



# Molecular and morphological evidences place the extinct New Zealand endemic *Turnagra capensis* in the Oriolidae

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## ABSTRACT

The affinities of Piopio *Turnagra capensis*, an extinct New Zealand passerine, remain poorly known. It has been included into or associated with several bird families (Calleatidae, Cracticidae, Pachycephalidae, Ptilonorhynchidae, Turdidae), often on tenuous grounds. We reassessed *Turnagra* phylogenetic relationships using nuclear and mitochondrial sequences and a set of morphological and behavioural traits. Molecular and phenotypic characters strongly suggest a novel hypothesis, congruently placing *Turnagra* in Oriolidae, a highly dispersive corvid family distributed from the Austro-Papuan landmass to Eurasia and Africa, but missing from the Pacific islands. We show also that the published molecular support to link *Turnagra* with Ptilonorhynchidae was biased by the use of incorrect genetic data and weak analyses.

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## 1. Introduction

New Zealand and its offshore islands host a peculiar avifauna with high endemism (OSNZ, 2010). The origin of New Zealand birds appears to be complex, with some taxa possibly representing vicariants deriving from the Gondwana break-up, while most lineages are more recent colonists (Trewick and Gibb, 2010; Lanfear and Bromham, in press).

The native passerines comprise 27–38 species-level taxa (depending on the taxonomic treatment, see Trewick and Gibb, 2010 and references therein). Some species are the result of local radiations and are currently classified as endemic families or endemic genera (Acanthisittidae, Callaeidae–Notiomystidae, *Mohoua*, *Turnagra*), but most species are closely related to non-New Zealand taxa. The molecular data identify 14 vicariance or dispersal events responsible for the build-up of the native passerine avifauna (Trewick and Gibb, 2010). The sister taxon of most passerine lineages have been clarified, either suggesting a vicariant origin (Acanthisittidae: Barker et al., 2002; Ericson et al., 2002a) or providing information on the time and direction of dispersal (e.g. Callaeidae: Barker et al., 2004; Meliphagidae: Driskell and Christidis, 2004; Petroicidae: Miller and Lambert, 2006). Some species have

never been included in molecular studies, but are nonetheless placed confidently in Australasian (*Gerygone*) or cosmopolitan (*Corvus*) genera based on morphological evidences (OSNZ, 2010). But the affinities of the endemic and now extinct *Turnagra capensis* remain poorly understood and several hypotheses were put forward.

At the time of human contact *Turnagra capensis* inhabited the entire New Zealand and some offshore islets (Worthy and Holdaway, 2002). Morphologically distinct forms existed in the South and North Islands, usually ranked at the subspecies level (*T. capensis capensis* and *T. capensis tanagra*, respectively). It was a still common forest bird at the time of European settlement, but disappeared shortly after 1900, probably due to the predation by introduced mammals (Tennyson and Martinson, 2006). In size, shape and colour *Turnagra* bears a vague resemblance to some *Turdus* thrushes, hence the common name of New Zealand thrush given by the first European settlers. The complex taxonomic history of *Turnagra* has been revised in detail by Olson et al. (1983). The species has been associated with no less than six passerine families: Calleatidae (Finsch, 1872), Cracticidae (Oliver, 1945), Pachycephalidae (Mayr and Amadon, 1951; Mayr, 1967), Ptilonorhynchidae (Sundevall, 1872; Finsch, 1874), Timaliidae (Sharpe, 1883), Turdidae (Buller, 1869; Sharpe, 1903), or segregated in the monotypic Turnagridae (Buller, 1887; Oliver, 1930; OSNZ, 1953, 1970).

Olson et al. (1983) reassessed the *Turnagra* affinities using a wide set of morphological characters, including general shape, plumage colour and structure, bill shape, development of rectal

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bristles, tarsal scutellation, pterylosis, myology, osteology. They concluded that *Turnagra* was unrelated to the Pachycephalidae, but likely “the most primitive member of the bird-of-paradise/bowerbird assemblage”. Olson et al.’s conclusions were, however, based on morphological similarity, without a formal cladistic analysis. A further problem with Olson et al.’s conclusion is represented by the polyphyly in the supposed “bird-of-paradise/bowerbird assemblage”. While the bowerbirds (Ptilonorhynchidae) belong to one of the most basal Oscine lineages, the typical birds-of-paradise (Paradisaeidae) are nested within the Core Corvoidea and the cnemophiline birds-of-paradise (Cnemophilidae) are at the base of the Passerida radiation (Barker et al., 2004; Irestedt and Ohlson, 2008). Nonetheless a mitochondrial molecular phylogeny seems to lend support to Olson et al.’ hypothesis (Christidis et al., 1996a), recovering *Turnagra* sister to the Ptilonorhynchidae. However the use of a single, fast evolving gene (cytochrome *b*) and the lack of representatives of the Paradisaeidae, the Cnemophilidae and many other passerine lineages make Christidis et al.’s finding in need of validation with a more robust dataset. In the present paper we revise *Turnagra* relationships using a multi-locus dataset and comprehensive taxon sampling. We also discuss its morphological and behavioural similarities with other bird lineages in the light of molecular findings.

## 2. Materials and methods

### 2.1. Taxon sampling strategy

We tested the phylogenetic hypotheses about the relationships of *Turnagra capensis* analysing a comprehensive dataset that includes representatives of all taxa associated with it in the past: Turdidae, Pachycephalidae, Ptilonorhynchidae, Cnemophilidae and Cracticidae. We included also representatives of all other passerine lineages that are or were known to occur in New Zealand: Acanthisittidae, Acanthizidae, Meliphagidae, *Mohoua*, Rhipiduridae, Corvidae, Callaeidae, *Notiomystis*, Petroicidae, Hirundinidae, Locustellidae, Zosteropidae and Motacillidae (Trewick and Gibb, 2010). From the results of several comprehensive passerine phylogenies (Barker et al., 2004; Alström et al., 2006; Jönsson and Fjeldså, 2006; Johansson et al., 2008; Norman et al., 2009) we selected representatives of all other deeper lineages, with special emphasis on the Core Corvoidea (*sensu* Barker et al., 2004). The tree was rooted with two parrots and two falcons as these are the sister lineages to the Passeriformes (Ericson et al., 2006a; Hackett et al., 2008). The dataset includes 81 species (77 ingroup and 4 outgroup taxa).

Table 1 provides the list of included taxa with sample accession numbers and the Genbank accession numbers of analyzed sequences. The *Turnagra* toepad was obtained from a specimen of the South Island form *Turnagra capensis capensis* housed in the Museo di Zoologia dell’Università di Torino (accession number MZUT Av2962).

### 2.2. DNA isolation and sequencing

Fresh tissue samples were extracted using the Qiagen DNA Mini Kit, following the manufacturer’s protocol. We used the Qiagen DNA Mini Kit for the toe-pad samples with a modified protocol as described in Zuccon (2005) and Irestedt et al. (2006).

We selected six nuclear (two exons and four introns) and three mitochondrial genes that are widely used in bird phylogenetic studies: the interphotoreceptor retinol-binding protein (IRBP), the zinc finger protein (ZENK), intron 11 of the glyceraldehyde-3-phosphodehydrogenase (GAPDH), intron 2 of the myoglobin gene, introns 6 and 7 of the ornithine decarboxylase

(ODC) gene, intron 9 of the phosphoenolpyruvate carboxykinase (PEPCK), cytochrome *b* (cytb), NADH dehydrogenase II and III genes (ND2 and ND3). The nine loci were amplified and sequenced using standard primers and amplification profiles as described in Fjeldså et al. (2010) for IRBP, Chubb (2004) for ZENK, Fjeldså et al. (2003) for GAPDH, Irestedt et al. (2002) for myoglobin, Allen and Omland (2003) for ODC, Sorenson et al. (2003) for PEPCK, Zuccon and Ericson (2010b) for cytb, Zuccon et al. (2006) for ND2 and Chesser (1999) for ND3. The toe-pad samples were amplified in a series of short, overlapping fragments of 200–300 bp, using a large set of internal primers (see Suppl. Material).

### 2.3. Gene characterisation and phylogenetic analyses

The nine loci were concatenated in a partitioned dataset. We excluded three long autapomorphic insertions for reducing the computational time: 630 bp in intron 6 of ODC in *Anthus*, 83 bp in intron 7 of ODC in *Rhipidura*, and 177 bp of PEPCK in *Acanthisitta*. Another 62 character positions that proved impossible to align unambiguously were excluded as well: 12 bp in ZENK, 31 bp in GAPDH, 16 bp in ODC, 3 bp in PEPCK. The final dataset, consisting of 7348 bp, was analyzed under the Bayesian inference and the maximum likelihood criteria.

Bayesian inference was carried out using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003), implemented on the freely available Biportal ([www.biportal.uio.no](http://www.biportal.uio.no)). A mixed model approach was implemented to account for the potential differences in evolutionary model parameters between the data partitions corresponding to the nine genes. The models best fitting the data were obtained with MrModelTest (Nylander, 2004), using the AIC criterion, 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 and Ronquist, 2001). Two independent runs of four incrementally heated Metropolis-coupled MCMC chains for 20 million generations were run, with sampling every 1000 generations, yielding 20,000 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 “burn-in” (15,000 trees).

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

Datasets including only the mitochondrial and the nuclear genes, respectively, were also analyzed under the Bayesian inference criterion using the same analytical parameters indicated above.

We explored the effect of missing data on the phylogenetic reconstruction under the Bayesian inference criterion. We analyzed a reduced dataset where we included only the species for which all gene were sequenced or only a single gene was missing (four species).

We compared alternative phylogenetic hypotheses using the Shimodaira–Hasegawa test (SH-test, Shimodaira and Hasegawa, 1999), as implemented in RAXML v. 7.0.3 (Stamatakis, 2006). The tested topologies were obtained enforcing *Turnagra* forming a monophyletic clade with selected taxa in the maximum likelihood searches in RAXML.

### 2.4. Morphological and behavioural characters

We scanned all the relevant literature on *Turnagra* and possibly related taxa and identified a series of morphological characters

**Table 1**  
 Samples and sequences included in the phylogenetic analysis with museum accession numbers. The nomenclature follows Dickinson (2003). GenBank accession numbers of sequences published previously are followed by their references. Museum acronyms: AM Australian Museum, Sydney; FMNH Field Museum of Natural History, Chicago; LSU Louisiana State University Museum of Natural History, Baton Rouge; MV Museum of Victoria, Melbourne; MZUT Museo di Zoologia dell'Università di Torino (now stored in Museo Regionale di Scienze Naturali, Torino); NRM Swedish Museum of Natural History, Stockholm; UWBM University of Washington, Burke Museum, Seattle; ZMUC Zoological Museum, University of Copenhagen. References: [1]: Fjeldså et al. (2010); [2]: Irestedt et al. (2008); [3]: Fjeldså et al. (2003); [4]: Irestedt and Ohlson (2008); [5]: Jönsson et al. (2010a); [6]: Fjeldså et al. (2005); [7]: Jönsson et al. (2010b); [8]: Fuchs et al. (2006); [9]: Fuchs et al. (2007); [10]: Jönsson et al. (2008a); [11]: Irestedt et al. (2006); [12]: Zuccon and Ericson (2010a); [13]: Fuchs et al. (2004); [14]: Ericson et al. (2002b); [15]: Norman et al. (2009); [16]: Johansson and Ericson (2003); [17]: Zuccon et al. (2006); [18]: Ericson and Johansson (2003); [19]: Alström et al. (2006); [20]: Jönsson et al. (2007); [21]: Irestedt et al. (2002); [22]: Mayr et al. (2003); [23]: Ericson et al. (2006b); [24]: Zuccon and Ericson (2010c); [25]: Johansson et al. (2008); [26]: Jönsson et al. (2008b); [27]: Ericson et al. (2006a); [28]: Harrison et al. (2004); [29]: Christidis et al. (1996b); [30]: Shepherd and Lambert (2007); [31]: Dor et al. (2010); [32]: Cracraft and Feinstein (2000); [33]: Alström et al. (2011); [34]: Cibois et al. (1999); [35]: Miller and Lambert (2006); [36]: Barker et al. (2004); [37]: Dumbacher et al. (2008); [38]: Driskell and Christidis (2004); [39]: Zuccon and Ericson (2010b); [40]: Wink et al. unpub.; [41]: Melo and O'Ryan (2007); [42]: Ribas et al. (2006); [43]: Hauber and Chong unpub.; [44]: Moyle et al. (2009); [45]: Warren et al. (2006).

Taxon	Accession N	IRBP	ZENK	GADPH	Myoglobin	ODC	PEPCK	cyt b	ND2	ND3
<i>Acanthisitta chloris</i>	NRM 569989 <sup>b</sup>	GU816860 [1] <sup>a</sup>	GU816947 [1] <sup>a</sup>	EU726202 [2] <sup>a</sup>	EU726212 [2] <sup>a</sup>	EU726220 [2] <sup>a</sup>	XXX JN614531	AY325307 [28]	AY325307 [28]	AY325307 [28]
<i>Acanthisitta pusilla</i>	Cockburn No.1	JN614765	JN614484	JN614818	JN614736	JN614595	JN614542	JN614867	JN614695	JN614643
<i>Ailuroedus crassirostris</i>	AM O65212	JN614761	JN614480	JN614814	JN614735	JN614591	JN614538	JN614865	JN614691	JN614639
<i>Anthornis melanura</i>		–	–	–	–	–	–	–	HM159185 [43]	–
<i>Anthus campestris</i>	DZC 20020427.01	JN614804	JN614523	JN614854	JN614754	JN614630	JN614583	JN614900	JN614730	JN614680
<i>Artamus leucorhynchus</i>	MV S3010	JN614773	JN614492	JN614825	FJ821079 [15] <sup>a</sup>	JN614602	JN614551	JN614874	JN614701	JN614651
<i>Batis crypta</i>	ZMUC O2953	JN614776	JN614495	JN614828	JN614739	JN614605	JN614554	JN614877	JN614704	JN614654
<i>Callaeva cinerea</i>	Mapara 196126	JN614800	JN614519	JN614849	JN614751	JN614626	JN614578	JN614896	JN614726	JN614676
<i>Campephaga flava</i>	ZMUC O11	GU816864 [1] <sup>a</sup>	GU816951 [1] <sup>a</sup>	AY336585 [3] <sup>a</sup>	AY165803 [16] <sup>a</sup>	GU816899 [1] <sup>a</sup>	JN614547	JN614872	GU816829 [1] <sup>a</sup>	GU816800 [1] <sup>a</sup>
<i>Certhia familiaris</i>	NRM 976184	GU816892 [1] <sup>a</sup>	GU816979 [1] <sup>a</sup>	JN614855	DQ466821 [17] <sup>a</sup>	GU816924 [1] <sup>a</sup>	JN614584	DQ008524 [19] <sup>a</sup>	DQ466857 [17] <sup>a</sup>	GU816820 [1] <sup>a</sup>
<i>Climacteris rufa</i>	MV 155	JN614762	JN614481	JN614815	AY064733 [14] <sup>a</sup>	JN614592	JN614539	U58501 [29]	JN614692	JN614640
<i>Cnemophilus loriae</i>	NRM 569572 <sup>b</sup>	JN614798	JN614517	EU272096 [4] <sup>a</sup>	EU272107 [4] <sup>a</sup>	EU272126 [4] <sup>a</sup>	JN614576	–	JN614724	JN614674
<i>Colluricincla harmonica</i>	MV 1422	JN614783	JN614502	JN614834	JN614743	JN614611	JN614561	JN614883	JN614710	GQ494125 [5] <sup>a</sup>
<i>Colluricincla megarhyncha</i>	–	–	–	GQ494038 [5]	GQ494067 [5]	GQ494050 [5]	–	EF592220 [37]	GQ494093 [5]	GQ494127 [5]
<i>Coracina lineata</i>	MV JCW073	JN614770	JN614489	JN614822	EU273398 [10] <sup>a</sup>	JN614599	JN614548	FJ821115 [15] <sup>a</sup>	EF052776 [9]	JN614648
<i>Corcorax melanorhamphos</i>	AM LAB1059	JN614793	JN614512	JN614844	AY064737 [14] <sup>a</sup>	JN614621	JN614571	AY064274 [14] <sup>a</sup>	JN614719	JN614669
<i>Cormobates placens</i>	MV E309	JN614763	JN614482	JN614816	AY064731 [14] <sup>a</sup>	JN614593	JN614540	JN614866	JN614693	JN614641
<i>Corvus cornix</i>	NRM 986167	JN614796	JN614515	JN614847	AY228327 [18] <sup>a</sup>	JN614624	JN614574	AY228087 [18] <sup>a</sup>	JN614722	JN614672
<i>Cyclarhis gujanensis</i>	NRM 966964	JN614789	JN614508	JN614840	JN614745	JN614617	JN614567	JN614889	JN614715	JN614665
<i>Dicrurus remifer</i>	NRM 20086565	JN614792	JN614511	JN614843	JN614748	JN614620	JN614570	JN614892	JN614718	JN614668
<i>Eopsaltria australis</i>	MV 1390	JN614802	JN614521	JN614851	AY064732 [14] <sup>a</sup>	JN614628	JN614580	AY064273 [14] <sup>a</sup>	JN614728	JN614678
<i>Epimachus albertisi</i>	MV C148	JN614794	JN614513	JN614845	AY064735 [14] <sup>a</sup>	JN614622	JN614572	JN614893	JN614720	JN614670
<i>Erpornis zantholeuca</i>	NRM 947312	JN614788	JN614507	JN614839	JN614744	JN614616	JN614566	JN614888	–	JN614664
<i>Falculunculus frontatus</i>	MV 1393	JN614787	JN614506	JN614838	FJ821086 [15] <sup>a</sup>	JN614615	JN614565	JN614887	JN614714	JN614663
<i>Furnarius cristatus</i>	NRM 966772	JN614759	JN614478	AY590066 [6] <sup>a</sup>	AY064255 [14] <sup>a</sup>	DQ435482 [23] <sup>a</sup>	JN614534	JN614861	JN614688	JN614635
<i>Gerygone igata</i>		–	–	–	–	–	–	–	HM159175 [43]	–
<i>Gymnorhina tibicen</i>	AM LAB1107	JN614774	JN614493	JN614826	JN614737	JN614603	JN614552	JN614875 DQ469300 [30]	JN614702 DQ469296 [30]	JN614652
<i>Heteralocha acutirostris</i>		–	–	–	–	–	–	GU460230 [31]	GU460295 [31]	–
<i>Hirundo neoxena</i>		–	–	–	–	–	–	GU460230 [31]	GU460295 [31]	–
<i>Hirundo rustica</i>	NRM 976238	JN614806	JN614525	JN614856	AY064258 [14] <sup>a</sup>	GQ242149 [24] <sup>a</sup>	JN614585	JN614901	GQ242090 [24] <sup>a</sup>	JN614682
<i>Lanius excubitor</i>	NRM 996541	JN614797	JN614516	JN614848	JN614750	JN614625	JN614575	JN614895	JN614723	JN614673
<i>Loboparadisaea sericea</i>	NRM 566737 <sup>b</sup>	JN614799	JN614518	EU272095 [4] <sup>a</sup>	EU272106 [4] <sup>a</sup>	EU272125 [4] <sup>a</sup>	JN614577	AF197843 [32]	JN614725	JN614675
<i>Malurus amabilis</i>	MV C803	JN614764	JN614483	JN614817	AY064729 [14] <sup>a</sup>	JN614594	JN614541	AY228088 [18] <sup>a</sup>	JN614694	JN614642
<i>Megalurus palustris</i>	NRM 20046786	JN614807	JN614526	JN614857	DQ008529 [19] <sup>a</sup>	EU680741 [25] <sup>a</sup>	JN614586	DQ008477 [19] <sup>a</sup>	JN614731	–
<i>Megalurus punctatus</i>		–	–	–	–	–	–	HQ706173 [33]	–	–

Table 1 (continued)

Taxon	Accession N	IRBP	ZENK	GADPH	Myoglobin	ODC	PEPCK	cyt b	ND2	ND3
<i>Menura novaehollandiae</i>	AM LAB1112	GU816863 [1] <sup>a</sup>	GU816950 [1] <sup>a</sup>	JN614812	JN614733	JN614589	JN614536	JN614863	JN614689	JN614637
<i>Microeca fascians</i>	UWBM 60797	JN614803	JN614522	JN614852	JN614753	JN614629	JN614581	JN614898	JN614729	JN614679
<i>Mohoua albicilla</i>		JN614772	JN614491	JN614824	FJ821091 [15]	JN614601	JN614550	FJ821127 [15]	JN614700	JN614650
<i>Mohoua novaeseelandiae</i>		–	–	–	–	–	–	–	HM159174 [43]	–
<i>Mohoua ochrocephala</i>		–	–	–	–	–	–	–	HM159168 [43]	–
<i>Notiomystis cincta</i>	NRM	JN614801	JN614520	JN614850	JN614752	JN614627	JN614579	JN614897	JN614727	JN614677
<i>Oreoica gutturalis</i>	MV W055	JN614771	JN614490	JN614823	FJ821094 [15] <sup>a</sup>	JN614600	JN614549	JN614873	JN614699	JN614649
<i>Oriolus brachyrhynchus</i>		–	–	GQ901791 [7]	–	GQ901709 [7]	–	–	GQ901762 [7]	GQ901733 [7]
<i>Oriolus flavocinctus</i>	MV 1603	JN614780	JN614499	JN614831	EF441258 [20] <sup>a</sup>	EF441243 [20] <sup>a</sup>	JN614558	JN614880	JN614708	GQ901728 [7] <sup>a</sup>
<i>Oriolus larvatus</i>		–	–	GQ901796 [7]	–	GQ901714 [7]	–	–	GQ901767 [7]	GQ901738 [7]
<i>Oriolus oriolus</i>	NRM 20036563	JN614781	JN614500	JN614832	JN614742	JN614609	JN614559	JN614881	EF052693 [9]	JN614658
<i>Oriolus xanthonotus</i>		–	–	GQ901794 [7]	–	GQ901712 [7]	–	–	GQ901765 [7]	GQ901736 [7]
<i>Oriolus xanthornus</i>		–	–	DQ406645 [8]	AY529929 [13]	EU272111 [4]	–	AF094615 [34]	AY529964 [13]	–
<i>Orthonyx temminckii</i>	MV B831	JN614767	JN614486	JN614820	AY064728 [14] <sup>a</sup>	JN614597	JN614544	JN614869	JN614697	JN614645
<i>Pachycephala olivacea</i>	MV B761	JN614785	JN614504	JN614836	FJ821097 [15] <sup>a</sup>	JN614613	JN614563	JN614885	JN614712	JN614661
<i>Pachycephala pectoralis</i>	MV 1419	JN614786	JN614505	JN614837	AY064727 [14] <sup>a</sup>	JN614614	JN614564	JN614886	JN614713	JN614662
<i>Pericrocotus divaricatus</i>	NRM 20016234	JN614769	JN614488	EF052818 [9]	EF052843 [9]	EU380450 [26]	JN614546	JN614871	EF052788 [9]	JN614647
<i>Petroica australis</i>		–	–	–	–	–	–	DQ469301 [30]	DQ469299 [30]	–
<i>Petroica macrocephala</i>		–	–	–	–	–	–	DQ359082 [35]	HM159177 [43]	–
<i>Philepitta castanea</i>	ZMUC S458	JN614757	JN614476	AY336591 [3] <sup>a</sup>	AY065790 [21] <sup>a</sup>	DQ785938 [11] <sup>a</sup>	JN614532	JN614859	JN614686	JN614633
<i>Philesturnus carunculatus</i>		–	–	–	–	–	–	DQ469303 [30]	DQ469297 [30]	–
<i>Picathartes gymnocephalus</i>	LSU B19213	GU816866 [1] <sup>a</sup>	GU816953 [1] <sup>a</sup>	JN614853	AY228314 [18] <sup>a</sup>	GU816900 [1] <sup>a</sup>	JN614582	JN614899	GU816831 [1] <sup>a</sup>	GU816802 [1] <sup>a</sup>
<i>Pitohui cristatus</i>		–	–	EU273389 [10]	EU273411 [10]	EU273370 [10]	–	AY443257 [36]	GQ494087 [5]	GQ494121 [5]
<i>Pitohui dichrous</i>	NRM 71252	JN614778	JN614497	EU273390 [10]	JN614740	JN614607	JN614556	EF592249 [37]	JN614706	JN614656
<i>Pitohui ferrugineus</i>	MV E611	JN614782	JN614501	JN614833	FJ821101 [15] <sup>a</sup>	JN614610	JN614560	JN614882	JN614709	JN614659
<i>Pitohui kirhocephalus</i>		–	–	EU273392 [10]	EU273414 [10]	–	–	EF592256 [37]	GQ494100 [5]	GQ494134 [5]
<i>Pitohui nigrescens</i>	MV E246	JN614784	JN614503	JN614835	EU273415 [10] <sup>a</sup>	JN614612	JN614562	JN614884	JN614711	JN614660
<i>Pitta erythrogaster</i>	FMNH 358346	JN614758	JN614477	DQ785909 [11] <sup>a</sup>	DQ785984 [11] <sup>a</sup>	DQ785948 [11] <sup>a</sup>	JN614533	JN614860	JN614687	JN614634
<i>Pomatostomus temporalis</i>	MV D257	JN614768	JN614487	JN614821	AY064730 [14] <sup>a</sup>	JN614598	JN614545	JN614870	JN614698	JN614646
<i>Prothemadera novaeseelandiae</i>		–	–	–	–	–	–	AY488380 [38]	AY488305 [38]	–
<i>Ptilonorhynchus violaceus</i>	AM LAB1099	JN614760	JN614479	JN614813	JN614734	JN614590	JN614537	JN614864	JN614690	JN614638
<i>Ptiloprora plumbea</i>	MV C173	JN614766	JN614485	JN614819	AY064736 [14] <sup>a</sup>	JN614596	JN614543	JN614868	JN614696	JN614644
<i>Rhipidura albicollis</i>	NRM 20046755	JN614790	JN614509	JN614841	JN614746	JN614618	JN614568	JN614890	JN614716	JN614666
<i>Rhipidura fuliginosa</i>	MV 1396	JN614791	JN614510	JN614842	JN614747	JN614619	JN614569	JN614891	JN614717	JN614667
<i>Sphecotheres viridis</i>	MV C398	JN614777	JN614496	JN614829	FJ821107 [15] <sup>a</sup>	JN614606	JN614555	JN614878	JN614705	JN614655
<i>Telophorus sulfureopectus</i>	NRM 20066991	JN614775	JN614494	JN614827	JN614738	JN614604	JN614553	JN614876	JN614703	JN614653
<i>Terpsiphone viridis</i>	ZMUC O1062	JN614795	JN614514	JN614846	JN614749	JN614623	JN614573	JN614894	JN614721	JN614671
<i>Turdus philomelos</i>	NRM 20036737	JN614805	JN614524	GU359037 [12] <sup>a</sup>	DQ466848 [17] <sup>a</sup>	GU358902 [12] <sup>a</sup>	GU358965 [12] <sup>a</sup>	GU237100 [39] <sup>a</sup>	DQ466886 [17] <sup>a</sup>	JN614681
<i>Turnagra capensis</i>	MZUT Av2962 <sup>b</sup>	JN614779	JN614498	JN614830	JN614741	JN614608	JN614557	JN614879	JN614707	JN614657
<i>Tyrannus savana</i>	NRM 976722	GU816862 [1] <sup>a</sup>	GU816949 [1] <sup>a</sup>	AY336579 [3] <sup>a</sup>	AY165826 [16] <sup>a</sup>	DQ435507 [23] <sup>a</sup>	JN614535	JN614862	GU816828 [1] <sup>a</sup>	JN614636

(continued on next page)



**Table 1** (continued)

Taxon	Accession N	IRBP	ZENK	GADPH	Myoglobin	ODC	PEPCK	cyt <i>b</i>	ND2	ND3
<i>Zosterops lateralis</i>		–	–	–	–	–	–	DQ328389 [45]	FJ460814 [44]	FJ460882 [44]
<i>Zosterops nigrorum</i>	ZMUC 02663	GU816897 [1] <sup>a</sup>	GU816984 [1] <sup>a</sup>	JN614858	GU816944 [1] <sup>a</sup>	GU816927 [1] <sup>a</sup>	JN614587	JN614902	GU816857 [1] <sup>a</sup>	JN614683
Outgroup										
<i>Falco subbuteo</i>	NRM 986329	GU816858 [1] <sup>a</sup>	GU816945 [1] <sup>a</sup>	JN614809	JN614732	JN614588	JN614528	EU233117 [40]	GU816825 [1] <sup>a</sup>	GU816797 [1] <sup>a</sup>
<i>Polyborus plancus</i>	NRM 947200	JN614755	JN614474	JN614808	AY233364 [22] <sup>a</sup>	DQ881770 [27] <sup>a</sup>	JN614527	EU233146 [40]	JN614684	JN614631
<i>Psittacus erithacus</i>	NRM 20066765	GU816859 [1] <sup>a</sup>	GU816946 [1] <sup>a</sup>	JN614810	GU816928 [1] <sup>a</sup>	GU816898 [1] <sup>a</sup>	JN614529	DQ335468 [41]	GU816826 [1] <sup>a</sup>	GU816798 [1] <sup>a</sup>
<i>Pyrrhura frontalis</i>	NRM 966989	JN614756	JN614475	JN614811	AY233367 [22] <sup>a</sup>	DQ881775 [27] <sup>a</sup>	JN614530	AY751643 [42]	JN614685	JN614632

<sup>a</sup> Published sequence obtained from the same sample used in this study.

<sup>b</sup> Toepad samples.

**Table 2**

Sequence characteristics of the loci analyzed. The numbers of variable and parsimony informative bases are calculated for the ingroup only. Three long synapomorphic insertions in ODC and PEPCK and 62 character positions impossible to align unambiguously have been excluded from the computation, see text for details.

Gene region	IRBP	ZENK	GADPH	Myoglobin	ODC	PEPCK	cyt <i>b</i>	ND2	ND3
Alignment length	1074	1158	467	768	839	677	972	1041	352
Number of variable bases (%)	497 (46.3%)	438 (37.8%)	279 (59.7%)	497 (64.7%)	464 (56.1%)	401 (59.2%)	487 (50.1%)	708 (68%)	212 (60.2%)
Number of parsimony informative bases (%)	278 (25.9%)	241 (20.8%)	190 (40.7%)	278 (36.2%)	297 (35.9%)	207 (30.6%)	448 (46.1%)	652 (62.6%)	195 (55.4%)
% A nucleotides (range)	25.9 (25.0–27.3)	23.7 (20.9–24.8)	21.3 (19.3–23.9)	27.9 (26.7–29.4)	28.0 (26.5–29.1)	29.8 (28.5–31.5)	28.1 (25.0–31.0)	30.2 (27.5–34.0)	27.9 (25.1–31.6)
% C (range)	24.1 (23.3–24.7)	35.8 (34.9–39.1)	19.0 (16.8–21.4)	22.3 (20.8–23.3)	17.2 (16.1–18.6)	19.8 (17.3–21.1)	33.1 (29.1–37.1)	33.6 (26.3–37.2)	32.8 (28.5–37.0)
% G (range)	27.1 (25.4–27.9)	18.9 (17.8–21.4)	34.7 (32.1–37.0)	23.6 (21.8–25.7)	20.7 (19.6–22.5)	18.5 (16.8–20.9)	14.0 (10.5–15.2)	11.3 (9.5–14.2)	12.8 (8.5–15.1)
% T (range)	23.0 (22.2–23.7)	21.7 (18.7–22.4)	25.0 (22.3–28.0)	26.2 (23.9–27.4)	34.1 (32.6–35.6)	31.9 (29.8–33.3)	24.7 (21.6–27.5)	24.8 (22.9–30.1)	26.5 (22.6–29.9)
Selected substitution model	K80 + I + $\Gamma$	GTR + I + $\Gamma$	GTR + $\Gamma$	SYM + $\Gamma$	GTR + $\Gamma$ + I	K80 + $\Gamma$	GTR + I + $\Gamma$	GTR + I + $\Gamma$	GTR + I + $\Gamma$

that were used to assess *Turnagra* relationships (Clench, 1985; Frith and Frith, 2004; Olson et al., 1983; Schodde and Mason, 1999; Worthy and Holdaway, 2002). These include eleven external characters (plumage, bill, wings and feet) and nine characters from internal morphology (Table 4).

Parsimony analyses were performed in PAUP\* v. 4.0b10 (Swofford, 2003). Taxa in which two or more states have been observed were interpreted as polymorphic. All characters were treated as unordered in the analyses. The searches were performed under the branch-and-bound option in PAUP\* and the estimated bootstrap support values are based on 10,000 replicates. Ptilonorhynchidae was used to root the tree as this taxon is presumed to be phylogenetically basal to the others (Ericson et al., 2002a, 2002b).

We also summarised some behavioural and ecological characters, including nest, eggs, mating systems, diet, vocalisation, over-water dispersal ability (Table 5). These characters are not easily scored for a formal cladistic analysis and they will be discussed below. The morphological characters, nests structure and eggs colour were re-assessed using the collections at the Natural History Museum, Tring.

### 3. Results

#### 3.1. Molecular evidences

We obtained almost full sequences for all taxa that we sequenced, but included partial sequences from GenBank for few

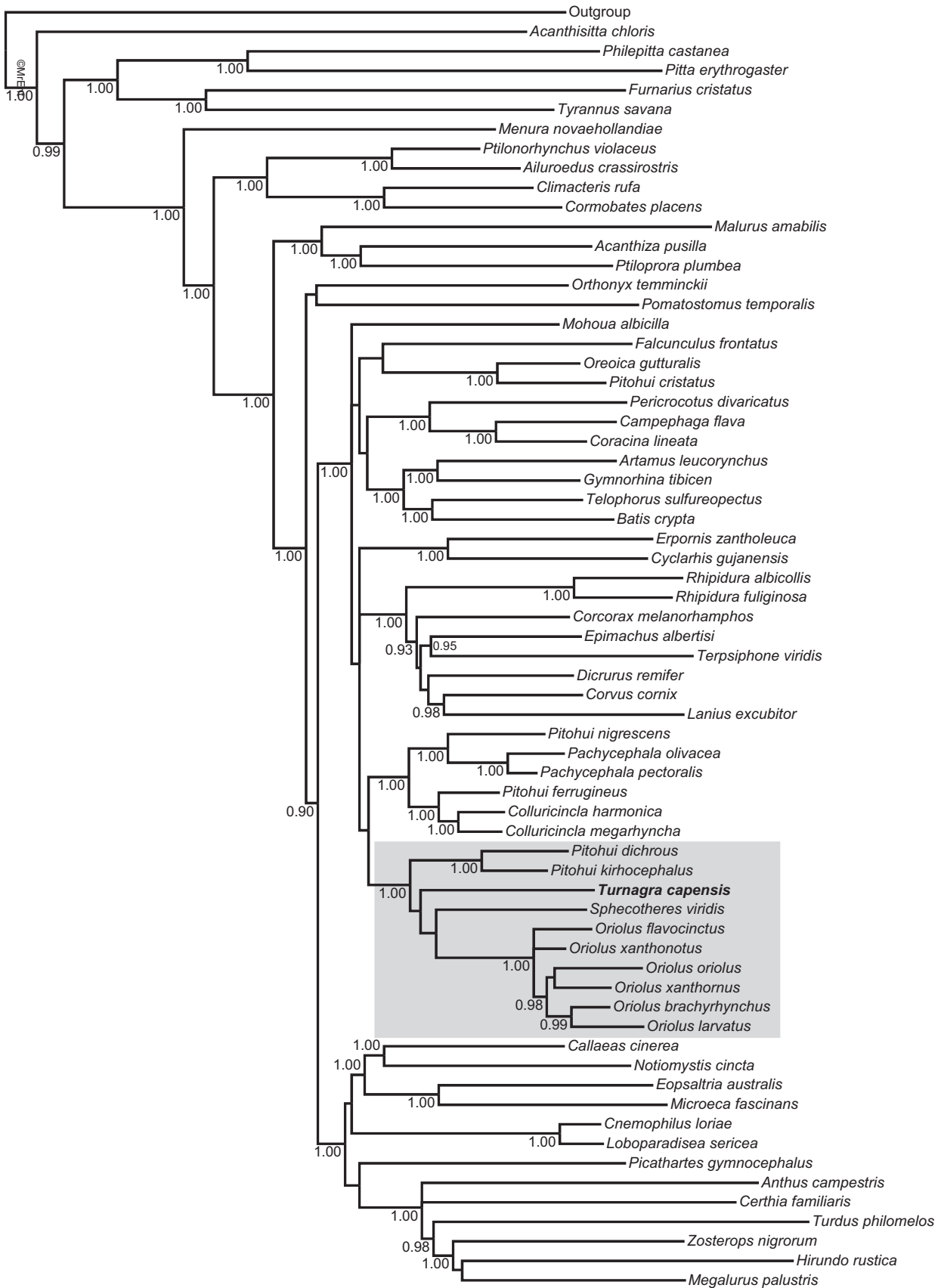
species for which we had no samples (Table 1). The amplification of fragmented DNA from old museum samples may increase the risk of amplifying contaminants. The *Turnagra* sequences were carefully inspected: the sequences were found to be unique (not identical to any other passerines amplified in our lab); no mismatches in overlapping regions of adjacent fragments or unusual mutations in coding regions were found; the codon variable positions in coding genes follow the usual frequency pattern (2nd < 1st < 3rd). The mitochondrial genes and the introns of Myoglobin and ODC were re-sequenced after several weeks or months, producing identical sequences. Based on these observations we are confident that the *Turnagra* sequences are correct.

Table 2 presents a summary of the molecular properties of each gene and the substitution models that were considered optimal according to the AIC criterion.

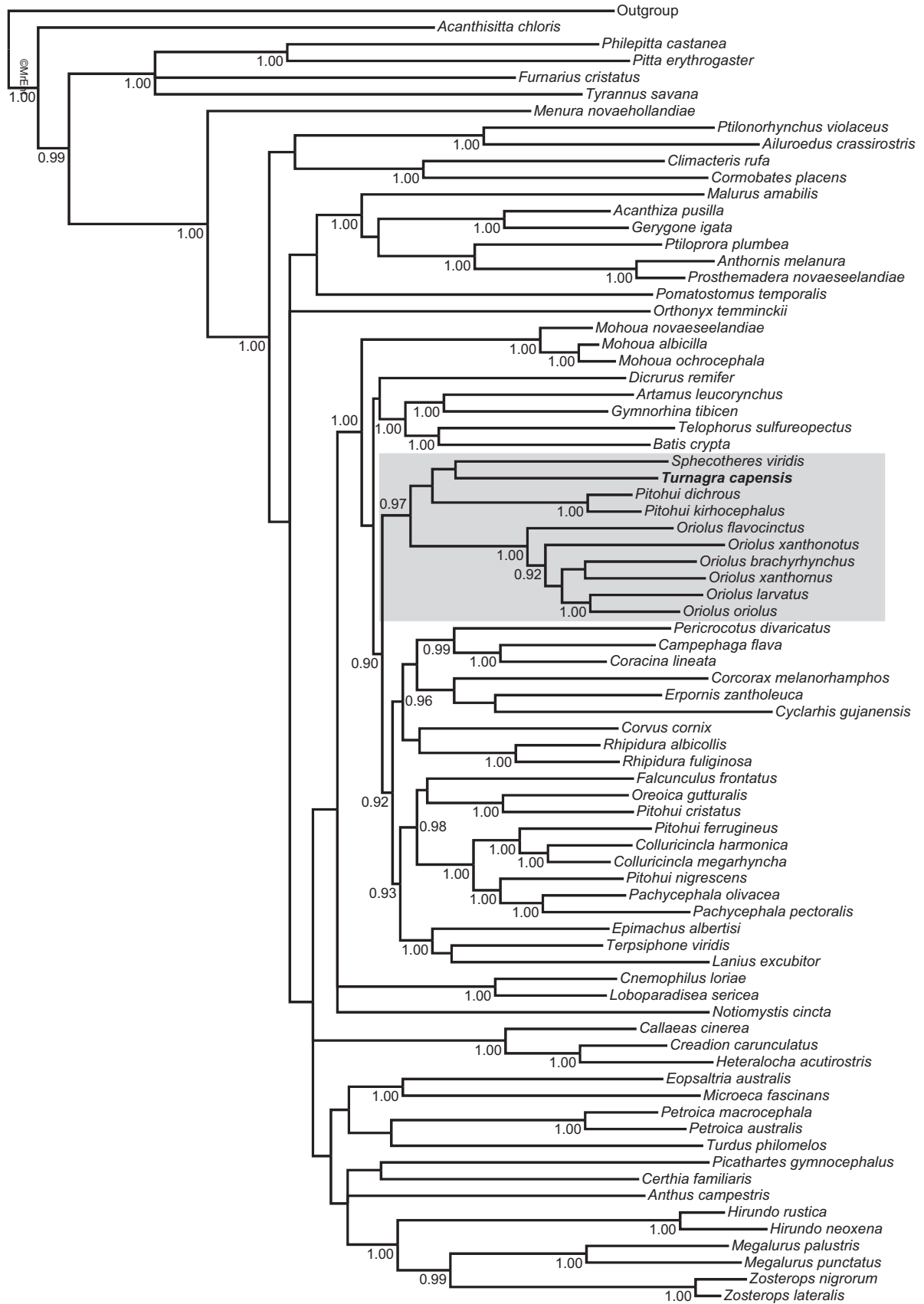
Bayesian and the Maximum Likelihood topologies obtained from the concatenated dataset are almost identical (Fig. 1). The major branching pattern agrees with current understanding of the passerine radiation that has been identified by several independent studies: *Acanthisitta* is basal to the major division Suboscines–Oscines, followed by the Basal Corvoidea lineages (*Menura*, Ptilonorhynchidae–Climacteridae, the Meliphagoidea clade, *Orthonyx* and *Pomatostomus*), the Crown Corvoidea and Passerida clades. Crown Corvoidea as a whole is poorly resolved, with most basal nodes receiving very low support values. On the other hand several subclades are strongly supported: *Mohoua*, *Erpornis* with *Cyclarhis*, *Falunculus*–*Oreoica*–*Pitohui cristatus*, Oriolidae (*sensu* Jönsson et al., 2010a), Pachycephalidae (*sensu* Jönsson et al., 2010b), Campephagidae, the “African” corvoid lineage (*sensu* Fuchs



**Fig. 1.** The majority-rule consensus tree obtained from the mixed-model Bayesian analysis of the concatenated dataset. The posterior probability values (threshold 0.70) and the bootstrap support values (threshold 70%) obtained from the maximum likelihood analysis are indicated at the node with a black and white dot, respectively. New Zealand native taxa are in bold. *Corvus corone* is used as lineage representative of the extinct *Corvus antipodum*, known only from fossil remains (OSNZ, 2010). *Anthus campestris* is used as lineage representative of *Anthus novaeseelandiae*. The black bars indicate the families associated in the past with *Turnagra*. The Oriolidae clade is highlighted in grey. The tree was edited in MrEnt v.2.2 (Zuccon and Zuccon, 2010).



**Fig. 2.** The majority-rule consensus tree obtained from the mixed-model Bayesian analysis of the nuclear dataset. The posterior probability values (threshold 0.90) are indicated at the node. The Oriolidae clade is highlighted in grey.



**Fig. 3.** The majority-rule consensus tree obtained from the mixed-model Bayesian analysis of the mitochondrial dataset. The posterior probability values (threshold 0.90) are indicated at the node. The Oriolidae clade is highlighted in grey.



**Table 3**

Comparison of alternative phylogenetic hypotheses using the Shimodaira–Hasegawa test performed with RAxML.  $\Delta$  –ln L: difference in tree likelihood compared to the best tree. Significant: significantly worse than the best topology,  $p < 0.05$ .

Topology tested	Tree likelihood	$\Delta$ –ln L	SH test
Best tree	–115752.068336		
<i>Turnagra</i> forming a monophyletic clade with			
Turdidae	–116030.739651	–278.671315	Significant
Ptilonorhynchidae	–116076.271860	–324.203524	Significant
Pachycephalidae	–115832.670289	–80.601953	Significant
Cnemophilidae	–115926.670096	–174.601760	Significant
Paradisaeidae	–115924.440474	–172.372138	Significant
Cracticidae	–115938.799709	–186.731373	Significant
Callaeidae	–115943.689436	–191.621100	Significant
Acanthisittidae	–116238.811083	–486.742747	Significant
Acanthizidae	–116028.224862	–276.156526	Significant
Meliphagidae	–116021.180352	–269.112016	Significant
<i>Mohoua</i>	–115834.727054	–82.658718	Significant
Rhipiduridae	–115895.884687	–143.816351	Significant
Corvidae	–115902.387579	–150.319243	Significant
Petroicidae	–115963.298713	–211.230377	Significant
Motacillidae	–116037.842779	–285.774443	Significant
Hirundinidae	–116072.385266	–320.316930	Significant
Locustellidae	–116101.575413	–349.507078	Significant

et al., 2006: *Artamus*, *Gymnorhina*, *Telophorus*, *Batis*) and the clade including *Rhipidura*, *Corvus*, *Lanius*, *Dicrurus*, *Epimachus*, *Corcorax* and *Terpsiphone*.

The analyses strongly support placing *Turnagra* within Oriolidae, where it forms a clade with *Sphecotheres*.

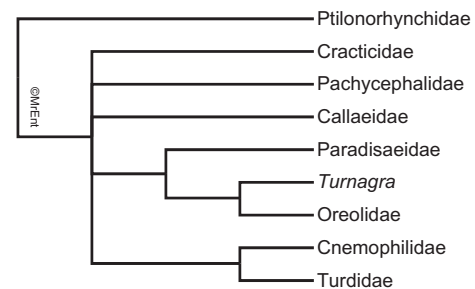
The separate analyses of the mitochondrial and nuclear genes recover less resolved trees, with poorer resolution in the basal nodes of the Corvoidea and Passeroidea lineages, but *Turnagra* remains firmly nested within Oriolidae (Figs. 2 and 3). The inclusion of only some genes for few species obtained from Genbank had no effect on the phylogenetic reconstruction. The topology obtained from the reduced dataset is almost identical, with minor rearrangements in the branching order within the Passeroidea clade. The position of *Turnagra* within Oriolidae and the nodes in the Corvida clade are not affected (Fig. S3).

All the traditional hypotheses about the taxonomic affinities of *Turnagra* have been rejected by the SH-test, as well any relationships with the other lineages of New Zealand passerines (Table 3).

Our cytochrome *b* sequence and that published by Christidis et al. (1996a) are too different to belong to the same species. A careful inspection of Christidis et al.'s sequence suggests that it does not represent a true *Turnagra* sequence (see Suppl. Material). Moreover, a re-analysis of Christidis et al.'s dataset also reveals that the association of their *Turnagra* sequence to the Ptilonorhynchidae is not supported (Fig. S2).

### 3.2. Morphological evidence

Most of the morphological characters included in the phylogenetic analysis exhibit a considerable degree of plasticity and homologies are difficult to ascertain. Thus the parsimony analysis of these characters did not result in a well-resolved phylogeny, and only two clades received bootstrap support exceeding 50% (Fig. 4). The first consists of Parasidaeidae, Oriolidae and *Turnagra*, which group together with a 53% bootstrap support. The other clade includes *Turnagra* and Oriolidae, a group that receives a 64% support. No unambiguous synapomorphies exist for these clades, however. A comparison of overall resemblance shows that *Turnagra* shares the same character states for many morphological characters with Oriolidae. The pars dorsalis of the pterygia spinalis is densely feathered in *Turnagra* and the Oriolidae, but much less so in the most corvid families (Olson et al., 1983; Clench, 1985).



**Fig. 4.** The strict consensus tree (36 steps long, C.I. = 0.61, R.I. = 0.58) calculated from the 20 morphological characters in Table 4.

Also, *Turnagra* and Oriolidae lack the small apterium between the pars dorsalis and the pars pelvica of the pterygia spinalis, a condition shared only with Cnemophilidae among the families considered here (Table 4). While most passerines have only nine secondaries (Jenni and Winkler, 1994), *Pitohui* and *Sphecotheres* have 10 secondaries and 10–11 secondaries occur in *Oriolus* (Schodde and Mason, 1999; Higgins et al., 2006). *Turnagra* has 10 secondaries as well. The alcoholic specimen in the Natural History Museum, used to re-assess this character, was heavily dissected in a previous study. Both wings are disarticulated from the body and the number of secondaries was easy to ascertain. The lower number reported by Frith and Frith (2004: eight secondaries) and Schodde and Mason (1999: nine secondaries) might be due to the difficulty of counting the innermost secondaries in a folded wing as it is usually prepared in round skins. The close similarity in morphology is also paralleled in many behavioural characters, as mating system, nest placement, and vocalisation. The tightly woven *Turnagra* nest and its eggs are also similar to those found in Oriolidae, and to a lesser degree to those of Pachycephalidae.

### 4. Discussion

A new bird family must be added to the New Zealand avifauna: *Turnagra* is an oriolid. This new hypothesis is strongly supported by molecular and morphological evidence and contradicts all previous ideas about *Turnagra* affinity. The Oriolidae occur over most of the Old World, but the centre of origin lays

**Table 4**

Data matrix used in the parsimony analysis of the morphological characters in *Turnagra* and some passerine families. For ease of presentation the matrix has been transposed. Oriolidae and Pachycephalidae are *sensu* Jönsson et al. (2010a) and Jönsson et al. (2010b), respectively. The character states were either scored using the collection of the Natural History Museum, Tring, or obtained from the literature (references indicated in square brackets), or both. References: [1]: Higgins et al. (2006); [2]: Oliver (1955); [3]: Olson et al. (1983); [4]: Worthy and Holdaway (2002); [5]: del Hoyo et al. (2008); [6]: Schodde and Mason (1999); [7]: Clench (1985); [8]: Higgins and Peter (2002); [9]: McEvey (1976); [10]: Frith and Beehler (1998); [11]: Clench (1992); [12]: Jenni and Winkler (1994).

	Turnagra	Oriolidae	Pachycephalidae	Cracticidae	Paradisaeidae	Cnemophilidae	Ptilonorhynchidae	Callaeidae	Turdidae
Sex dimorphism, plumage (0 – dimorphic; 1 – monomorphic) [1,5,6,8,10]	1	0	0	1	0/1	0	0/1	1	0/1
Juvenile plumage like adults (0 – absent; 1 – present) [1,5,6,8,10]	1	1	1	0	1	0	1	1	0
Legs and feet (0 – weak; 1 – strong) [1,6,10]	1	1	1	1	1	0	1	1	1
Tarsal scutellation (0 – booted; 1 – scutellated) [2,6]	1	1	0/1	1	0/1	0	0/1	0	0
Bill shape stout, notch upper tomium (0 – absent; 1 – present) [1,6,10]	1	1	1	0	0	0	1	0	0
Bristles (0 – absent; or only poorly developed; 1 – well-developed) [1]	1	1	1	1	0	0	0	0	0
Tail length (0 – short; 1 – long) [1,6]	1	1	1	1	0/1	0	0/1	0/1	1
Tail shape (0 – pointed; 1 – squared) [1,6]	1	1	1	1	0/1	0/1	1	0	1
Wing shape (0 – long; pointed; 1 – broad; rounded) [1,6]	1	0/1	1	0/1	1	1	1	1	0
Number of secondaries (0–9 or less; 1–10; 2–11; 3–12 or more) [1,6,12]	1	1/2	0	1/2	1/2/3	3	2/3	0	0
Dorsal pterylosis, basal gap (0 – absent; 1 – present) [3,6,7,11]	0	0	1	1	1	0	1	1	?
Skull, nasal region (0 – ossified; 1 – non-ossified) [3,6,12]	0	0	0	0	0	1	1	1	1
Skull, maxillopalatines (0 – reduced; 1 – expanded) [1,9,12]	1	1	1	?	0	1	1	1	0
Skull, transpalatine process (0 – pointed; 1 – truncated) [1,3,6,12]	1	0/1	0	0	1	0	0	1	0
Skull, lacrymal (0 – absent; 1 – present) [1,3,6,12]	0	0	0	0	0/1	0	1	1	0
Skull, ectethmoid foramen (0 – single; 1 – double) [1,6,9]	0	0	0	0	0/1	0	0	1	1
Skull, postorbital and zygomatic process (0 – poorly developed; 1 – well-developed) [3,6,12]	1	1	0	1	1	0	1	0	0
Temporal fossa (0 – small; 1 – medium; 2 – large) [1,6,12]	1	1	0	2	1	0	2	2	0
Humeral fossa (0 – single; 1 – double) [1,6]	0	0	0	0	0	?	0	0	1
Proximal caudal foramen in the femur (0 – absent; 1 – present) [4]	1	1	1	0	1	?	0	1	1

in Australasia, with *Sphecotheres* and *Pitohui* and the basal *Oriolus* lineages restricted to Australia and New Guinea (Jönsson et al., 2010a). The family is known for its bright yellow, green or red plumages, at odds with the brown, quite non-descript *Turnagra*. However, *Turnagra* plumage resembles the females of some *Oriolus* species. The loss of plumage dimorphism in island taxa is a well known pattern and is attributed to the combination of reduced sexual selection to avoid heterospecific mating and the effect of natural selection, favouring a less conspicuous, female-like plumages (Newton, 2003).

The oriolids are clearly a dispersive group that colonised most of the Old World (Jönsson et al., 2010a). Several oriolids form foraging flocks, especially *Sphecotheres*, the *Turnagra* sister lineage. Flocking behaviour is one of the factors assumed to favour the colonisation of oceanic islands (Bock, 1960). Nonetheless *Turnagra* has been the only oriolid lineage that colonised the Pacific east of the Australo-Papuan continental shelf.

Historical hypotheses on *Turnagra* relationships tried to establish a connection with lineages endemic to New Zealand (Callaeidae) or occurring in the Australasian region (Turdidae),

**Table 5**  
Ecological and behavioural characters in *Turnagra* and some passerine families. Oriolidae and Pachycephalidae are *sensu* Jönsson et al. (2010a) and Jönsson et al. (2010b), respectively. The character states were either scored using the collection of The Natural History Museum, Tring (indicated by !), or obtained from the literature (reference indicated in square brackets), or both. References: [1]: Higgins et al. (2006); [2]: Buller (1887); [3]: del Hoyo et al. (2008); [4]: Schodde and Mason (1999); [5]: North (1901–1904); [6]: Higgins and Peter (2002); [7]: del Hoyo et al. (2007); [8]: Frith and Beehler (1998); [9]: del Hoyo et al. (2009); [10]: Frith and Frith (2004); [11]: del Hoyo et al. (2005).

Taxon	<i>Turnagra</i>	Oriolidae	Pachycephalidae	Cracticidae	Paradisidae	Cnemophilidae	Ptilonorhynchidae	Callaeidae	Turdidae
Diet	Fruits and insects [1]	Mostly frugivorous plus insects [3]	Insectivorous [9]	Mostly insectivorous or scavenger [9]	Omnivorous [8]	Obligate frugivorous [8]	Fruits, shoots and leaves [10]	Omnivorous [1]	Insectivorous, frugivorous or omnivorous [11]
Nest structure	Compact deep cup at a tree fork; mostly grasses, almost no leaves, finer lining inside [1,1]	Deep cup at a tree fork; compact structure, tightly woven to the branches, made mostly of grasses ( <i>Oriolus</i> ) or more vinelets and few twigs ( <i>Sphecotheres</i> ) [1,3,5]	Deep cup at a tree fork; rather coarsely woven, made of twigs and bark, with some leaves and roots [4]	Rather coarse and flimsy cup-shaped nest in outer tree forks [4]	Rather loose cup of tree leaves within an exterior of fresh green material and lined with fine stems of epiphytic orchids, roots and mosses [1,8]	Domed, made of mosses and ferns, lined with stems of epiphytic orchids and few sticks [8]	Rough bulky cup-shaped nest of twigs [1,4]	Large cup-shaped nest loosely constructed, among branches, in tree or epiphyte hollows or on ground [1]	Bulky fibrous cup-shaped nest, in shrubbery or crevices [4]
Clutch size	2–3 [1]	2–3 [1]	2–3 [6]	2–4 [1]	1–2 [8]	1 [9]	1–2 [4]	2–3 [1]	2–6 [1]
Eggs, background colour	Whitish [!]	Whitish, cream or pale pinkish, but bluish in <i>Sphecotheres</i> [!]	Mostly whitish, pale pinkish or pale buff [!]	Brown, greenish or greyish [!]	Dark cream or pinkish or brownish [!]	Pale pinkish [!]	Cream, pale grey or pale brown [!]	Greyish or brownish [!]	Variable, brown, grey, greenish or blue [!]
Eggs, marking	Small black or brown blotching, mostly at the blunt end [!]	Small to medium blotching with black, brown or rusty, mostly at the blunt end [!]	Blotching with black, brown, olive green or grey over most of the surface, more intense at the blunt end [!]	Freckled or vermiculated over most of the surface with brown, rufous or black [!]	Strong marking, with blotch, spot or streaks, with dark brown and grey [!]	Finely blotched in rufous and purple, with denser marking at the blunt end [!]	Variable: unmarked, vermiculated or bolding blotched in grey, brown or black [!]	Blotching with brown or olive green [!]	Variable, from plain or faintly spotted to heavily marked or vermiculated [!]
Mating system	Presumed monogamy [1]	Monogamy [4]	Monogamy [4]	Monogamy, polygyny in <i>Gymnorhina</i> [1]	Monogamy or polygyny [8]	Polygyny [8]	Polygyny (but monogamy in <i>Ailuroedus</i> ) [4]	Monogamy [1]	Monogamy [4]
Song	Musical [1]	Musical [3]	Musical [7]	Musical [1]	Harsh [9]	Harsh [8]	Harsh [9]	Musical [1]	Musical [11]
Song mimicry	Yes [2]	Yes [3]	Yes [6]	Yes [1]	Not recorded [9]	Not recorded [9]	Yes [4]	Yes [1]	Yes [11]
Over-water dispersal	Yes [1]	Yes [3]	Yes [7]	No [8]	No [8]	No [8]	No [10]	No [1]	Yes [11]

Callaeidae, Ptilonorhynchidae, Cracticidae, Pachycephalidae). However, among these only the Turdidae and the Pachycephalidae are clearly dispersive groups with wide Pacific distributions, while the other families are confined to the Australo-Papuan continental plate, apparently unable to cross water stretches (del Hoyo et al., 2008, 2009). The alleged molecular support for a *Turnagra*–Ptilonorhynchidae link was indeed interpreted by Christidis et al. (1996a) as evidence of an undetected case of bowerbird dispersal outside the Australian–New Guinean landmass.

Mistaken phylogenetic relationships have often been ascribed to cases of extreme morphological divergence among related taxa (e.g. drepanids, Pratt, 2005) or to cases of phenotypic convergence of unrelated lineages (e.g. “coerebids”, Remsen, 2003). *Turnagra* does not fit either case: although not so “oriole-like” in plumage colour, the analysis of the anatomical traits clearly links it to Oriolidae. Despite extensive investigations (Olson et al., 1983; Schodde and Mason, 1999; Frith and Frith, 2004; Higgins et al., 2006) all comparisons were post hoc driven: only those families that were assumed to be likely relatives were included in comparative analyses.

Mayr and Amadon (1951) acknowledged that *Turnagra* was clearly not a thrush, following Oliver’s study of the palate (Oliver, 1945), and suggested a possible link with Pachycephalidae. At that time Pachycephalidae was a loose assemblage of passerines at least in part insectivorous, characterised by a bill with a tomial notch, a rather unspecialized morphology and a general Australasian distribution. *Turnagra* would have fit well within such a group. However,

while *Pachycephala*, *Colluricincla* and part of *Pitohui* do form a monophyletic clade (Jönsson et al., 2010b), the other, mostly monotypic genera (*Hylocitrea*, *Rhagologus*, *Eulacestoma*, *Falcunculus*, *Oreoica*: Spellman et al., 2008; Norman et al., 2009) proved to belong elsewhere.

A perceived similarity between *Turnagra capensis capensis* and the bowerbird *Scenopoeetes dentirostris* guided Olson et al.’s (1983) reappraisal. The two taxa are indeed surprisingly similar in general shape and plumage pattern. In birds with striped breast the feathers have a typical pale background with a darker central stripe. In the South Island form of *Turnagra* and in *Scenopoeetes* the pattern is reversed, with a cream central stripe on a dark brown feather. Olson et al. identified a number of similarities between *Turnagra* and the Ptilonorhynchidae, but failed to appreciate that the two taxa differ in several other traits and none of the similarities can be regarded as an unambiguous synapomorphy. Regrettably the Ptilonorhynchidae hypothesis was strengthened by a biased molecular phylogeny (Christidis et al., 1996a), and these results were readily included in checklists and major taxonomic works (e.g. Heather and Robinson, 2005; OSNZ, 2010).

However, more thorough evaluations of the same morphological characters used by Olson et al. questioned the Ptilonorhynchidae hypothesis (Schodde and Mason, 1999; Frith and Frith, 2004; Higgins et al., 2006). Although these authors recognised a better match with the Pachycephalidae, the lack of a thorough

comparison with a wider selection of corvid groups precluded the placement of *Turnagra* in Oriolidae.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.10.013.

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