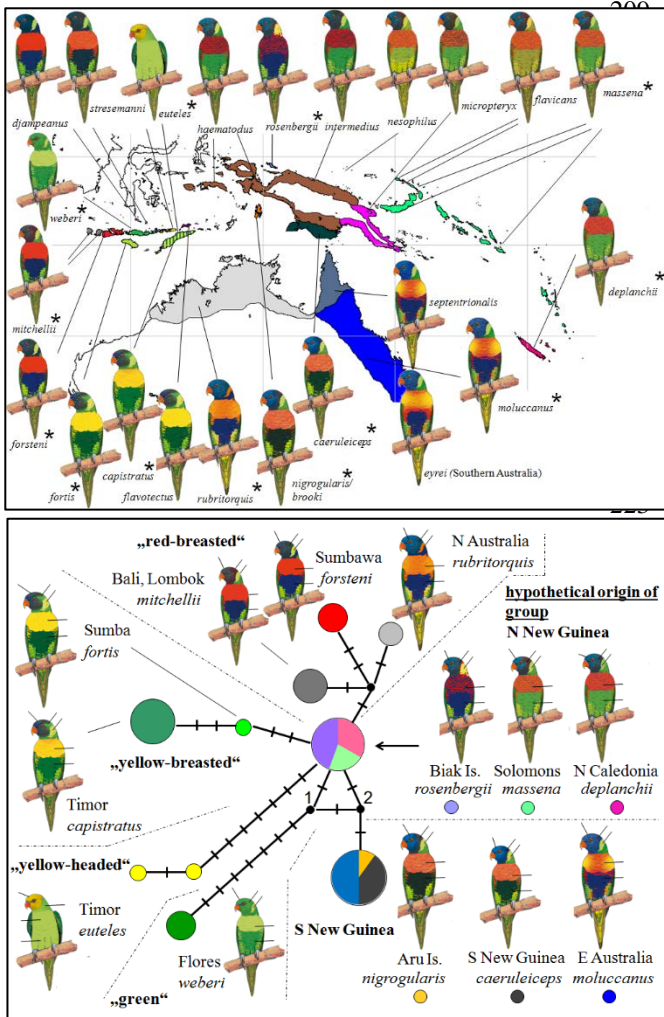
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200 *Trichoglossus haematodus* Linnaeus, 1771

201 In contrast, the colourful Rainbow Lorikeet, which does not exhibit a pronounced sexual dichromatism, is an
 202 abundant, social, nectarivorous parrot (Forshaw 2010). It is found in open woodland in the tropical lowlands, and
 203 commonly occurs in urban areas of Australia. It competes with similarly sized birds for nest holes (Franklin 1997;

204 Waterhouse 1997; Shukuroglou & McCarthy 2006; Legault et al. 2011). *T. haematodus* is strikingly diverse, the
 205 number of taxa differs – according to authors – between 20 (Forshaw 2010) and 22 subspecies (Arndt 2012), see
 206 Figure 4.

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239 independent genetic lineages. Drawings are with courtesy of Thomas Arndt.

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241 The taxonomy of the *Trichoglossus-haematodus*-complex is currently under discussion. Del Hoyo et al. (2014)
 242 distinguish the following taxa, using criteria of Tobias et al. (2010): (1) *T. rosenbergii* (monotypic), (2) *T. forsteni*
 243 (incl. *mitchellii*, *djampeanus* and *stresemanni*), (3) *T. weberi* (monotypic), (4) *T. haematodus* (all taxa from New
 244 Guinea North and South including satellite islands and Solomons), (5) *T. moluccanus* (incl. *septentrionalis*), (6)
 245 *T. capistratus* (incl. *fortis* and *flavotectus*), and (7) *T. rubritorquis* (monotypic). (8) *T. euteles* is treated as a
 246 separate species. Molecular evidence is still insufficient for this group and was not a basis for the arrangement of

Figure 3 – (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*) ($\epsilon=0$). 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., characteristic 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

247 del Hoyo et al. (2014). The taxon *T. h. brooki* Ogilvie-Grant, 1907 (Aru Islands) is regarded taxonomically invalid,
 248 as the two known museum specimen are of captive origin, most likely to be juveniles of *T. h. nigrogularis* (T. A.).

249 MATERIALS AND METHODS

250 Sampling

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

256

257 Table 1 *Eclectus* & *Trichoglossus*: sample information of the current study. Origin: LPF: Loro Parque
 258 Fundación, Tenerife, Spain;
 259 CMH: C. Mettke-Hofmann. *T. euteles* sequences were retrieved from GenBank.

260

Scientific Name	IPMB ID.	Accession number	GI number	Origin	Distribution	Wild/Captive
<i>Chamosyna papou</i>	49578	KM372511		LPF	New Guinea	c
<i>Psitteuteles goldiei</i>	31315	KM372512		LPF	New Guinea	c
<i>Melopsittacus undulatus</i>	-	EF450826			Australia	c
<i>Psittacula alexandri abbotti</i>	34985	KM372495		LPF	Nicobar Islands	c
<i>Eclectus roratus aruensis</i>	34683	KM372496		LPF	Aru Islands	c
<i>Eclectus roratus aruensis</i>	34684	KM372497		LPF	Aru Islands	c
<i>Eclectus roratus cornelia</i>	34685	KM372498		LPF	Sumba	c
<i>Eclectus roratus cornelia</i>	34686	KM372499		LPF	Sumba	c
<i>Eclectus roratus polychloros</i>	34687	KM372500		LPF	New Guinea	c
<i>Eclectus roratus riedeli</i>	34688	KM372501		LPF	Tanimbar Island	c
<i>Eclectus roratus riedeli</i>	34689	KM372502		LPF	Tanimbar Island	c
<i>Eclectus roratus riedeli</i>	34692	KM372503		LPF	Tanimbar Island	c
<i>Eclectus roratus</i>		AB177948		Astuti et al. (2006)	Moluccas	w?
<i>Eclectus roratus roratus</i>	34693	KM372504		LPF	Buru, Seram	c
<i>Eclectus roratus solomonensis</i>	34680	KM372506		LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c
<i>Eclectus roratus solomonensis</i>	34682	KM372507		LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c
<i>Eclectus roratus solomonensis</i>	34697	KM372508		LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c
<i>Eclectus roratus solomonensis</i>	34698	KM372509		LPF	Solomon Islands, Bismarck & Admiralty Archipelagos	c

<i>Eclectus roratus roratus</i>		34701	KM372505		LPF	Moluccas	c
<i>Eclectus</i> ssp. unknown origin		34702	MG429727		LPF	presumably New Guinea	c
<i>Trichoglossus euteles</i>			AB177963	121308487	Astuti et al. (2006)	Timor, Lomblen to Nila & Babar	w?
<i>Trichoglossus euteles</i>			AB177943	121308447	Astuti et al. (2006)	Timor, Lomblen to Nila & Babar	w?
<i>Trichoglossus nigrogularis</i>	<i>haematodus</i>	9353			CMH	Aru Islands	c
			KM372513				
<i>Trichoglossus caeruleiceps</i>	<i>haematodus</i>	35195			LPF	S New Guinea	c
			KM372514				
<i>Trichoglossus caeruleiceps</i>	<i>haematodus</i>	35196			LPF	S New Guinea	c
			KM372515				
<i>Trichoglossus caeruleiceps</i>	<i>haematodus</i>	35197	MG429705		LPF	S New Guinea	c
<i>Trichoglossus caeruleiceps</i>	<i>haematodus</i>	35198	MG429706		LPF	S New Guinea	c
<i>Trichoglossus capistratus</i>	<i>haematodus</i>	35199	MG429709		LPF	Timor	c
<i>Trichoglossus capistratus</i>	<i>haematodus</i>	35200			LPF	Timor	c
			KM372516				
<i>Trichoglossus capistratus</i>	<i>haematodus</i>	35201			LPF	Timor	c
			KM372517				
<i>Trichoglossus capistratus</i>	<i>haematodus</i>	35202	MG429707		LPF	Timor	c
<i>Trichoglossus capistratus</i>	<i>haematodus</i>	31259	MG429708		LPF	Timor	c
<i>Trichoglossus capistratus</i>	<i>haematodus</i>	9346	MG429724		CMH	Timor	c
<i>Trichoglossus deplanchii</i>	<i>haematodus</i>	35205	MG429710		LPF	New Caledonia & Loyalty Islands	c
<i>Trichoglossus deplanchii</i>	<i>haematodus</i>	35206			LPF	New Caledonia & Loyalty Islands	c
			KM372519				
<i>Trichoglossus deplanchii</i>	<i>haematodus</i>	35207	MG429711		LPF	New Caledonia & Loyalty Islands	c
<i>Trichoglossus forsteni</i>	<i>haematodus</i>	35209	KM372520		LPF	Sumbawa Island	c
<i>Trichoglossus forsteni</i>	<i>haematodus</i>	35210	MG429713		LPF	Sumbawa Island	c
<i>Trichoglossus forsteni</i>	<i>haematodus</i>	35211	MG429712		LPF	Sumbawa Island	c
<i>Trichoglossus forsteni</i>	<i>haematodus</i>	35212			LPF	Sumbawa Island	c
			KM372521				
<i>Trichoglossus haematodus fortis</i>	<i>haematodus</i>	9354	MG429726		CMH	Sumba Island	c
<i>Trichoglossus massena</i>	<i>haematodus</i>	35213	MG429714		LPF	Karkar, Archipelago Islands & Bismarck Solomon	c
<i>Trichoglossus massena</i>	<i>haematodus</i>	35214	MG429715		LPF	Karkar, Archipelago Islands & Bismarck Solomon	c
<i>Trichoglossus mitchellii</i>	<i>haematodus</i>	35215			LPF	Bali & Lombok	c
			KM372525				
<i>Trichoglossus mitchellii</i>	<i>haematodus</i>	35216			LPF	Bali & Lombok	c
			KM372526				
<i>Trichoglossus mitchellii</i>	<i>haematodus</i>	35217	MG429716		LPF	Bali & Lombok	c
<i>Trichoglossus mitchellii</i>	<i>haematodus</i>	35218	MG429717		LPF	Bali & Lombok	c
<i>Trichoglossus moluccanus</i>	<i>haematodus</i>	35221	MG429718		LPF	eastern Australia to Tasmania	c
<i>Trichoglossus moluccanus</i>	<i>haematodus</i>	35222			LPF	eastern Australia to Tasmania	c
			KM372527				

<i>Trichoglossus moluccanus</i>	<i>haematodus</i>	35223	KM372528	LPF	eastern Australia to Tasmania	c
<i>Trichoglossus moluccanus</i>	<i>haematodus</i>	9312	MG429722	CMH	eastern Australia to Tasmania	c
<i>Trichoglossus moluccanus</i>	<i>haematodus</i>	9323	MG429723	CMH	eastern Australia to Tasmania	c
<i>Trichoglossus rosenbergii</i>	<i>haematodus</i>	35224	MG429719	LPF	Biak Island	c
<i>Trichoglossus rosenbergii</i>	<i>haematodus</i>	35226	KM372529	LPF	Biak Island	c
<i>Trichoglossus rosenbergii</i>	<i>haematodus</i>	35227	KM372530	LPF	Biak Island	c
<i>Trichoglossus rosenbergii</i>	<i>haematodus</i>	9347	MG429725	CMH	Biak Island	c
<i>Trichoglossus rubritorquis</i>	<i>haematodus</i>	35225	KM372531	LPF	N Australia	
<i>Trichoglossus rubritorquis</i>	<i>haematodus</i>	35228	KM372532	LPF	N Australia	c
<i>Trichoglossus rubritorquis</i>	<i>haematodus</i>	35229	MG429720	LPF	N Australia	c
<i>Trichoglossus weberi</i>	<i>haematodus</i>	35231	KM372533	LPF	Flores Island	c
<i>Trichoglossus weberi</i>	<i>haematodus</i>	35232	KM372534	LPF	Flores Island	c
<i>Trichoglossus weberi</i>	<i>haematodus</i>	35233	MG429721	LPF	Flores Island	c

262 **DNA isolation, PCR, sequencing**

263 DNA was obtained from blood and tissue samples and stored in EDTA buffer (Carl Roth, Karlsruhe). Total DNA
 264 was isolated using standard proteinase K (Merck, Darmstadt) and phenol/chloroform protocols (Sambrook et al.
 265 1989). Fragments of the mitochondrial cytochrome *b* gene (*cyt b*) were amplified using specific primers, see Table
 266 2. The PCR amplifications were performed in 50 µl reaction volumes containing 1 × PCR buffer (Bioron,
 267 Ludwigshafen), 100 µM dNTPs, 0.2 units of *Taq* DNA polymerase (Bioron, Ludwigshafen), 200 ng of DNA and
 268 5 pmol of primers. PCR was carried out under the following conditions: 5 min at 94°C, followed by 35 cycles of
 269 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
 270 precipitated with 4 M NH₄Ac and ethanol (1:1:12) followed by a centrifugation for 15 min (13,000 rpm).

271 Sequencing was performed by capillary electrophoresis using a MegaBACE™ 1000 sequencer (Molecular
 272 Dynamics, Amersham Pharmacia). DNA length of *cyt b* sequences were 1,140 nucleotides (Braun 2014).

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277

278 Table 2 – Primers used for PCR amplification (amp) and DNA sequencing (seq) of cytochrome *b* gene (*cyt b*),
 279 being 1,140 nt in Psittaciformes. f= forward, r = reverse; L = light strand, H = heavy strand; Sequencing: X=CY5
 280 fluorescent label;
 281

Cyt <i>b</i> – 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	GTCTTACCATGAGGTCAAATATC	f	amp/seq (L)	Braun (2014)
L15558	TGTGAYAAAATCCCATCCACCC	f	amp/seq (L)	Braun (2014)
H15400	AAGAATCGGGTTAGGGTGGGG	r	amp/seq (H)	Braun (2014)
H15494	CCTAGGGGRTTRTTTGACC	r	amp/seq (H)	Braun (2014)
L14764_MW	TGATACAAAAAATAGGMCCMGAAGG	f	amp/seq (L)	modified from Sorenson et al. (1999)

282

283 Alignment

284 The nucleotide sequences were aligned using the CLUSTAL W algorithm (Thompson et al. 1994) with BIOEDIT
285 version 7.0.9.0 (Hall 1999). DNA sequences were checked for their quality manually, and for their vertebrate
286 mitochondrial origin by translating them into amino acids. No internal stop codons or frame-shifts were observed
287 in the sequences. Basic statistics, Neighbor-joining trees and average uncorrected p -distances were calculated with
288 MEGA 5.2.2 (Tamura et al. 2011).

289 Model selection

290 For the best fitting evolutionary model, JMODELTEST (Guindon & Gascuel 2003; Posada 2008; Darriba et al. 2012)
291 was used. The model Hasegawa, Kishino and Yano plus invariant sites (HKY+I) (Hasegawa et al. 1985) was
292 proposed to be the best fitting evolutionary model for both *Trichoglossus* and *Eclectus* mtDNA according to
293 Bayesian information criterion (BIC).

294 Maximum-Likelihood analysis

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

300 Bayesian analysis, tree editing

301 Bayesian inferences were performed with BEAST v.1.4.8 (Drummond & Rambaut 2008) and BEAST on XSEDE
302 (Miller et al. 2010). The searches were conducted under HKY model with four rate (gamma) categories as model
303 of evolution. The MCMC chain length was set to 10,000,000, logging parameters every 1,000 steps, resulting in
304 10,000 trees. The burnin was set to 1,000 (cut off the first 10% of trees). Results of the log files have been
305 statistically evaluated using the program TRACER v.1.4 (Rambaut & Drummond 2007). Additional Bayesian
306 analysis was performed using MRBAYES 3.2.2 (Ronquist et al. 2012) on XSEDE (Miller et al. 2010) with HKY
307 and equal rates. Phylogenetic trees were arranged and edited using FIGTREE v1.4.0 (Rambaut 2012).

308 Network

309 Mitochondrial haplotype alignments (cyt *b*) were analyzed using NETWORK v. 4.6.1.1 (Polzin & Daneshmand
 310 2012). The network was calculated using the Median Joining method (MJ) (Bandelt et al. 1999) with epsilon=0 in
 311 order to keep the shortest tree. The dataset was formatted in NETWORK 4.6.1.1 and redrawn for publication.

312 **Molecular clock**

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

318 **RESULTS**

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

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

Taxon + IPMB ID	haplotype/site	1	1	1	1	1	1	1	2	2	3	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
<i>aruensis</i> 34683	NG	-	-	-	-	-	T	A	T	C	C	C	C	A	T	T	C	C	C	A	A	C	T	T	A
<i>aruensis</i> 34684	NG	-	-	-	-	-
<i>solomonensis</i> 34680	NG	-	-	-	-	-	G	C	.
<i>solomonensis</i> 34682	NG	-	-	-	-	-	G	C	.
<i>solomonensis</i> 34697	NG	-	-	-	-	-	G	C	.
<i>solomonensis</i> 34698	NG	-	-	-	-	-	G	C	.
<i>polychloros</i> 34687	NG	-	-	-	-	-
unknown origin 34702	NG	-	-	-	-	-	T	C	.
<i>cornelia</i> 34685	SUM	-	-	-	-	-	.	.	T	A	C	C	.
<i>cornelia</i> 34686	SUM	-	-	-	-	-	.	.	T	A	C	C	.
<i>riedeli</i> 34688	TAN	C	A	C	A	A	C	.	.	T	.	T	.	C	.	T	C	.	G
<i>riedeli</i> 34689	TAN	C	A	C	A	A	C	.	.	T	.	T	.	C	.	T	C	.	G
<i>riedeli</i> 34692	TAN	C	A	C	A	A	C	.	.	T	.	T	.	C	.	T	C	.	G

<i>roratus</i> AB177948	MOL	- G A G G . G C . . T . . . G . A A G C . C . .
<i>roratus</i> 34693	MOL	T A T A A . . C G . . C . .
<i>roratus</i> 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 0 0 0 0 0 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
<i>aruensis</i> 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
<i>aruensis</i> 34684	NG	. .
<i>solomonensis</i> 34680	NG T
<i>solomonensis</i> 34682	NG T
<i>solomonensis</i> 34697	NG T
<i>solomonensis</i> 34698	NG T
<i>polychloros</i> 34687	NG	. .
unknown origin 34702	NG T C
<i>cornelia</i> 34685	SUM	A G C . . . C T . G T . C . T . . C . G G C
<i>cornelia</i> 34686	SUM	A G C . . . C T . G T . C . T . . C . G G C
<i>riedeli</i> 34688	TAN	A G C T T C . . C G T C . C . C T . T . . . C C
<i>riedeli</i> 34689	TAN	A G C T T C . . C G T C . C . C T . T . . . C C
<i>riedeli</i> 34692	TAN	A G C T T C . . C G T C . C . C T . T . . . C C
<i>roratus</i> AB177948	MOL	A G C G T . . C
<i>roratus</i> 34693	MOL	A G C G T . . C
<i>roratus</i> 34701	MOL	A G C G T . . C

329

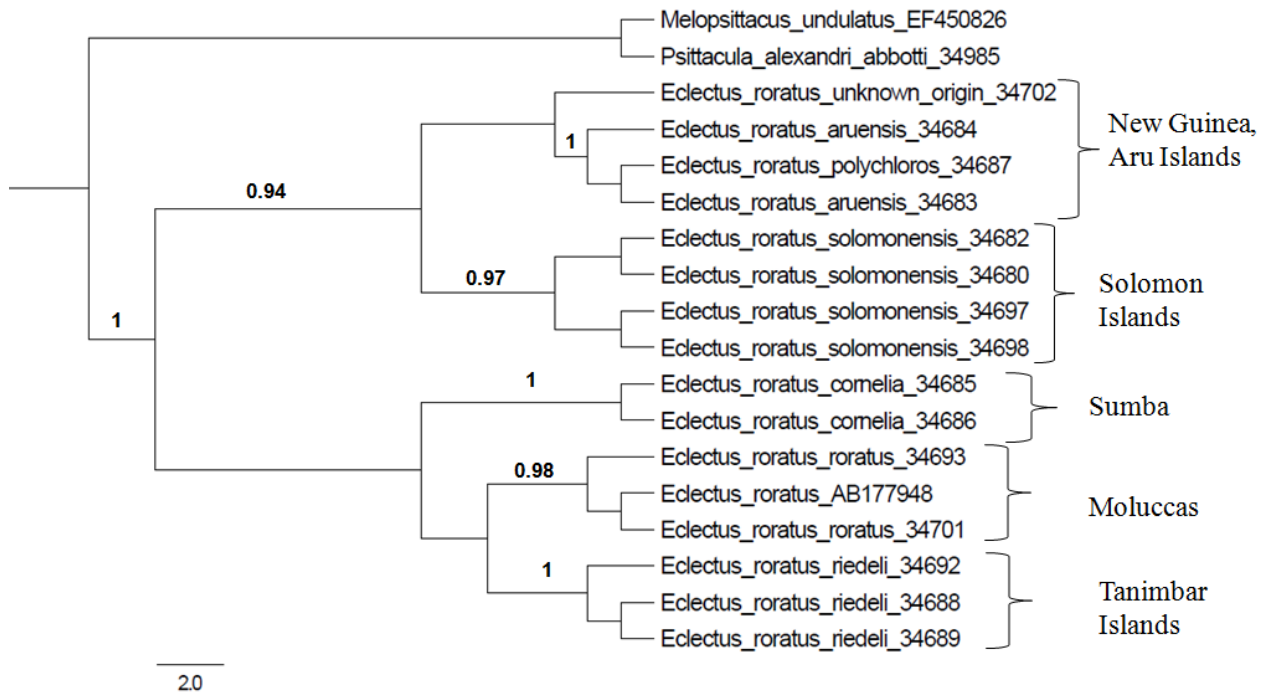
330

331 ***Eclectus-roratus*-complex: haplotype network, Wallacean origin and molecular clock**

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

339 The Bayesian analysis is documented in Figure 3. Based on a molecular rate of 2.1% divergence per one million
 340 years for cytb in birds (Weir & Schluter 2008), divergence in the stem clades in *Eclectus* is set to a maximum of
 341 1.38 million years ago (p-distance=0.029, see Table 5). The population on the Tanimbar Islands (*E. r. riedeli*)
 342 became isolated at around 1.38 Ma and the Sumba population (*E. r. cornelia*) at around 0.67-0.90 Ma. The

343 populations of New Guinea, the adjacent land mass (today e.g. represented by Aru Islands), and the Solomon
 344 Islands diverged within the past 0.43-0.81 Ma.



345
 346 Figure 4 – Bayesian analysis using BEAST v.1.4.8: maximum clade credibility tree of *Eelectus* (cyt *b*, 1,140 nt).
 347 Clades corresponding to different islands, also reported in the network analysis are well supported. Support values
 348 (posterior probabilities) above 0.9 are displayed.
 349

350

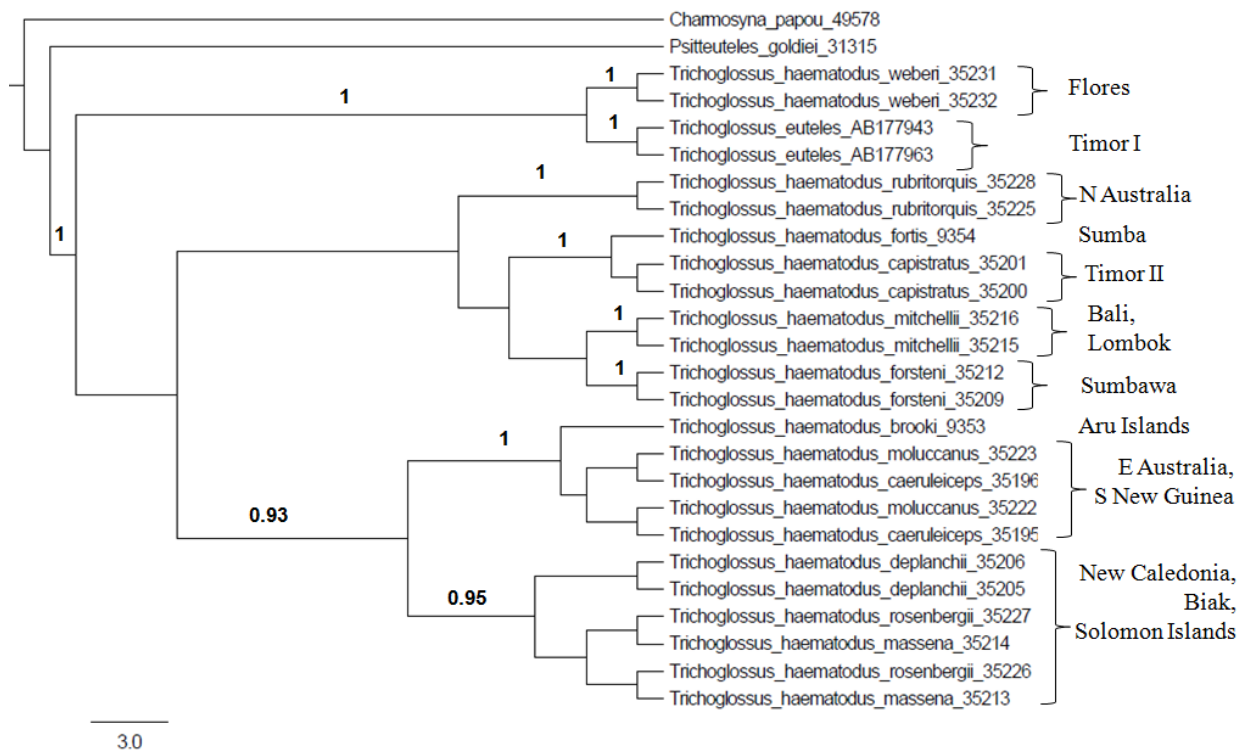
351 Table 4 – Pairwise p-distance values for 16 taxa of *Eclectus roratus* used in the phylogenetic analysis, based on
 352 1,140 mtDNA
 353 nucleotides of cytochrome *b* (cyt *b*). The analysis was calculated in MEGA 5.2.2 (Tamura et al. 2011).

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

354
355

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

357 The haplotype network for the *Trichoglossus-haematodus*-complex is illustrated in Figure 4, the Bayesian analysis
 358 is given in Figure 5. Based on the network data, the evolutionary origin of the *Trichoglossus*-complex might be
 359 situated in N New Guinea, so a non-Wallacean origin is proposed for this group. Based on the molecular rate of
 360 2.1%-rule (Weir & Schluter 2008) and the maximum divergence time within the group (N New Guinea lineage as
 361 source population to oldest lineages), the evolutionary time frame for the examined taxa of *Trichoglossus*
 362 *haematodus* is set to 0.80 million years ago (p-distance = 0.017, see Figure 4).



363
 364 Figure 5 – Bayesian Analysis using BEAST v.1.4.8: maximum clade credibility tree of *Trichoglossus* (cyt *b*,
 365 1,140 nt). Clades defined in Network 4.6.1.1 are well supported as distinct lineages while the clades “N New
 366 Guinea” (*rosenbergii*, *massena*, *deplanchii*) and “S New Guinea” (*nigrogularis*, *caeruleiceps*, *moluccanus*)
 367 remain unresolved. Support values (posterior probabilities) above 0.9 are displayed.
 368

369 The most likely origin of the *Trichoglossus-haematodus*-group is northern New Guinea, as shown in Figure 4.
 370 Several genetic lineages may be distinguished: (1) “yellow-headed” lorikeets (*T. euteles*) on Timor, (2) “green”
 371 lorikeets (*T. h. weberi*) on Flores, (3) “yellow-breasted” taxa on Sumba (*T. h. fortis*) and as a second lineage on
 372 Timor (*T. h. capistratus*), (4) Bali and Lombok (*T. mitchellii*); (5) Sumbawa (*T. forsteni*), with the closely related
 373 (6) “red-necked” lorikeet in N Australia (*T. h. rubritorquis*). The two main lineages of New Guinea split at around
 374 0.33 Ma between (7) N New Guinea clade (*T. h. rosenbergii*, *T. h. massena*, *T. h. deplanchii*) and (8) S New
 375 Guinea/Aru Islands/E Australia clade (*T. h. caeruleiceps*, *T. h. nigrogularis*, *T. h. moluccanus*). The most recent
 376 divergence events took place in the late Pleistocene, within the lineages N New Guinea and S New
 377 Guinea/Australia. The genetic distance (p-distance<0.001) suggests evolution within less than 50,000 years BP,
 378 probably younger than 18,000 years BP (last glacial maximum), see Figure 6.

379

380 Table 5 – Variable sites of the network dataset of *Trichoglossus-haematodus-complex*. Taxon names and
 381 haplotype names given. Sites as numbers top down.
 382 abbreviation of haplotypes: TIM= Timor I clade; FLOR = Flores clade; NNG = N New Guinea; SNG = S New Guinea;
 383 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
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
rubritorquis 35228	AUS	C	A	G	G	A	C	.	.	T	.	.	.	C	A	.	.	.	A	.
taxon	haplotype/site	5	5	6	6	6	7	7	7	7	8	8	8	8	8	9	9	9	9	9	9	0	0	
		4	8	2	9	9	0	2	2	5	2	4	6	7	9	1	2	5	5	7	0	1	6	
		3	2	1	6	9	0	2	6	3	2	3	4	0	4	2	7	0	4	2	2	7	9	
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	.	
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	.	.	

<i>fortis</i> 9354	SUM	. . T G . G . C A . C C C T C
<i>forsteni</i> 35209	SMBW	. . T . . G G C A T C C C T . . C . .
<i>forsteni</i> 35212	SMBW	. . T . . G G C A . C . G . . C C T . . C . .
<i>mittchellii</i> 35215	BAL	. . T . . G . C A . C A C C T . . C . .
<i>mittchellii</i> 35216	BAL	. . T . . G . C A . C A C C T . . C . .
<i>rubritorquis</i> 35225	AUS	. . T . C G . C A . C C C T . . C . C
<i>rubritorquis</i> 35228	AUS	. . T . C G . C A . C C C T . . C . C

384

385 **DISCUSSION**386 **Vicariance and dispersal**

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

397 **Speciation events in Australasia**

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

405 The distribution patterns of land birds in the Wallacea which are younger than 5 million years are apparently due
406 to long distance dispersal and not due to tectonic activity (concept see Carstensen et al. 2012). Based on the finding

407 that speciation in the two examined parrot complexes is much younger, it is clear that tectonic activity can neither
 408 explain speciation in *Electus*, nor in *Trichoglossus*. Their occurrence on oceanic islands should be attributed to
 409 long distance dispersal or vicariance during the Pleistocene.

410 **Genetic origin inside or outside the Wallacea**

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

413 *Electus* scenario: *out-of-Moluccas-hypothesis*

414 As shown in Figure 2, the most likely origin of *Electus* spp. is in the Moluccas (*roratus*). The Lesser Sunda
 415 Islands with Sumba (*cornelia*), the Tanimbar islands (*riedeli*) and New Guinea (*polychloros*, *solomonensis*,
 416 *aruensis*) had presumably been colonized from there, very likely also N Australia (*macgillivrayi*) which was not
 417 included in the dataset. *Electus* is capable of long-distance dispersal: Pleistocene and Holocene fossils were found
 418 on Tonga, c. 2,700 km SE of the current distribution, probably also on Rota (Mariana Is.) (Steadman 1993). An
 419 explanation for the low genetic distance across the Sahul Shelf may be land bridges during the Pleistocene (Voris
 420 2000) or recent dispersal.

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

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

427 The finding of the populations in N Australia and the Lesser Sunda Islands being closely related is puzzling
 428 because the taxa are found more than 1,000 km from each other. A similar biogeographic pattern as in
 429 *mitchellii/forsteni/rubritorquis* (Lesser Sunda Islands and N Australia) can be found in fruit doves. *Ptilinopus*
 430 *alligator* lives in N Australia, *P. cinctus* on the Lesser Sunda Islands except Sumba, and *P. dohertyi* on Sumba
 431 (Cox. 1997). This finding may be explained by the smaller geographic distance between Lesser Sunda Islands and
 432 the Sahul Shelf during the Pleistocene.

433 ***Eclectus* and *Trichoglossus*: rapid evolution and implications for taxonomy**

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

440

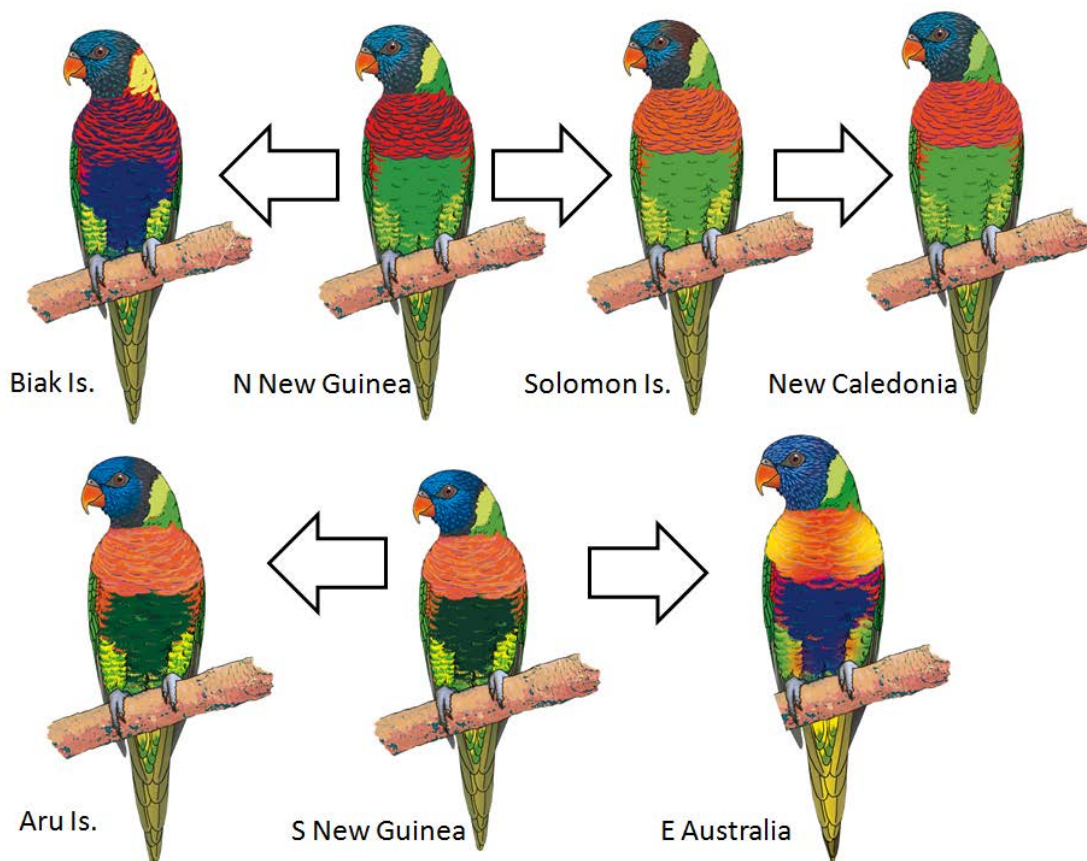
441 Table 6– Suggested taxonomic revision of *Eclectus roratus* based on phylogenetic units. Only taxa used in the
 442 study are displayed.

<i>Species</i>	<i>includes</i>
<i>Eclectus roratus</i>	<i>E. r. roratus</i>
<i>Eclectus cornelia</i>	<i>E. r. cornelia</i>
<i>Eclectus riedeli</i>	<i>E. r. riedeli</i>
<i>Eclectus polychloros</i>	<i>E. r. polychloros</i>
	<i>E. r. aruensis</i>
	<i>E. r. solomonensis</i>

443

444 In case of the cryptic Western Ground Parrot (*Pezoporus wallicus flaviventris*) p-distance values of 4.4–5.1%
 445 between western and eastern populations of Australia were equal to a divergence time of 2 Ma, suggesting a
 446 separate species status for the western population *P. wallicus* (Murphy et al., 2011). In the *Trichoglossus*-
 447 *haematodus*-complex, the situation is more complicated. The distribution of the *T. haematodus* taxa reflects the
 448 Checkerboard distribution pattern (Diamond 1975), meaning that two closely related species never occur on the
 449 same islands, based on the presence of competitors (Newton 2003). The case of *T. (h.) euteles* and *T. h. capistratus*
 450 is puzzling as both are occurring on the island of Timor, which is contradictory to the Checkerboard distribution
 451 for closely related species. The sympatry of *euteles* and *capistratus* suggests that both taxa are evolutionary
 452 sufficiently distinct from each other to form two distinct species. Given the p-distance of 1.7% and the time frame
 453 of 800,000 years, a rapid evolution into two distinct species took place. This is the highest p-distance value within
 454 the *T. haematodus* complex. The smaller *T. (h.) euteles* lives at altitudes from sea level to 2,400 m and seems to
 455 be commoner than the larger *T. h. capistratus* on Timor, replacing *capistratus* at higher altitudes and on several

456 nearby islands (Juniper & Parr, 2003). *T. h. rosenbergii* is considered a full species by del Hoyo et al. (2014) based
 457 on its different colour pattern and the isolated population on the island of Biak. Our data shows identical haplotype
 458 together with other taxa from the islands north of New Guinea (*massena*, *deplanchii*). It is a case of dramatically
 459 rapid evolution within less than 50,000 years, probably less than 18,000 years BP, see Figure 6. The same situation
 460 is present in the Australia-S New Guinea clade. *T. h. moluccanus* (E Australia), *T. h. nigrogularis* (Aru Is.) and *T.*
 461 *h. caeurleiceps* (S New Guinea) share a common haplotype. A similar case of very recent speciation is known
 462 from the swift complex *Apus apus/A. pallidus*, which are considered distinct species, but share a common
 463 haplotype. The same is true for the complex *A. affinis/A. nipalensis* Päckert et al. (2012). Other examples of rapid
 464 radiation within the parrot family is the genus *Psittacula* (Braun et al., 2016) with the South Asian Ring-necked
 465 Parakeet showing a new breeding behavior or rapid morphological changes in a different climate such as in
 466 temperate Europe (Braun, 2007, 2014; Le Gros et al., 2016).



467 Figure 6 – Divergence in *T. haematodus* can occur very quickly. The youngest lineages (N New Guinea vs. S
 468 New Guinea) evolved by dispersal and/or isolation (arrows) from New Guinea during the Pleistocene, less than
 469 50,000 years ago, probably as young as 18,000 years ago (last glacial maximum). Drawings are with courtesy of
 470 Thomas Arndt.
 471
 472

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

480
 481 Table 7 – Suggested taxonomic revision of *Trichoglossus haematodus* based on phylogenetic units. Only taxa
 482 used in the study are displayed.

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

483
 484

485 **Implications for conservation and further research**

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

490 The study shows that speciation is underway in Australasia. Diversification took place in both *Eclectus* and
 491 *Trichoglossus*. This highlights the importance of areas of endemism, in which the Wallacea clearly belongs. For
 492 conservation reason, several taxa are suggested being elevated to species level under the criteria of Tobias et al.
 493 (2010). Although *T. haematodus* has been regarded as a common species with a conservation status of “Least

494 Concern” (Stattersfield et al. 2014), the elevation of several populations to species level will lead to a different
 495 situation (see Taylor 2013). Several populations are now under decline, especially due to the trapping pressure,
 496 especially on Biak (*T. h. rosenbergii*) with a population < 10,000 birds, but also on Flores (*T. h. weberi*), on
 497 Bali/Lombok (*T. h. mitchellii*), on Sumbawa (*T. h. forsteni*) and other populations on smaller islands (Taylor 2013).
 498 The taxon *mitchellii* currently is in the situation of being ‘extinct in the wild’ from both Bali and Lombok (T.A.,
 499 R. Wüst, pers. comm., 2015), the status of many other taxa is still insufficiently known.

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

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

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

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514

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726 forsteni-as-near-threatened/](http://www.birdlife.org/globally-threatened-bird-forums/2013/09/rainbow-lorikeet-trichoglossus-haematodus-is-being-split-list-t-rosenbergii-as-vulnerable-and-t-weberi-and-t-forsteni-as-near-threatened/) (accessed 20.07.2014).
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747

748 Biosketch

749 Michael Peter Braun did his doctorate at Heidelberg University in Germany. His main research interests are the
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752 Author contributions: M.P.B. and M.W., conceived the ideas; M.R., R.Z., A.H., H.G., D.W., L.N., T.A., H.S.-G.,
753 and C.M.-H. contributed data; M.P.B., with help from T.D. and H.S.G., analysed the data; M.P.B. led the writing;
754 all authors made significant comments on and improvements to the manuscript.

755

757 Table 8 – Pairwise p-distance values for 24 taxa of *Trichoglossus* used in the phylogenetic analysis, based on mitochondrial 1,140 nucleotides of cytb. The analysis was
 758 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