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The Cinnamon Ibon *Hypocryptadius cinnamomeus* is a forest canopy sparrow

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The Cinnamon Ibon inhabits the canopy of cloud-forest of Mindanao Island in the Philippines, and has until now been classified as an aberrant member of the Zosteropidae (white-eyes). We assessed the systematic position of this enigmatic species using DNA sequence data (two mitochondrial markers, two nuclear introns and two nuclear exons) and broad taxon sampling. The species was robustly placed among the granivorous passeroid clades, as a basal branch in the family of true sparrows, Passeridae. Morphological data lend further support, as the Cinnamon Ibon shows similar specialization of the skull as other granivorous passeroids. The species' restricted distribution in the montane cloud-forest of the island of Mindanao, which is of oceanic origin, is difficult to explain without assuming an over-water dispersal event.

Keywords: Passeridae, Passeriformes, passerines, Passeroidea, phylogeny, systematics, zoogeography, Zosteropidae.

The Cinnamon Ibon *Hypocryptadius cinnamomeus* is an enigmatic bird of the cloud-forest of the southern Philippine island of Mindanao (Delacour & Mayr 1946, Kennedy *et al.* 2000, van Balen 2008). The species was placed in the family Zosteropidae (white-eyes) with little supporting evidence except that it has a reduced 10th primary and is sexually monomorphic with no indication of a distinctive juvenile plumage. It tends to move around in groups, often in mixed feeding parties together with white-eyes (Mountain White-eye *Zosterops montanus*, Mindanao Ibon *Lophozosterops goodfellowi*). Thus, the earlier taxonomic decision may reflect the tendency of the past to try to accommodate aberrant species within larger and ecologically similar groups of the same biogeographical region. However, the Cinnamon Ibon differs from white-eyes by its heavier build, distinctly longer wingtips and shorter legs, rich cinnamon-brown plumage and absence of an eye-ring, as well as by having a rather thick and broad bill with aberrant, round nostrils and a less specialized tongue (Hachisuka 1930, Mees 1969). Thus, Hachisuka (1930) erected a separate subfamily for it, and Mees (1969) did not think it belonged in the Zosteropidae at all, but could offer no alternative placement. It has therefore remained in the Zosteropidae in all later classifications.

Members of the Zosteropidae feed largely from flowers and fruit, and consequently show similar morphological specializations as sunbirds (Nectariniidae), honeyeaters (Meliphagidae) and Neotropical honeycreepers ('Coerebidae'). They were therefore placed near sunbirds and honeyeaters in Wetmore (1960) and remained there until molecular data were available and revealed the independent evolution of specializations for nectar feeding in different groups (Sibley & Ahlquist 1990, see Fleischer *et al.* 2001 for Drepanidae, Remsen 2003 for 'Coerebidae' and Fleischer *et al.* 2008 for Mohoidae). In the traditional interpretation of white-eye evolution (Delacour & Mayr 1946, Mees 1969) the large genus *Zosterops* was regarded as 'primitive' and close to the ancestral form of the family, whereas aberrant species were regarded as derived and placed in separate small or monotypic genera. The current DNA-based

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phylogenetic hypothesis rejects this 'centrifugal' view by placing many aberrant taxa among the fulvettas (*Stachyris*, *Yuhina*) in the Timaliidae (babblers, Gelang *et al.* 2009) basal to a rapidly radiating group of *Zosterops* species, but with a few island forms with aberrant colours (*Woodfordia*, *Rukia* and *Speirops*) nested within it (Moyle *et al.* 2009).

In the phylogenetic analysis of white-eyes by Moyle *et al.* (2009), the Cinnamon Ibon was placed among the outgroup taxa. However, based on the taxon sampling used in this study it could not be concluded whether the Cinnamon Ibon was a member of the broader babbler radiation (Timaliidae) or a member of another clade of oscines. Since the work of Newton (1896), the circumscription of the Timaliidae has been considered particularly problematic as it traditionally has accommodated many birds of uncertain affinities. Modern molecular phylogenetic methods have now defined a more inclusive and monophyletic Timaliidae (Cibois 2003a,b, Gelang *et al.* 2009), although the family remains heterogeneous in terms of the diversity of adaptive forms, and no morphological characters have been found that can clearly unite all members of the Timaliidae.

The present paper is based on a study of a series of Cinnamon Ibon specimens collected in Mindanao in 1951–52 during the second Danish Galathea expedition. This series served as a source of morphological information and also yielded DNA for amplifying nuclear DNA. In this paper we present new evidence that unexpectedly transfers the Cinnamon Ibon from the white-eyes to another major branch of the radiation of songbirds, the Old-World sparrows, Passeridae.

METHODS

Morphological data

Sixteen specimens of the Cinnamon Ibon, collected between November 1951 and January 1952 on Katanglad Volcano in the Hilong-hilong Hills on Mindanao, were examined. One study skin was reworked to produce a partial skeleton with an almost complete skull (except pterygoids, part of the sphenoid and the occipital region), as well as the bones of the wings and legs for morphological comparison. This was compared with skeletons of representatives of most families of the Passerida, including *Zosterops* and other babblers, and all families of Passeroidea (with Passeridae represented by the House Sparrow *Passer domesticus*, Tree Sparrow *Passer montanus* and Bush Petronia *Gymnoris* (*Petronia*) *dentata*), as well as with X-rays of the heads of study skins of several other species (White-winged Snowfinch *Montifringilla nivalis*, Afghan Snowfinch *Pyrgilauda theresae*, White-browed Sparrow-weaver *Plocepasser mahali* and Grey-capped Social-weaver *Pseudonigrita arnaudi*). The last two species group with the weavers (Ploceidae) in the molecular analysis of Groth (1998), but share many morphological characters with sparrows (Bentz 1979).

Taxon sampling for molecular analysis

For a balanced taxon sampling, we scrutinized the results of several comprehensive oscine phylogenies (Alström *et al.* 2006, Jønsson & Fjeldså 2006, Johansson *et al.* 2008) and selected representatives of all deeper lineages. However, we did not include *Regulus* (Kinglets) and representatives of the bombycillid radiation (waxwings, silky flycatchers), as these are very difficult to place with high confidence in a phylogenetic analysis, although they certainly represent deep branches within the Passerida. Preliminary results placed the Cinnamon Ibon together with some seed-eaters in the Passeroidea and we expanded the sampling of that clade accordingly, with special emphasis on the Old-World seed-eaters (Estrididae, Fringillidae, Passeridae, Ploceidae and Viduidae). The sampling of the remaining Passeriformes was completed with the inclusion of a Rifleman *Acanthisitta chloris* and two suboscines (*Pitta* and *Tyrannus*). A growing consensus places parrots and falcons as the sister lineages to Passeriformes (Ericson *et al.* 2006a, Hackett *et al.* 2008) and we used one representative of each as outgroups (Table 1).

Laboratory procedures

The DNA of the Cinnamon Ibon was extracted from toe-pads of study skins, following the procedure described in Zuccon (2005) and Irestedt *et al.* (2006). To exclude contamination or amplification errors we replicated our efforts by sequencing a second Cinnamon Ibon sample. The sequence divergence between the two individuals was minimal (0–1.15%) and we included only one individual in subsequent analyses. The fresh tissue samples of the other species were extracted using

Table 1. Samples and sequences included in this study, with museum and GenBank accession numbers. The taxonomy follows Dickinson (2003).

Taxon	Sample	IRBP	ZENK	Myoglobin	ODC	ND2	ND3
Hypocryptadius cinnamomeus	ZMUC 1425	GU816884	GU816971	GU816939	GU816916	FJ460769 [14]*	FJ460837 [14]*
Hypocryptadius cinnamomeus	ZMUC 1435**	GU816885	GU816972	GU816940	GU816917	–	–
Acanthisitta chloris	NRM 569989	GU816860	GU816947	EU726212 [1]	EU726220 [1]	AY325307 [12]*	AY325307 [12]*
Alauda arvensis	NRM 966614	GU816896	GU816983	AY228284 [2]	GU816926	GU816856	GU816824
Ammodramus humeralis	NRM 966958	GU816890	GU816977	GU816942	GU816922	GU816853	GU816818
Anthus trivialis	NRM 976393	GU816887	GU816974	AY228285 [2]	GU816919	GU816850	GU816815
Campephaga flava	ZMUC O11	GU816864	GU816951	AY165803 [3]	GU816899	GU816829	GU816800
Catharus ustulatus	NRM 20016340	GU816894	GU816981	GU358709 [4]	GU358837 [4]	GU237101 [13]	GU816822
Certhia familiaris	NRM 976184	GU816892	GU816979	DQ466821 [5]	GU816924	DQ466857 [5]	GU816820
Chloropsis aurifrons	NRM 20026694	GU816873	GU816960	GU816933	GU816906	GU816838	–
Cryptospiza reichenovii	ZMUC O785	GU816878	GU816965	AY228293 [2]	GU816911	GU816843	–
Dicaeum australe	ZMUC O3737	GU816870	GU816957	AY228294 [2]	GU816903	GU816835	GU816805
Dinemellia dinemelli	NRM 20076168	GU816875	GU816962	GU816935	GU816908	GU816840	–
Euplectes ardens	ZMUC O1706	GU816876	GU816963	AY228299 [2]	GU816909	GU816841	GU816809
Fringilla montifringilla	NRM 20046395	GU816888	GU816975	GU816941	GU816920	GU816851	GU816816
Irena puella	UWBM 82069	GU816872	GU816959	GU816932	GU816905	GU816837	GU816807
Kakamega poliothorax	NRM 20086268	GU816869	GU816956	GU816930	GU816902	GU816834	EU686374 [16]*
Lanius collurio	NRM 986403	GU816865	GU816952	AY228328 [2]	DQ881748 [8]	GU816830	GU816801
Loxia curvirostra	NRM 976546	GU816889	GU816976	AY228303 [2]	GU816921	GU816852	GU816817
Menura novaehollandiae	AM LAB1112	GU816863	GU816950	AY064744 [6]*	EF441242 [9]*	AY064754 [6]*	NC_007883 [17]*
Modulatrix stictigula	ZMUC 118848	GU816868	GU816955	EU680619 [7]	EU680743 [7]	GU816833	GU816804
Montifringilla ruficollis	IZAS uncat	GU816883	GU816970	AY228306 [2]	GU816915	GU816848	GU816813
Motacilla alba	NRM 976193	GU816886	GU816973	AY228307 [2]	GU816918	GU816849	GU816814
Nectarinia olivacea	ZMUC O3401	GU816871	GU816958	GU816931	GU816904	GU816836	GU816806
Padda oryzivora	NRM 20046261	GU816879	GU816966	GU816937	GU816912	GU816844	EF100769 [18]*
Passer luteus	NRM 20106041	GU816881	GU816968	GU816938	GU816913	GU816846	GU816811
Passer montanus	NRM 976359	GU816880	GU816967	AY228311 [2]	DQ785937 [10]	GU816845	GU816810
Petronia petronia	IZAS uncat	GU816882	GU816969	AY228312 [2]	GU816914	GU816847	GU816812
Picathartes gymnocephalus	LSU B19213	GU816866	GU816953	AY228314 [2]	GU816900	GU816831	GU816802
Pitta angolensis	ZMUC S1027	GU816861	GU816948	AY165820 [3]	DQ785940 [10]	GU816827	GU816799
Promerops gurneyi	UWBM 70395	GU816867	GU816954	GU816929	GU816901	GU816832	GU816803
Prunella modularis	NRM 976138	GU816874	GU816961	GU816934	GU816907	GU816839	GU816808
Saltator atricollis	NRM 966978	GU816891	GU816978	AY228320 [2]	GU816923	GU816854	GU816819
Sturnus vulgaris	NRM 966615	GU816895	GU816982	AY228322 [2]	EF441253 [9]	DQ146346 [15]	GU816823
Troglodytes aedon	NRM 947056	GU816893	GU816980	GU816943	GU816925	GU816855	GU816821
Tyrannus savana	NRM 976722	GU816862	GU816949	AY165826 [3]	DQ435507 [11]	GU816828	–
Vidua macroura	NRM 20026168	GU816877	GU816964	GU816936	GU816910	GU816842	–
Zosterops nigrorum	ZMUC O2663	GU816897	GU816984	GU816944	GU816927	GU816857	FJ460876 [14]*

Table 1. (*Continued*)

Taxon	Sample	IRBP	ZENK	Myoglobin	ODC	ND2	ND3
Outgroup							
Psittacus erithacus	NRM 20066765	GU816859	GU816946	GU816928	GU816898	GU816826	GU816798
Falco subbuteo	NRM 986329	GU816858	GU816945	–	–	GU816825	GU816797
Falco rufigularis	NRM uncat	–	–	DQ881850 [8]	DQ881734 [8]	–	–

Museum acronyms: AM, Australian Museum; IZAS, Institute of Zoology, Chinese Academy of Science; LSU, Louisiana State University, Museum of Natural Sciences; NRM, Swedish Museum of Natural History; UWBM, University of Washington, Burke Museum; ZMUC, Zoological Museum, University of Copenhagen.
References: [1] Irestedt *et al.* (2008), [2] Ericson and Johansson (2003), [3] Johansson and Ericson (2003), [4] Zuccon and Ericson (2010a), [5] Zuccon *et al.* (2006), [6] Ericson *et al.* (2002a,b), [7] Johansson *et al.* (2008), [8] Ericson *et al.* (2006a,b), [9] Jønsson *et al.* (2007), [10] Irestedt *et al.* (2006), [11] Ericson *et al.* (2006a,b), [12] Harrison *et al.* (2004), [13] Zuccon and Ericson (2010b), [14] Moyle *et al.* (2009), [15] Fuchs *et al.* (2006), [16] Nguembock *et al.* (2009), [17] Slack *et al.* (2007), [18] R. Susanti *et al.* (unpubl. data).
*Published sequences obtained from samples different from those used in this study.
**The sequences obtained from this individual of *Hypocryptadius* were used only as a control and were not included in the phylogenetic analysis.

the Qiagen DNA Mini kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol.

For the molecular phylogenetic analyses we utilized six loci: the mitochondrial NADH dehydrogenase subunit II (ND2) and subunit III (ND3), two nuclear introns, intron 2 of myoglobin and introns 6–7 of ornithine decarboxylase (ODC), and two nuclear exons, the interphotoreceptor retinol-binding protein (IRBP) and the zinc finger protein (ZENK). Different substitution rates among the included loci provide good resolution across a wide evolutionary window.

For all loci except IRBP, we used previously published primers and procedures (ND2: Sorenson *et al.* 1999, ND3: Chesser 1999; myoglobin: Irestedt *et al.* 2002; ODC: Allen & Omland 2003, ZENK: Chubb 2004). The IRBP gene encodes a large glycoprotein that plays a key role in the transport of retinoids between the retinal pigment epithelium and the photoreceptors (Fong *et al.* 1990). Although this locus has been extensively used to resolve the mammalian high-level phylogeny (e.g. Stanhope *et al.* 1996, Madsen *et al.* 2001) it has thus far not been used in avian molecular systematics. By using the published sequences of *Gallus*, *Homo* and *Didelphis* we developed two new IRBP primers for passerine birds. These two new primers, IRBP-F2 (5′-GGGAATGCAAGAAGCCATTGAACAAGCA-3′) and IRBP-R2 (5′-AAGACAGTATCCACCAAGGCATGCAGCA-3′), amplify a region of 1134 bp located in the first exon. The amplification profile was: initial denaturation for 5 min at 95 °C, followed by 35–40 cycles of denaturation for 40 s at 95 °C, annealing for 40 s at 58 °C, an extension for 60 s at 72 °C, with a final extension of 5 min at 72 °C. The nuclear genes from the Cinnamon Ibon study skins were amplified in a series of short, overlapping fragments of 200–300 bp, using a large set of specific primers. The primer sequences and the amplification conditions are listed in Supporting Information Table S1. PCR products were cleaned using the QIAquick PCR Purification Kit (Qiagen) and run on an ABI Prism 3100 automated DNA sequencer (Perkin-Elmer Applied Biosystems, Waltham, MA, USA). The DNA sequences were aligned with MEGALIGN™ (DNAStar, Madison, WI, USA) and adjusted manually by eye.

Phylogenetic analyses

The concatenated dataset and each gene partition were analysed using Bayesian inference and the

maximum likelihood optimality criteria. Bayesian inference analyses were carried out using MRBAYES 3.1.2 (Ronquist & Huelsenbeck 2003), implemented on the freely available BIOPORTAL (http://www.bioportal.uio.no). A mixed-model approach was implemented to account for the potential differences in evolutionary model parameters between the six data partitions corresponding to the six genes. The most appropriate nucleotide substitution models for each gene partition were determined with MRMODELTEST (Nylander 2004) using Akaike's information criterion (AIC) in conjunction with PAUP* (Swofford 2003). We assumed uniform interval priors for the parameters, except for base frequencies, which were assigned a Dirichlet prior (Huelsenbeck & Ronquist 2001). Two independent runs of four incrementally heated Metropolis-coupled MCMC chains were run for 10 million generations, sampling every 1000 generations, to yield 10 000 trees. We used the online version of AWTY (Nylander *et al.* 2008) to assess the convergence of the MCMC chains and to estimate the number of generations to discard as the 'burn-in' (2000 trees).

Maximum likelihood searches of the partitioned dataset were conducted with RAXML v. 7.0.3 (Stamatakis 2006) using a GTR+Γ+I model and random starting tree, with α-shape parameters, GTR rates and empirical base frequencies estimated and optimized for each partition. Nodal support was estimated using 100 bootstrap pseudoreplicates.

Individual gene partitions and two combined datasets including only the mitochondrial and the nuclear genes, respectively, were also analysed using the Bayesian inference and maximum likelihood optimality criterion. The same analytical parameters as indicated above were used, with the exception that a single gene partition was used with the respective evolutionary model, for an individual gene dataset.

Estimates of divergence time

To relate the origin of the Cinnamon Ibon to the well-documented geological history of the Philippine archipelago (Hall 2002), we estimated the divergence time based on the concatenated dataset of all genes using a relaxed clock model implemented in BEAST 1.4.8 (Drummond *et al.* 2002, 2006, Rambaut & Drummond 2007). To calibrate the tree we used the geological split between New Zealand and Antarctica, as this has been associated with the basal separation of the *Acanthisitta* lineage from all other passerines (Barker *et al.* 2002, Ericson *et al.* 2002a). The dating of this split has often been assumed to be around 85–82 Mya (Lawver *et al.* 1991, Cooper & Millener 1993), but more recently the timing of this split has been suggested to be less certain, 85–65 Mya (McLoughlin 2001, Ladiges & Cantrill 2007). To account for this uncertainty we used a normal distributed tree prior with a median at 76 Mya and a standard deviation of 8 (2.5% = 60.3 Mya, 5% = 62.8 Mya, 95% = 89.2 Mya and 97.5% = 91.7 Mya). For the other priors, we used the default settings, except for the tree prior, which was set to a Yule process under an uncorrelated log-normal distribution for the molecular clock model. We used a GTR+Γ model and ran MCMC chains for 25 million generations.

RESULTS

Phylogenetic relationships

We obtained complete sequences for all taxa with the exception of five species, for which we lack ND3 (Table 1). As amplification of fragmented DNA from old museum samples may increase the risk of amplifying contaminants, the sequences obtained from the Cinnamon Ibon samples have been carefully inspected. The sequences were found to be unique (not identical to any other passerines amplified in our laboratory). No mismatches in overlapping regions of adjacent fragments or unusual mutations in coding regions were found. The variable positions in coding genes follow the usual frequency pattern (2nd < 1st < 3rd). The slow evolving exon sequences from the two Cinnamon Ibon specimens were found to be identical, whereas the p-distances between the more variable introns were compatible with the expected intraspecific variability (0.7% in ODC and 1.4% in myoglobin). Based on these observations, we are confident that the sequences obtained from the Cinnamon Ibon toe-pads are correct.

The two members of the Motacillidae (*Anthus* and *Motacilla*) sampled share a long synapomorphic insertion of 643 bp in intron 6 of ODC that was excluded from the final alignment to reduce the computational time. Without this long ODC insertion, the six genes were concatenated into a single dataset of 5120 bp (Table 2).

Table 2. Sequence characteristics of the six loci analysed. The numbers of variable and parsimony-informative sites were calculated for the ingroup taxa only. The synapomorphic insertions in ODC were excluded from all analyses (see text for details).

Gene region	IRBP	ZENK	Myoglobin	ODC	ND2	ND3
Alignment length	1074	1155	766	732	1041	352
No. of variable sites (%)	380 (35.4)	346 (30.0)	386 (50.4)	405 (55.3)	655 (62.9)	202 (57.4)
No. of parsimony-informative sites (%)	192 (17.9)	161 (13.9)	151 (19.7)	220 (30.0)	579 (55.6)	171 (48.6)
% A nucleotides (range)	26.0 (25.4–26.9)	23.9 (22.0–25.0)	28.1 (26.8–29.2)	28.1 (27.1–29.3)	30.6 (28.0–33.4)	27.7 (24.8–31.9)
% C (range)	24.0 (23.0–24.8)	35.4 (34.6–38.3)	22.2 (21.1–23.1)	16.8 (15.5–18.1)	34.9 (32.6–37.1)	32.7 (25–36.8)
% G (range)	27.1 (26.4–27.7)	18.6 (17.5–20.3)	23.3 (21.8–24.5)	20.4 (19.2–21.4)	10.8 (9.2–12.3)	14.0 (9.4–25.0)
% T (range)	23.0 (22.3–23.7)	22.0 (19.4–23.0)	26.4 (24.2–28.0)	34.7 (32.7–35.8)	23.7 (21.4–27.9)	25.6 (22.4–27.9)
Selected substitution model	SYM+I+Γ	GTR+I+Γ	GTR+Γ	GTR+I+Γ	GTR+I+Γ	GTR+I+Γ

A GTR+Γ+I substitution model was considered optimal for the mitochondrial genes, ODC and ZENK, a GTR+Γ model for myoglobin and the SYM+Γ+I model for IRBP. Our phylogenetic tree obtained from the concatenated dataset (Fig. 1) recovered the expected branching pattern in the passerine radiation that has been identified by several independent studies, with the Rifleman basal to the major division of the split between the Suboscines and Oscines, followed by the Basal Corvoidea, Crown Corvoidea and Passerida clades. The basal nodes in the Passerida are best regarded as a polytomy. Neither the Bayesian inference nor the maximum likelihood analysis was able to support the branching pattern among the four major lineages Passeroidea, Certhoidea, Muscicapoidea and Sylvoidea, and the two methods conflict as to the placement of the Certhioidea, which is either placed sister to the Muscicapoidea in the maximum likelihood topology or basal to Muscicapoidea + Sylvioidea in the Bayesian tree. Within the Passeroidea, most nodes received strong statistical support, with three well-identified lineages: (1) the accentors (*Prunella*), (2) a group uniting members of the Ploceidae, Estrildidae and Viduidae, and (3) a group uniting members of the Passeridae, Motacillidae and Fringillidae *sensu lato*. In the third lineages, all nodes are strongly supported, with the Cinnamon Ibon as the basal branch among the true sparrows Passeridae. A synapomorphic deletion of 16 bp in intron 7 of ODC is shared by all taxa in the Passeroidea, further supporting the removal of the Cinnamon Ibon from the Sylvioidea.

The analysis of the nuclear genes alone recovered a topology congruent with the tree obtained from the entire dataset, with almost all nodes in the Passeroidea receiving high posterior probability support (Fig. 2). The mitochondrial dataset failed to resolve the deeper relationships among the Oscines, resulting in a large polytomy (Fig. 2). However, the Cinnamon Ibon was recovered as sister to the Passeridae, in agreement with the other datasets. The topologies obtained from the Bayesian analysis of the individual genes are generally poorly resolved, with low nodal support (Supporting Information Figs S1–S3). However, the analysis of three partitions (IRBP, myoglobin and ODC) recovered, with significant posterior probability values, a clade where the Cinnamon Ibon is sister to the representatives of sparrows (*Passer*, *Montifringilla* and *Petronia*) included in this study. For the other genes, the topology collapsed into large polytomies (ND3) or the basal nodes received very low posterior probability values (ND2 and ZENK). In all partitions, none of the nodes with significant posterior probability values conflicted with the topology obtained from the combined dataset.

The topology obtained in the BEAST tree is almost fully congruent with the topology discussed above, expect for the position of the Dunnock, which is shifted to the base of the Ploceidae/Estrildidae/Viduidae clade (Fig. 3), and the *Kakamega-Modulatrix* clade, which is placed sister to the *Dicaeum-Nectarinia* clade rather than basal to it. Based on our calibration points the Passeridae emerged around 35 Mya and the Cinnamon Ibon diverged from the typical sparrows *c.* 31 Mya. The radiation of the typical sparrows (*Passer*, *Petronia* and *Montifringilla*) occurred later, around 25 Mya.

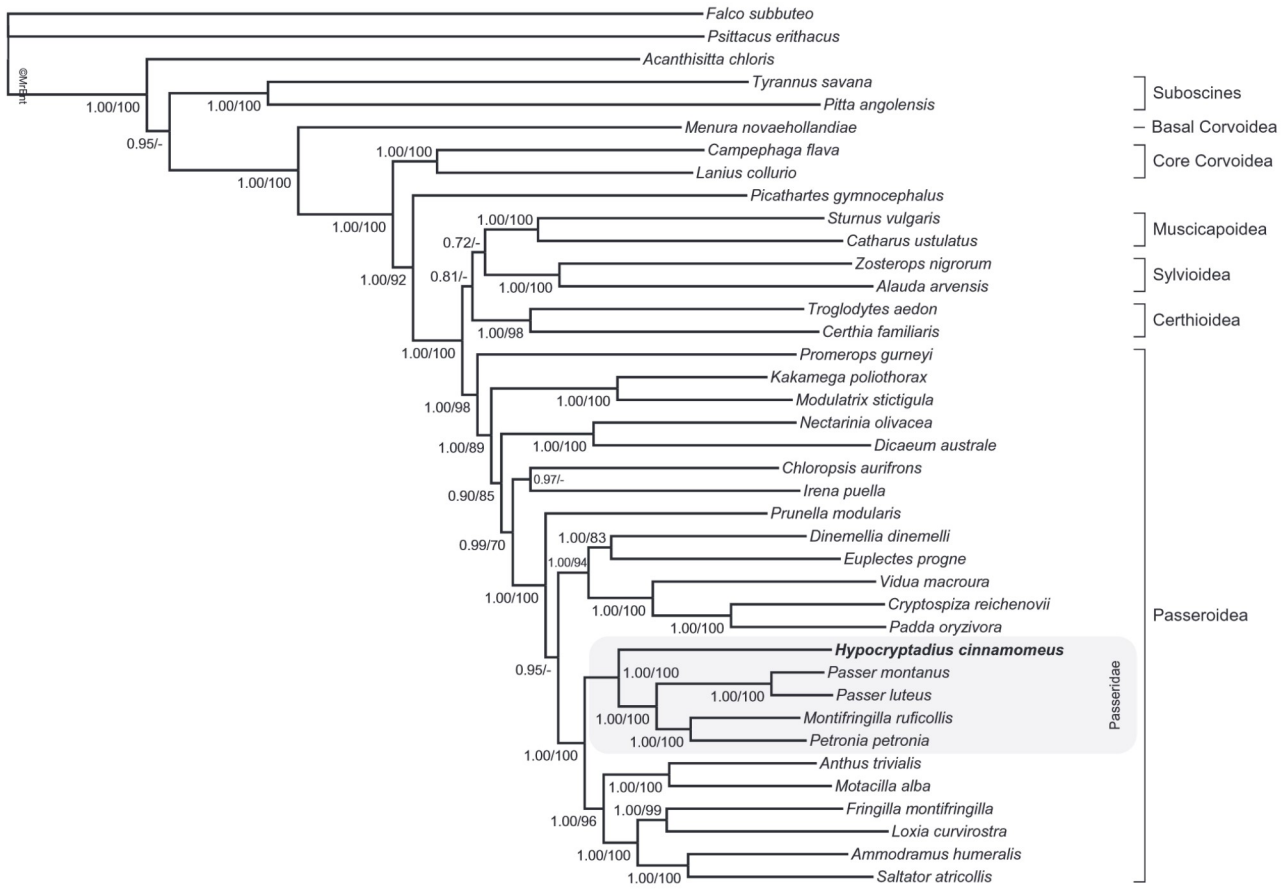

Figure 1. The 50% majority rule consensus tree obtained from the mixed-model Bayesian analysis of the concatenated dataset. The nodal values represent the Bayesian posterior probability and the bootstrap support obtained from the maximum likelihood analysis. The major passerine clades are indicated on the left and the position of the Cinnamon Ibon *Hypocryptadius cinnamomeus* within the Passeridae is highlighted.

Morphology

The Cinnamon Ibon is sexually monomorphic, with no clear-cut age-related variation (three of the Copenhagen specimens, which are young judging from the condition of the rectrices, have insignificantly paler colours, with fuscous pigmentation only in the terminal part of the rectrices, in contrast to the more uniform dark rectrices in adults). In this respect, the Cinnamon Ibon resembles babblers, including white-eyes. The rich cinnamon-brown colour (ranging from Sanford's Brown dorsally and Auburn on the wing coverts to pinkish white on the central underparts) sets it clearly apart from most white-eyes. Although some white-eyes and many other babblers have brown colours, it is not the same deep cinnamon hue. However, such colours are found in many sparrows.

The general shape is sparrow-like (judging from the photographic material that is available online), compact, with a relatively short, squared tail. The wings are long (the wing is 10 mm longer than in the largest white-eye) with the tips of the closed wing projecting 16 mm beyond the secondaries, which form a parallelogram with a well-marked rear corner (unlike the more rounded 'elbow' of white-eyes). A reduced tenth primary is shared by white-eyes as well as sparrows. Furthermore, the strong feet and pattern of scales (scutellate and acutiplantar) on the short (18 mm) tarsi is more similar to that of sparrows and weavers than white-eyes. The soles of the feet are also similar to sparrows and weavers, characterized by small pads separated by many folds, unlike in most passeriform birds (including white-eyes), which have 13 well-developed toe-pads (typically separated by a furrow or one to

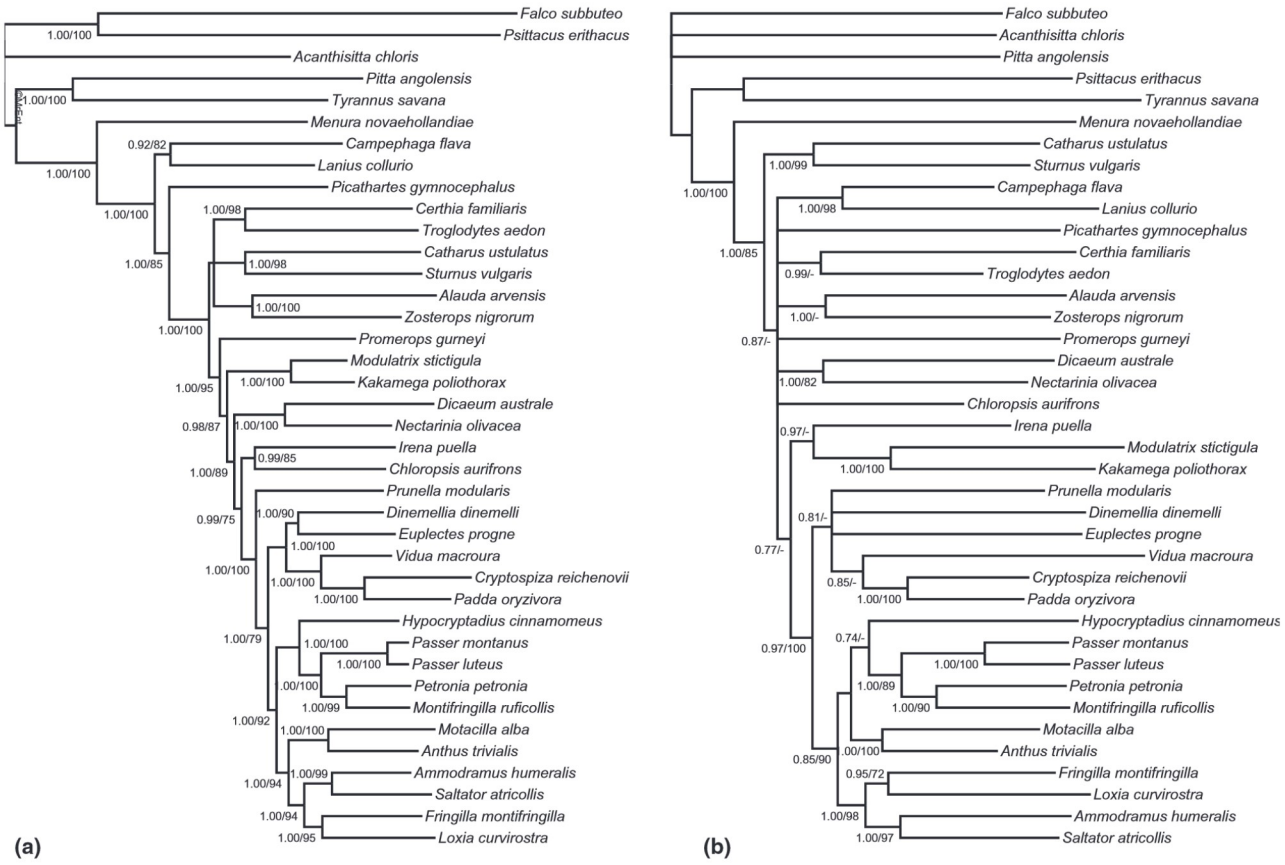

Figure 2. The 50% majority rule consensus trees obtained from the mixed-model Bayesian analysis of the combined nuclear (a) and mitochondrial loci (b). The nodal values represent the Bayesian posterior probability and the bootstrap support obtained from the maximum likelihood analysis.

two folds) to facilitate grasping of slender branches (Lennerstedt 1973).

Compared with white-eyes, the bill is strong (Hachisuka 1930, Mees 1969), conical and slightly curved, and has round nasal openings entirely closed posteriorly by an operculum, as in most granivorous passeroid groups, but unlike white-eyes, which have long, slit-like nostrils placed below an elongate horizontal operculum. Open nostrils are also seen in the Bonin White-eye *Apalopteron familiare*, which may be related to the Golden White-eye *Cleptornis marchei* (Springer *et al.* 1995) or the *Stachyris* group of babblers (Moyle *et al.* 2009). The tongue of the Cinnamon Ibon is reported to have only a slight bifurcation and short lateral fringes (Mees 1969), unlike that usually reported for white-eyes, although Beecher (1953, p. 291), who dissected four *Zosterops* species, refers to only one of these (Cape White-eye *Zosterops virens*) as being specialized.

The skull

The Cinnamon Ibon skull (Fig. 4a) differs in all aspects from white-eyes (Fig. 4b) and other babblers but comes close to that of granivorous passeroids. The palate resembles that of a sparrow (*Passer*; see Jollie 1958). The upper mandible is reinforced, as in most granivorous birds, by extensive ossification of the internasal septum and the fusing of the maxillary processes of the anterior palatines. The attachments for mandibular adductors and protractor muscles of the quadrate bone are prominent, resembling those of sparrows, weavers and waxbills. The zygomatic process is a long, straight structure, as in weavers, including the sparrow-like genera *Plocepasser* and *Pseudonigrita* (Bentz 1979), but not thickened and rigid as in a typical sparrow (*Passer* in Fig. 4d). The articular end of the lower mandible is shallow in the Cinnamon Ibon, as in basal passeroid groups

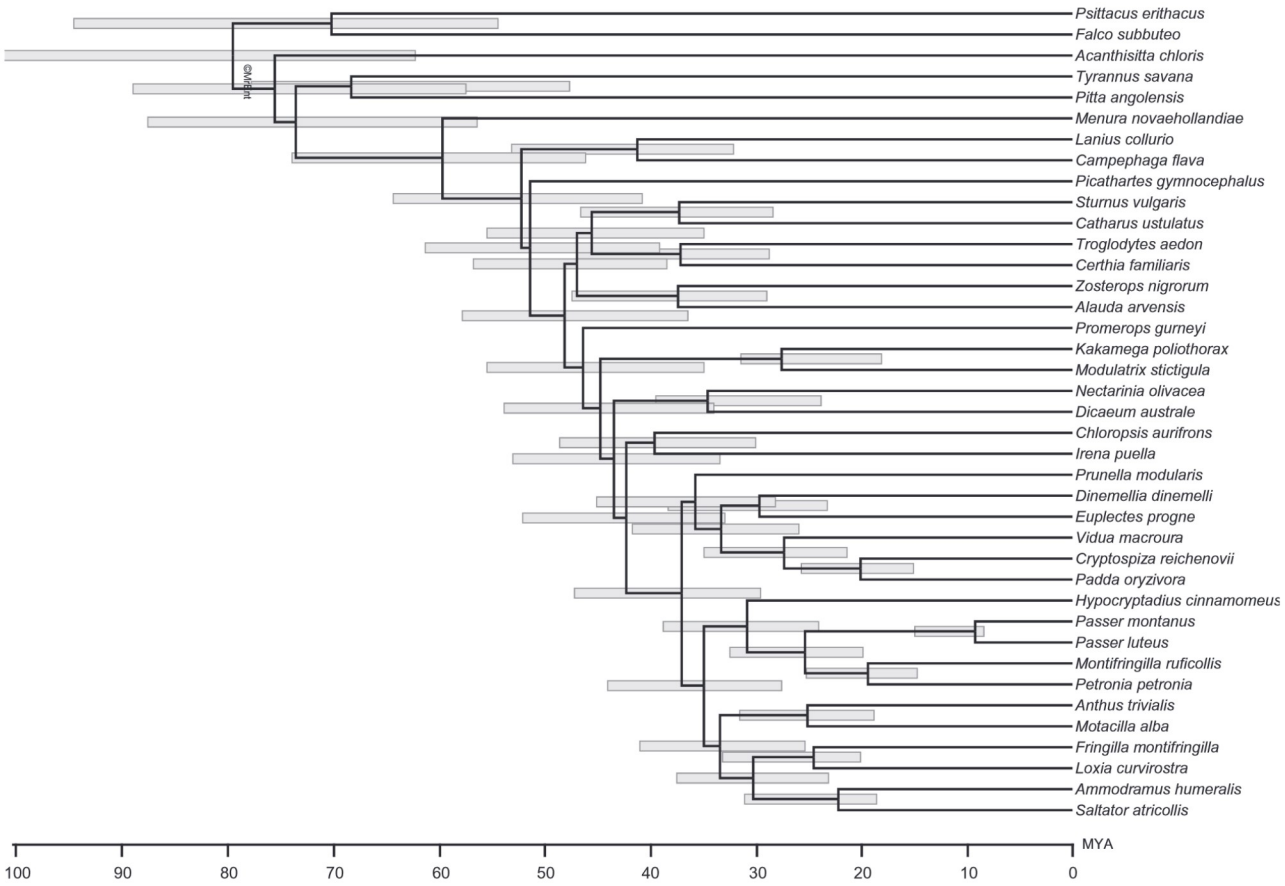

Figure 3. The chronogram estimated under a relaxed clock model with BEAST 1.4.8 and calibrated with the postulated separation of the Rifleman (*Acanthisitta*) from all other passerines at 76 ± 8 Mya. The error bars indicate 95% highest posterior density (HPD) intervals.

(Prunellidae, Ploceidae, *Plocepasser* and *Pseudonigrita*), but unlike the more blunt or truncated shape in the more specialized granivores (*Passer*, Fringillidae and Emberizidae). Ectethmoid foramina are of a 'pinched' type (Beecher 1953), intermediate between the two-hole state in basal passeroids and Ploceidae and the single-hole (derived) state of *Gymnornis* and *Passer*.

Based on the partial skeletal material of the Cinnamon Ibon that was available, it was not possible to record any appendicular muscle attachments that are phylogenetically informative according to the analysis by Bentz (1979).

DISCUSSION

The molecular evidence consistently supports the removal of the Cinnamon Ibon from the Zosteropidae. The combined analysis of nuclear and mitochondrial loci, as well as the mitochondrial and nuclear partitions alone, congruently identify the Cinnamon Ibon as the sister lineage to the Passeridae. The morphological evidence, notably the structure of the skull, would seem to support this placement and contradict the traditionally accepted systematic placement of the Cinnamon Ibon with the white-eyes. Few attempts have been made to deduce phylogenetic relationships of passerine birds from morphology. The most comprehensive such analysis, by Beecher (1953), used characters of the skull and jaw muscles, and adopted the logical principle that simple character states are primitive and can serve as a basis for arranging taxa in transformation series ending with highly specialized (derived) character states. Unfortunately, modern molecular phylogenetics does not lend much support to the phylogenetic hypothesis proposed by Beecher. Scrutiny of his character states nevertheless suggests that some of his described morphological transitions may be

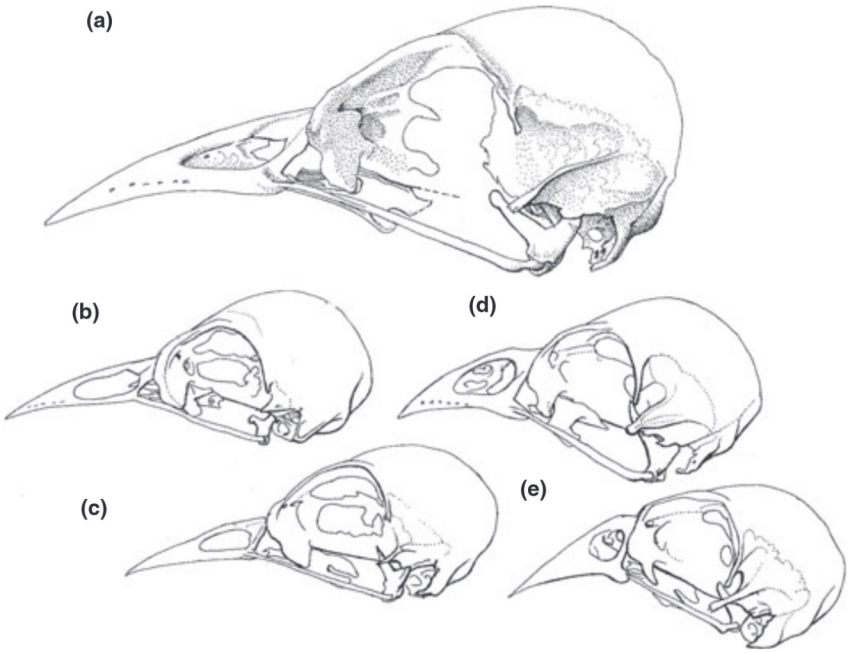

Figure 4. Skull of Cinnamon Ibon *Hypocryptadius cinnamomeus* (a) and more simplified drawings of African Yellow White-eye *Zosterops senegalensis* (b), Dunnock *Prunella modularis* (c), House Sparrow *Passer domesticus* (d) and Red-throated Twinspot *Hypargos niveoguttatus* (e). Note that the pterygoids and part of the sphenoid region are missing in the examined Cinnamon Ibon skull, and the pterygoids have therefore been omitted on the other illustrated skulls.

systematically informative. Thus, whereas most of the basal and corvoid songbird groups (Corvida of Sibley & Ahlquist 1990) have free lacrymals, a large ectethmoid foramen and complex mandibular muscles, the deeper branches of the Passerida (as outlined by Johansson *et al.* 2008) can be characterized by the loss of free lacrymals, double ectethmoid foramina and restricted attachment areas for simple, parallel-fibred mandibular adductors. Within the Sylvoidea, *Zosterops* and the majority of other timaliid lineages evolved a single ectethmoid foramen. In the Passeroidea, the Spot-throat *Modulatrix stictigula* conforms well with basal members of the Passerida, whereas the other deep branches (*Promerops*, *Diceum*, *Nectarinia*, *Irena* and *Chloropsis* in Fig. 1) have very weak mandibular adductors but a reinforced depressor mechanism, possibly an adaptation to access nectar sources. The more terminal radiation of granivorous birds (*Prunella* to *Ammodramus* in Fig. 1) are, with the exception of the family Motacillidae, characterized by complex and pinnate mandibular adductors and greatly expanded temporal fossa with distinct structures for muscle attachments such as strongly developed postorbital and zygomatic processes and orbital process of the quadrate (Fig. 4c–e) and corresponding reinforced muscle attachments on the lower mandible.

The Cinnamon Ibon skull resembles most closely that of the granivorous passeroids, although the bill and associated muscle attachments are less extreme than in specialized seed-eaters. Its diet is varied, and may require some strength for crushing. According to label data for the 16 available specimens in the ZMUC from Mindanao, most had insect remains in their stomachs, specified as beetles (or even 'lots of beetles') on some labels, plus many larvae, fruit pulp, berries and some seeds. This food must mainly have been taken from the vegetation, but Hachisuka (1930) suggests that the Cinnamon Ibon may also feed like a flycatcher.

Unfortunately, very little information is available about the biology of the Cinnamon Ibon. It feeds in all strata in the forest, from understorey bushes to the canopy, but may be most typical of the interior of mature forest with an open understorey (Hachisuka 1930). It is generally found in groups and often as a core species of mixed flocks with white-eyes (*Zosterops montanus*, *Lophozosterops goodfellowi*), fantails (Black-and-cinnamon Fantail *Rhipidura nigrocinnamomea*), warblers (Mountain Leaf-warbler *Phylloscopus trivirgatus*)

and tits (Elegant Tit *Periparus elegans*), which glean prey from small branches and leaves (van Balen 2008).

The call notes of the Cinnamon Ibon are reported to resemble those of a sparrow (*Passer*; van Balen 2008), and it is not melodious (Hachisuka 1930), but apart from this, little of what is known about its biology seems to resemble that of sparrows. Most peculiar is its association with the cloud-forest canopy, unlike all other sparrows. This could be an ancestral adaptation, considering that some of the deeper branches of the passeroid group (sunbirds, flowerpeckers and leafbirds) inhabit arboreal habitat. However, the morphology of the foot soles of the Cinnamon Ibon, with small toe-pads and multiple folds and furrows, resembles those of weavers and sparrows and other terrestrial clades (Lennerstedt 1973). This seems to suggest a secondary specialization to its cloud-forest habitat.

Biogeography

The Cinnamon Ibon has a restricted distribution on the southern Philippine island of Mindanao, where it inhabits montane cloud-forest on the Malindang, Misamis oriental, Kitanglad, Hilong-hilong, Mitutum, Mayo and Apo Mountains (Kennedy *et al.* 2000).

Mindanao is located at the southeastern margin of the geographical range of the sparrow family, as the highest taxonomic diversity among sparrows occurs in mountainous parts of Asia, and only one species, the Tree Sparrow, with a rather terminal position in the family, is represented with marginal populations in the Philippines. In addition, most of the deeper passeroid lineages seem to be rooted in continental Asia, with secondary radiations in Africa and in the New World (Barker *et al.* 2002; exceptions are some relictual taxa including the sugarbirds, the Spot throat and others in Africa, and the high diversity of flowerpeckers in the Philippines).

The isolated occurrence of the Cinnamon Ibon on Mindanao is even more remarkable when we take into account that the southern Philippine islands originated as a group of volcanic islands far out in the Pacific Ocean, with no near contact with Gondwana or other subaerial land areas (Hall 2002). At 30 Mya (corresponding to the origin of the *Hypocryptadius* lineage in Fig. 3), the southern Philippine islands were still positioned far out in the ocean north of New Guinea. However, volcanoes along the island arc that now constitute Sangihe and northern Sulawesi may have provided potential stepping-stones for dispersal from the Greater Sunda Area.

Any attempt to interpret the isolated distribution on Mindanao must necessarily be speculative, as we still lack a densely sampled phylogeny of the passeroid clade. However, considering the length of the *Hypocryptadius* branch in Figure 3, it seems plausible to refer to it as a relictual form and representative of a clade that originated somewhere else.

CONCLUSIONS

Molecular and morphological evidence strongly indicates that the Cinnamon Ibon is a member of the radiation of granivorous passeroid birds. The cranial morphology places it within the radiation of granivorous passeroids, but suggests a basal position with less strong specialization than seen in the true sparrows (*Passer*, *Petronia*). However, the state of the palate and ectethmoid foramina is in agreement with the basal position of the typical sparrow clade, as suggested by the molecular phylogeny. The agreement of morphological and molecular evidence strongly supports the transfer of the Cinnamon Ibon from the Zosteropidae to the Passeridae *sensu* Voous (1977). However, *Hypocryptadius* should be retained in a distinct, monotypic subfamily, Hypocryptadiinae Hachisuka 1930, to indicate its differences from the typical Passeridae (*Passer*, *Petronia*, *Gymnornis*, *Montifringilla* and *Pyrgilauda*).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figures S1–S3. Trees recovered from the Bayesian analysis of the individual genes. S1: IRBP (left) and ZENK (right); S2: myoglobin intron 2 (left) and ornithine decarboxylase introns 6–7 (right); S3: NADH dehydrogenase II (left) and NADH

dehydrogenase III (right). The posterior probability values are indicated at the node (threshold 0.95).

Table S1. Primer pairs used for the amplification and sequencing of the nuclear genes of *Hypocryptadius cinnamomeus*.

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