

A multi-gene phylogeny disentangles the chat-flycatcher complex (Aves: Muscicapidae)

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We reconstructed the first well-sampled phylogenetic hypothesis in the chat-flycatcher complex combining nuclear and mitochondrial sequences. The dichotomy between chats-terrestrial feeders and flycatchers-aerial feeders does not reflect monophyletic groups. The flycatching behaviour and morphological adaptations to aerial feeding (short tarsi, broad bill, rictal bristles) evolved independently from chat ancestors in three different lineages. The genera *Aethya*, *Brachypteryx*, and *Myiophonus* are nested within the Muscicapidae radiation and their morphological and behavioural similarities with the true thrushes Turdidae are presumably the result of convergence. The postulated close relationships among *Erythacus*, *Luscinia* and *Tarsiger* cannot be confirmed. *Erythacus* is part of the African forest robin assemblage (*Cichladusa*, *Cossypha*, *Pogonocichla*, *Pseudaethya*, *Sbeppardia*, *Stiphrornis*), while *Luscinia* and *Tarsiger* belong to a large, mainly Asian radiation. *Enicurus* belongs to the same Asian clade and it does not deserve the recognition as a distinct subfamily or tribe. We found good support also for an assemblage of chats adapted to arid habitats (*Monticola*, *Oenanthe*, *Thamnolaea*, *Myrmecocichla*, *Pentholaea*, *Cercomela*, *Saxicola*, *Campicoloides*, *Pinarocbrea*) and a redstart clade (*Phoenicurus*, *Chaimarrornis* and *Rhyacornis*). Five genera (*Muscicapa*, *Copsychus*, *Thamnolaea*, *Luscinia* and *Ficedula*) are polyphyletic and in need of taxonomic revision.

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Introduction

The chats and flycatchers (Muscicapidae *sensu* Dickinson 2003) are a speciose clade of small oscine passerines. They represent significant components of tropical and temperate bird communities across the Old World, including some renowned songbirds and several common garden birds. Several species are hole-nesters and their aptitude to accept nest-boxes has made them classical model species in ecological and behavioural studies (e.g. Lundberg & Alatalo 1992).

Following a long standing view chats and flycatchers are usually associated with thrushes (Turdidae) (Hartert 1910; Mayr & Amadon 1951; Wetmore 1960). Their close relationship is supported by two morphological synapomorphies: a cryptic spotted juvenile plumage and the so called 'turdine thumb', a derived syrinx morphology (Ames 1975). Other morphological characters purported to link Turdidae and Muscicapidae, the double humeral fossa

(Bock 1962) and the 'passeroid' carpometacarpal condition (Pocock 1966), are actually plesiomorphies shared with several other unrelated oscines (Sibley & Ahlquist 1990). However, the traditionally assumed closer relationship of thrushes with chats is not supported by either DNA–DNA hybridization (Sibley & Ahlquist 1990) or nucleotide sequences (e.g. Cibois & Cracraft 2004; Zuccon *et al.* 2006). These studies not only provide compelling evidence that chats and flycatchers constitute a monophyletic clade to the exclusion of thrushes, but they also suggest that the division between more terrestrial species, i.e. chats (subfamily Saxicolinae), and more arboreal aerial foragers, i.e. flycatchers (subfamily Muscicapinae), might not be natural. Preliminary analyses by Cibois & Cracraft (2004) and Voelker & Spellman (2004) were based on too few species, but both studies placed with high support *Copsychus*, a chat, among the flycatchers, and *Ficedula*, a typical flycatcher, among the chats. Voelker & Spellman (2004)

went further to re-define the limits of Turdidae and Muscicapidae. They suggested the transfer of the chats *Cercotrichas* and *Copsychus* to the Muscicapinae, and re-allocated the flycatchers *Ficedula* and *Cyornis* and the thrushes *Aletbe*, *Brachypteryx*, and *Monticola* to the Saxicolinae.

No comprehensive cladistic treatment of the family exists and the perceived relationships at the genus level are generally dictated by overall similarity and geographic proximity. Hence, Vaurie (1953) revised the flycatchers using characters like bill, wing and tail shapes, plumage patterns, body proportions, development of rictal bristles. He identified two broad assemblages following mostly their geographic distribution: the African flycatchers (*Bradornis*, *Empidonax*, *Fraseria*, *Melaenornis*, *Sigelus*) on one side, and the south-east Asian taxa (*Cyanoptila*, *Cyornis*, *Eumyias*, *Ficedula*, *Muscicapella*, *Niltava*) plus *Muscicapa* on the other and with *Rhinomyias* somewhat intermediate.

Overall similarity guided also Ripley's (1952) revision of thrushes and chats. He recognized an enlarged genus *Erithacus* that included also *Luscinia*, *Tarsiger*, *Pogonocichla*, *Sheppardia* and *Stiphrornis*. This move was generally not followed, but the idea of a close association between *Erithacus*, *Luscinia* and *Tarsiger* persisted (e.g. Vaurie 1955, 1959; Sibley & Monroe 1990; Dickinson 2003). Ripley associated his broad genus *Erithacus* with the African forest robins (*Cossypha*, *Pseudocossyphus*, *Cicladusa*, *Aletbe*). A somewhat similar African assemblage was postulated also by Irwin & Clancey (1974) and Jensen (1990), but without the Eurasian species (i.e. without *Erithacus*, *Luscinia* and *Tarsiger*). Ripley identified also a large group of typical chats occurring in arid habitats (*Saxicola*, *Oenanthe*, *Cercomela*, *Myrmecocichla* and *Thammolaea*). The redstarts (*Phoenicurus*, including *Chaimarrornis* and *Rhyacornis*) were associated with *Hodgsonius* and *Cinclidium*, while similarities were noted between *Cercotrichas* and *Copsychus* (including *Trichixos*). The chats ended with *Saxicoloides*, associated with *Prunella* (now classified in a distinct, unrelated family, Ericson & Johansson 2003; Barker *et al.* 2004). *Monticola* and *Myiophonus* were placed at the beginning of the true thrushes probably because of their larger size, although Ripley noted that *Monticola* was 'closely related to the chats and wheatears'.

For few genera there is no consensus and their affinities are much debated. The Namibian endemic *Namibornis berero* has been linked to the flycatchers for similarities in nest, eggs and begging call (Vaurie 1953; Taylor & Clement 2006), while its anatomy, call note and habits are more chat-like (Jensen & Jensen 1971; Keith *et al.* 1992).

The *Enicurus* forktails are rather common Asian birds occurring along montane streams, characterized by long tails and bold pattern in black and white. Now their placement among chats is not questioned, although they are

generally assumed to be fairly isolated from the other taxa and sometimes placed in their own subfamily/tribe Enicurinae/Enicurini to mark their distinctiveness (e.g. Voous 1977; Cramp 1988; Collar 2005).

DNA-DNA hybridization evidence prompted Sibley & Ahlquist (1990) to remove the genera *Aletbe* and *Brachypteryx* from the chats and transferred them to the true thrushes. While Dickinson (2003) followed their decision, Rasmussen & Anderton (2005) and Collar (2005) retained both genera among chats.

Although no comprehensive cladistic analysis for the family exists, several molecular studies addressed the relationships within selected genera: *Erithacus* (Seki 2006), *Ficedula* (Outlaw & Voelker 2006), *Monticola* and *Pseudocossyphus* (Goodman & Weigt 2002; Outlaw *et al.* 2007; Zuccon & Ericson in press), *Oenanthe* and *Cercomela* (Alibadian *et al.* 2007; Outlaw *et al.* in press), *Saxicola* (Illera *et al.* 2008), *Sheppardia* (Roy *et al.* 2001; Beresford *et al.* 2004), *Stiphrornis* (Beresford & Cracraft 1999; Schmidt *et al.* 2008).

A taxonomically more inclusive analysis (Beresford 2003) investigated the relationships among the African forest robins, a group of forest-dwelling chats dominated by the genera *Cossypha*, *Sheppardia* and *Aletbe* first proposed by Irwin & Clancey (1974). Not only did Beresford's study fail to recover a monophyletic clade for the African robins, but it showed that none of the three main genera in the complex is monophyletic. In particular, two species of *Aletbe* were unexpectedly recovered far away from the core African robins complex. However, the inadequate sampling outside the African robins makes those findings preliminary.

Limited molecular data are available to test the chat and flycatcher relationships predicted by morphology and behaviour. We present the first densely sampled phylogeny for this speciose clade using nuclear and mitochondrial sequence data and re-evaluate their systematics.

Methods

Taxon sampling strategy

The phylogenetic relationships in the chat-flycatcher complex are reconstructed from a selection of species that cover the entire morphological and ecological diversity observed in the group. Among the chats (Saxicolinae), we selected 46 species representing 34 out of 40 (85%) genera accepted by Collar (2005) in the most recent taxonomic revision of the group. The flycatcher genera *Culicicapa* and *Stenostira*, traditionally placed in the Muscicapidae, are part of a different lineage not related to the chat-flycatcher complex (Barker *et al.* 2004; Beresford *et al.* 2005; Fuchs *et al.* 2009) and are not considered here. Among the remaining flycatchers (Muscicapidae) recognized by Taylor

Table 1 Samples and sequences included in the phylogenetic analysis, with museum accession numbers and collection localities.

Taxon	Accession no.	G3P	Myoglobin	ODC	PEPCK	ND2	Locality
Saxicolinae (typical chats)							
<i>Alethe castanea</i>	NRM 89836	GU358968	GU358705	GU358833	GU358906	GU358775	Uganda, Mabira
<i>Alethe diademata</i>	NRM 89837	GU358969	GU358706	GU358834	GU358907	GU358776	Ghana, Ashanti
<i>Brachypteryx montana</i>	NRM 20046739	GU358970	GU358707	GU358835	GU358908	GU358777	Vietnam, Yen Bou
<i>Campicoloides bifasciatus</i>	NMBV 06249	GU358973	GU358710	GU358838	–	GU358779	South Africa, Free State
<i>Cercomela familiaris</i>	NRM 680265	GU358974	GU358711	GU358839	GU358911	GU237102 [4]	Botswana, Francistown
<i>Cercotrichas podobe</i>	NRM 89609	GU358976	GU358713	GU358841	GU358913	GU358781	Sudan, Atbara
<i>Chaimarrornis leucocephalus</i>	NRM 88997	GU358977	GU358714	GU358842	GU358914	GU358782	Vietnam, N Tonkin
<i>Cichladusa guttata</i>	NRM 20076178	GU358978	GU358715	GU358843	GU358915	GU358783	Captivity, unknown origin
<i>Cinclidium frontale</i>	BMNH 1930.7.16.66	GU358980	GU358717	GU358845	GU358917	GU358785	Vietnam, Tonkin
<i>Copsychus malabaricus</i>	NRM 20036774	GU358982	DQ466823 [1]	GU358847	GU358919	DQ466859 [1]	Vietnam, Kon Tum
<i>Copsychus saularis</i>	NRM 20026683	GU358983	GU358719	GU358848	GU358920	GU358787	Vietnam, Hanoi bird market
<i>Cossypha albicapilla</i>	NRM 20036522	GU358984	GU358720	GU358849	GU358921	GU358788	Captivity, unknown origin
<i>Cossypha niveicapilla</i>	NRM 20086252	GU358985	GU358721	GU358850	GU358922	GU358789	Nigeria, Obudu
<i>Cossypha semirufa</i>	NRM 89734	GU358986	GU358722	GU358851	GU358923	GU358790	Ethiopia, Sidamo
<i>Enicurus leschenaulti</i>	NRM 20076682	GU358990	GU358726	GU358855	–	GU358794	Vietnam, Quang Tri
<i>Enicurus schistaceus</i>	NRM 20046993	GU358991	GU358727	GU358856	GU358927	GU358795	Vietnam, Quang Tri
<i>Erithacus rubecula</i>	NRM 976377	GU358992	AY228296 [2]	GU358857	GU358928	DQ466861 [1]	Sweden, Blekinge
<i>Erythropygia hartlaubi</i>	NRM 89876	GU358975	GU358712	GU358840	GU358912	GU358780	Belgian Congo, Rutshuru
<i>Heinrichia calligyna</i>	NRM 85472	GU359000	GU358735	GU358865	GU358936	GU358803	Indonesia, North Sulawesi
<i>Hodgsonius phaenicuroides</i>	NRM 90636	GU359001	GU358736	GU358866	GU358937	GU358804	China, Yunnan
<i>Irania gutturalis</i>	NRM 89820	GU359002	GU358737	GU358867	GU358938	GU358805	Somalia, Dire Daua
<i>Luscinia luscinia</i>	NRM 986236	GU359003	GU358738	GU358868	GU358939	GU358806	Sweden, Gotland
<i>Luscinia sibilans</i>	NRM 20046835	GU359004	GU358739	GU358869	GU358940	GU358807	Vietnam, Quang Tri
<i>Monticola gularis</i>	NRM 20036789	GU359006	GU358741	GU358871	–	GU237106 [4]	Vietnam, Kon Tum
<i>Monticola solitarius</i>	NRM 20016756	GU359007	GU358742	GU358872	GU358942	GU358808	Captivity, unknown origin
<i>Myiomela diana</i>	ZMH 53.170	GU358979	GU358716	GU358844	GU358916	GU358784	Indonesia, Java
<i>Myiomela leucurum</i>	NRM 20046748	GU358981	GU358718	GU358846	GU358918	GU358786	Vietnam, Yen Bou
<i>Myiophonus caeruleus</i>	NRM 947317	GU359014	GU358749	GU358879	GU358949	GU358813	Vietnam, Hanoi bird market
<i>Myiophonus melanurus</i>	NRM 87901	GU359015	GU358750	GU358880	–	GU358814	Indonesia, West Sumatra
<i>Myrmecocichla nigra</i>	NRM 570041	GU359017	GU358752	GU358882	GU358950	GU237119 [4]	Angola, Dembos
<i>Oenanthe deserti</i>	NRM 20046660	GU359019	GU358754	GU358884	GU358952	GU237121 [4]	Iran, Mashhad
<i>Oenanthe oenanthe</i>	NRM 966643	GU359020	GU358755	GU358885	–	GU358816	Sweden, Stockholm
<i>Pentholaea arnotti</i>	NRM 558901	GU359016	GU358751	GU358881	–	GU358815	South Africa, Transvaal
<i>Phoenicurus erythrogaster</i>	NRM 20026510	GU359021	GU358756	GU358886	–	GU358817	Captivity, unknown origin
<i>Phoenicurus phoenicurus</i>	NRM 20016219	GU359022	GU358757	GU358887	GU358953	GU237122 [4]	Sweden, Stockholm
<i>Pinarhocihla sordida</i>	NRM 558924	GU359040	GU358774	GU358905	–	GU358832	Ethiopia, Addis-Abeba
<i>Pogonocichla stellata</i>	NRM 89914	GU359023	GU358758	GU358888	GU358954	GU358818	Kenya, Mt Elgon
<i>Pseudaethe poliocephala</i>	NRM 89840	GU359024	GU358759	GU358889	GU358955	GU358819	Kenya, Mt Kenya
<i>Rhyacomis fuliginosa</i>	NRM 20016563	GU359026	GU358761	GU358891	GU358957	GU358821	Captivity, unknown origin
<i>Saxicola ferrea</i>	NRM 90616	GU359027	GU358762	GU358892	–	GU358822	Vietnam, S Annam, Dalat
<i>Saxicola rubetra</i>	NRM 20016186	GU359028	GU358763	GU358893	GU358958	GU237123 [4]	Sweden, Stockholm
<i>Saxicoloides fulicatus</i>	RMNH 145771	GU359029	GU358764	GU358894	GU358959	GU358823	Sri Lanka
<i>Sheppardia cyornithopsis</i>	NRM 89313	GU359030	GU358765	GU358895	GU358960	GU358824	Cameroon, Centre Province
<i>Stiphronis xanthogaster</i>	NRM 66656	GU359032	GU358767	GU358897	GU358962	GU358826	Belgian Congo, Kartoushi
<i>Tarsiger cyanurus</i>	NRM 20076746	GU359033	GU358768	GU358898	GU358963	GU358827	Vietnam, Quang Tri
<i>Thamnolaea cinnamomeiventris</i>	NRM 20086147	GU359034	GU358769	GU358899	GU358964	GU358828	Nigeria, Jos
<i>Thamnolaea semirufa</i>	NRM 570040	GU359035	GU358770	GU358900	–	GU237125 [4]	Ethiopia, Sidamo
<i>Trichixos pyrropygus</i>	NRM 76680	GU359036	GU358771	GU358901	–	GU358829	Malaysia, Perak
Muscicapinae (typical flycatchers)							
<i>Bradornis mariquensis</i>	NRM 680263	GU358971	GU358708	GU358836	GU358909	GU358778	Botswana, Francistown
<i>Cyanoptila cyanomelana</i>	NRM 20056744	GU358987	GU358723	GU358852	GU358924	GU358791	Vietnam, Ha Tinh
<i>Cyornis rubeculoides</i>	NRM 20046863	GU358988	GU358724	GU358853	GU358925	GU358792	Vietnam, Quang Tri
<i>Empidonis semipartitus</i>	NRM 67321	GU358989	GU358725	GU358854	GU358926	GU358793	Uganda, Nabilantuk
<i>Eumyias thalassina</i>	NRM 20076755	GU358993	GU358728	GU358858	GU358929	GU358796	Vietnam, Quang Tri
<i>Ficedula buruensis</i>	ZMUC 133499	GU358994	GU358729	GU358859	GU358930	GU358797	Indonesia, Buru
<i>Ficedula monileger</i>	NRM 20076651	GU358995	GU358730	GU358860	GU358931	GU358798	Vietnam, Quang Tri

Table 1 (Continued).

Taxon	Accession no.	G3P	Myoglobin	ODC	PEPCK	ND2	Locality
<i>Ficedula parva</i>	NRM 996601	GU358996	GU358731	GU358861	GU358932	GU358799	Sweden, Blekinge
<i>Ficedula sapphira</i>	NRM 67529	GU358997	GU358732	GU358862	GU358933	GU358800	India, Darjeeling
<i>Ficedula westermanni</i>	NRM 20076456	GU358998	GU358733	GU358863	GU358934	GU358801	Captivity, unknown origin
<i>Fraseria ocreata</i>	NRM 67430	GU358999	GU358734	GU358864	GU358935	GU358802	Congo, Lesse
<i>Melaenornis edolioides</i>	NRM 20076771	GU359005	GU358740	GU358870	GU358941	GU237104 [4]	Nigeria, Jos
<i>Muscicapa caerulescens</i>	NRM 67853	GU359008	GU358743	GU358873	GU358943	GU358809	South Africa, W Pondoland
<i>Muscicapa muttui</i>	NRM 20086578	GU359009	GU358744	GU358874	GU358944	GU358810	Vietnam, Ha Giang
<i>Muscicapa striata</i>	NRM 20046170	GU359010	GU358745	GU358875	GU358945	GU237117 [4]	Sweden, Stockholm
<i>Muscicapella hodgsoni</i>	NRM 67707	GU359011	GU358746	GU358876	GU358946	GU358811	India, Sikkim
<i>Myioparus plumbeus</i>	NRM 68032	GU359013	GU358748	GU358878	GU358948	GU358812	Congo, Zambia
<i>Niltava sundara</i>	NRM 947301	GU359018	GU358753	GU358883	GU358951	GU237120 [4]	Vietnam, Vinh Phu
<i>Rhinomyias ruficauda</i>	NRM 67431	GU359025	GU358760	GU358890	GU358956	GU358820	Borneo, Sarawak
<i>Sigelus silens</i>		–	DQ125957 [3]	–	–	DQ125984 [3]	
Outgroup							
<i>Catharus ustulatus</i>	NRM 20016340	GU358972	GU358709	GU358837	GU358910	GU237101 [4]	USA, California
<i>Myadestes occidentalis</i>	NRM 20066505	GU359012	GU358747	GU358877	GU358947	GU237118 [4]	El Salvador, Monte Cristo
<i>Sialia sialis</i>	NRM 20036253	GU359031	GU358766	GU358896	GU358961	GU358825	USA, New York
<i>Turdus philomelos</i>	NRM 20036737	GU359037	DQ466848 [1]	GU358902	GU358965	DQ466886 [1]	Sweden, Uppsala
<i>Zoothera citrina</i>	NRM 20046884	GU359038	GU358772	GU358903	GU358966	GU358830	Vietnam, Quang Tri
<i>Zoothera dauma</i>	NRM 20056740	GU359039	GU358773	GU358904	GU358967	GU358831	Vietnam, Ha Tinh

The taxonomy follows Collar (2005) for the Saxicolinae and Taylor & Clement (2006) for the Muscicapinae. GenBank accession numbers of sequences published previously are followed by their references.

BMNH, The Natural History Museum, Tring; NMBV, National Museum, Bloemfontein; NRM, Swedish Museum of Natural History, Stockholm; RMNH, Naturalis, Leiden; ZMH, Zoologisches Museum, Hamburg; ZMUC, Zoological Museum, University of Copenhagen.

References: [1] Zuccon *et al.* (2006); [2] Ericson & Johansson (2003); [3] Fuchs *et al.* (2006); [4] Zuccon & Ericson (in press).

& Clement (2006) we obtained samples of 20 species representing 14 out of 16 genera (88%). The few missing genera are all monotypic and are unlikely to alter the major findings of our analysis. For larger genera we selected more than one species as a preliminary test to assess their monophyly.

The relationships among the thrushes (Turdinae) have been clarified by Klicka *et al.* (2005) and Nylander *et al.* (2008a). Following their results, our outgroup selection includes six species representative of the major thrush lineages.

DNA isolation and sequencing

The fresh tissue samples were extracted using the Qiagen DNA Mini Kit, following the manufacturer protocol. We used the Qiagen DNA Micro Kit for the toe-pad samples with a modified protocol as described by Zuccon (2005) and Irestedt *et al.* (2006).

We selected one mitochondrial and four nuclear genes that are widely used in bird phylogenetic studies: the NADH dehydrogenase II gene (ND2), the intron 2 of the myoglobin gene, the introns 6 and 7 of the ornithine decarboxylase (ODC) gene, the intron 11 of the glyceraldehyde-3-phosphodehydrogenase (GAPDH) gene and intron 9 of the phosphoenolpyruvate carboxykinase

(PEPCK). The ND2 gene and the introns were amplified and sequenced using standard primers and amplification profiles as described in Zuccon *et al.* (2006), Irestedt *et al.* (2002), Allen & Omland (2003), Fjeldså *et al.* (2003) and Sorenson *et al.* (2003), respectively. The toe-pad samples were amplified in a series of short, overlapping fragments of 200–300 bp, using a large set of internal primers, whose sequences are available from the authors. PCR products were cleaned using QIAquick PCR Purification Kit (Qiagen) and run on an ABI Prism 3100 automated DNA sequencer (Perkin-Elmer Applied Biosystems).

Gene characterization and phylogenetic analyses

The five loci were concatenated in a partitioned dataset analyzed under the Bayesian inference and the maximum likelihood criterion.

The Bayesian inference was carried out using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003), implemented on the freely available Biportal (<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 five genes. The models best fitting the data were obtained with MrModelTest (Nylander 2004), using the AIC criterion, in conjunction with PAUP* (Swofford 2003).

Table 2 Comparison of alternative phylogenetic hypotheses using the Shimodaira-Hasegawa test performed with RAxML.

Topology tested	Tree likelihood	Δ -ln L	SH test
Best tree	-42824.225399		Best
Monophyly of flycatchers vs. chats	-43141.834914	-177.917635	Significant
Monophyly of <i>Alethe</i> + <i>Pseudaethe</i>	-43125.042445	-161.125166	Significant
Monophyly of <i>Cinclidium</i> + <i>Myiomela</i>	-42990.192249	-26.274971	Significant
Monophyly of <i>Erithacus</i> + <i>Luscinia</i> + <i>Tarsiger</i>	-43084.384716	-120.467438	Significant
Monophyly of <i>Oenanthe</i> + <i>Campicoloides</i>	-42984.344885	-20.427606	Significant
Monophyly of <i>Saxicola</i> + <i>Campicoloides</i>	-42985.601013	-21.683734	Significant
Monophyly of <i>Ficedula</i>	-43098.138443	-134.221164	Significant
Monophyly of <i>Muscicapa</i>	-42974.251231	-10.333952	NS
Monophyly of <i>Thamnolaea</i>	-43100.917040	-136.999762	Significant

Δ -ln L: difference in tree likelihood compared to the best tree. NS, not significantly worse than the best topology; significant, $P < 0.05$.

MrModelTest output suggested as the best fit the HKY + Γ model for GAPDH, the GTR + Γ model for myoglobin and PEPCK, and the GTR + Γ + I model for ODC and ND2. 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 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.* 2008b) to assess the convergence of the MCMC chains and to estimate the number of generations to discard as '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 replicates.

Individual gene partitions were analysed under the Bayesian inference and maximum likelihood criterion under the same conditions indicated above, except for using a single partition and the respective evolutionary models for each gene. The ND2 gene accounts for half of the parsimony informative characters. To evaluate a possible bias in the phylogenetic signal caused by ND2, we analysed also a concatenated dataset under the same condition indicated above, but including only the nuclear loci.

We compared alternative phylogenetic hypotheses using the Shimodaira-Hasegawa test (SH test, Shimodaira & Hasegawa 1999), as implemented in RAxML v. 7.0.3 (Stamatakis 2006). The tested topologies were obtained enforcing the monophyly of selected genera or group of genera (see Table 2) in the maximum likelihood searches in RAxML.

Results

We obtained full sequences for almost all taxa (Table 1). However, the PEPCK gene is missing for 12 species, while for *Sigelus silens*, whose sequences were obtained from Genbank, only ND2 and myoglobin genes are available. We checked the possible amplification of pseudogenes translating the protein coding gene into amino acids sequences, but no unexpected stop codons or unusual amino acidic substitutions were observed. The sequence alignment was straightforward, thanks to the limited number of indels in the four introns. The five genes were concatenated in a single dataset of 3553 bp. Table 3 presents a summary of the molecular properties of each partition.

The Bayesian inference and the maximum likelihood analysis recovered almost identical, well resolved topologies from the concatenated dataset and the large majority of nodes received high support values in both analyses (Fig. 1). One of the major lineages includes three clades: the *Alethe* *s.s.* as the basal-most branch (clade 1 in Fig. 1), followed by a large clade comprising the African flycatchers (*Bradornis*,

Table 3 Sequence characteristics of the five loci analysed. The numbers of variable and parsimony informative bases are calculated for the ingroup only.

Gene region	G3P	Myoglobin	ODC	PEPCK	ND2
Alignment length	336	767	732	677	1041
Number of variable bases (%)	192 (57.1%)	315 (41.1%)	343 (46.9%)	278 (41.1%)	633 (60.8%)
Number of parsimony informative bases (%)	114 (33.9%)	131 (17.1%)	182 (24.9%)	117 (17.3%)	555 (53.3%)
% A nucleotides (range)	21.5 (19.2–25.0)	28.8 (27.8–29.8)	28.0 (25.0–29.2)	29.4 (25.0–31.3)	30.5 (28.9–32.5)
% C (range)	21.5 (19.5–25.0)	22.5 (21.8–23.2)	16.6 (15.5–25.0)	21.2 (17.3–25.0)	34.5 (32–36.5)
% G (range)	32.6 (25.0–34.6)	22.8 (21.4–23.8)	20.7 (19.8–25.0)	18.6 (17.0–25.0)	11.4 (9.8–12.7)
% T (range)	24.4 (21.3–27.3)	26.0 (24.7–27.8)	34.8 (25.0–36.0)	30.8 (25.0–33.6)	23.6 (21.7–26.0)
Selected substitution model	HKY + Γ	GTR + Γ	GTR + Γ + I	GTR + Γ	GTR + Γ + I

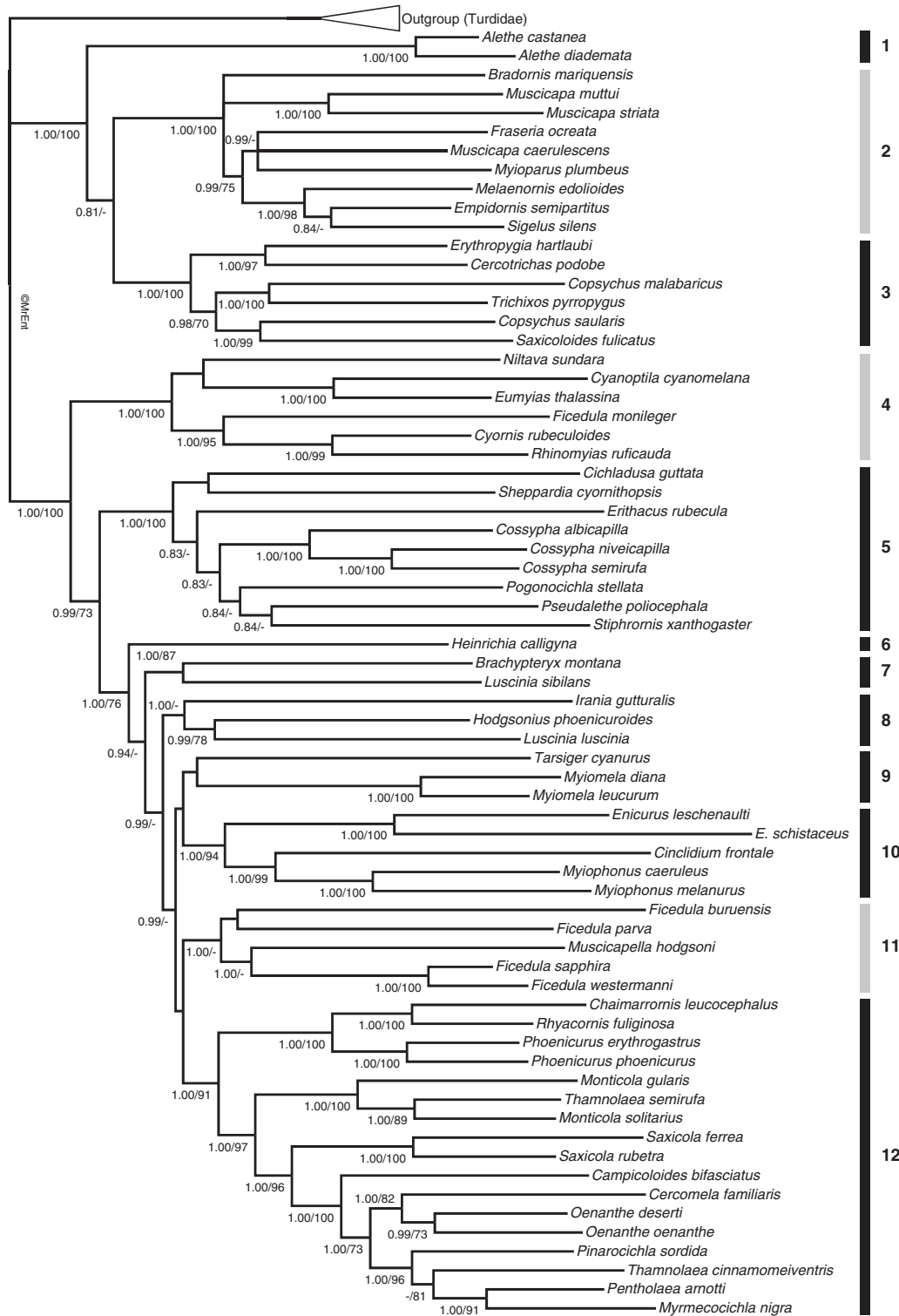


Fig. 1 The majority rule consensus tree obtained from the mixed-model Bayesian analysis of the concatenated dataset. The support values indicated at the node are the posterior probability (threshold 0.70) and the bootstrap support (threshold 70%) obtained from the Bayesian inference and the maximum likelihood analysis, respectively. Numbers on the right refer to the clades discussed in the text. The black and grey bars denote the chats (Saxicolinae) and the flycatchers (Muscicapinae), respectively.

Empidonax, *Fraseria*, *Melaenornis*, *Myioparus* and *Sigelus*) and *Muscicapa* (clade 2), which are sister to the scrub robins (*Erythropygia* and *Cercotrichas*) plus the magpie-robins and shamas (*Copsychus*, *Trichixos* and *Saxicoloides*) (clade 3).

In the other major lineage a clade with some Asian flycatchers (*Cyanoptila*, *Cyornis*, *Eumyias*, *Niltava*, *Rhinomyias* and *Ficedula moniliger*) branches off at the base (clade 4), followed by the African forest robins (*Cicladusa*, *Cossypha*, *Pogonocicbla*, *Pseudalethe*, *Sheppardia* and *Stiphrornis*) plus *Eritbacus rubecula* (clade 5), a lineage composed by the monotypic *Heinrichia* (clade 6), then the clade *Brachypteryx* plus *Luscinia sibilans* (clade 7) and a branch with *Irania*, *Hodgsonius* and *Luscinia luscinia* (clade 8). The remaining species form four well identified clades, but the basal nodes are poorly supported. The genera *Tarsiger* and *Myiomela* (clade 9) are recovered as sisters to the clade comprising *Enicurus*, *Myiophonus* and *Cinclidium* (clade 10), although that node lacks support. Another lineage includes the Eurasian flycatchers, with *Muscicapella* nested within a paraphyletic *Ficedula* (clade 11). The redstarts (*Phoenicurus*, *Chaimarrornis* and *Rhyacornis*) are at the base of a well resolved clade together with the rock-thrushes (*Monticola*), the stonechats (*Saxicola*) and several open-habitat chats (*Campicoloides*, *Cercomela*, *Myrmecocicbla*, *Oenanthe*, *Pentbolaea*, *Pinarocbroa* and *Thamnolaea*) (clade 12).

The analysis of the nuclear introns alone supports a similar topology, while the ND2 gene alone recovers a less resolved tree (Figs S1 and S2). The individual introns provide poorly resolved trees with few nodes receiving a significant support. However, none of the supported nodes is in conflict with the topology obtained from the combined dataset.

Our results are reinforced by the SH test that reject almost all alternative hypotheses tested. The reciprocal monophyly of chats and flycatchers, the monophyly in some genera (*Ficedula*, *Thamnolaea*) or pair of genera are refused (Table 2). Only the tree obtained enforcing the monophyly of the genus *Muscicapa* is not significantly worse than our best topology.

Discussion

Our analysis provides the first clear picture of the phylogenetic relationships among the chats and flycatchers. We are able to confirm several hypotheses based on morphology, but a number of relationships are novel and often at odds with traditional views.

Preliminary analyses have suggested that flycatchers are polyphyletic (Cibois & Cracraft 2004; Voelker & Spellman 2004). With a denser sampling we can confirm this, and show that the long proposed dichotomy between chats and flycatchers has no relevance. The most parsimonious hypothesis suggests that the flycatching behaviour has

evolved independently from chat ancestors at least three times (3 steps vs. 4 steps assuming flycatcher ancestors). The division in chats-terrestrial foragers and flycatchers-aerial foragers is actually an oversimplification that minimizes more diversified foraging habits. While some chats are strictly terrestrial feeders (e.g. *Alethe*, *Cercotrichas*, *Cossypha*, *Oenanthe*, *Cercomela*), some smaller taxa like *Sheppardia*, *Pogonocicbla*, *Stiphrornis* and *Tarsiger* forage at least in part by aerial sallying (Collar 2005). Likewise, aerial sallying is not always the predominant feeding technique among flycatchers. *Rhinomyias* are almost exclusive foliage gleaners, while *Melaenornis* and *Bradornis* are mostly perch-hunters that capture preys on the ground (Taylor & Clement 2006).

Aerial foraging has emerged several times in the oscine clade. The use of the same foraging niche and the convergence to the same ecotype (e.g. short tarsi, rictal bristles, broad bill) has obscured the phylogenetic relationships of several groups. The monarch flycatchers (Monarchidae), the fantails (Rhipiduridae), the batis and wattle-eyes (Platysteiridae), the stenostirids (Stenostiridae), the Australasian robins (Petroicidae) and the whistlers (Pachycephalidae) were all merged in an enlarged family Muscicapidae (Hartert 1910; Mayr & Amadon 1951; Wetmore 1960). DNA hybridization (Sibley & Ahlquist 1990) and sequence data (e.g. Barker *et al.* 2004; Beresford *et al.* 2005) have progressively dismantled the concept of a single, monophyletic clade embracing all flycatchers, leaving only the Old World typical flycatchers. Our results provide a further step in the same direction, indicating that even in this case the apparent uniformity is the result of convergence.

The first of the three flycatcher clades (clade 2) comprises all the African species plus two Eurasian *Muscicapa*. Except for the inclusion of *Muscicapa*, the clade is similar to the African group identified by Vaurie (1953). The basal node is an unresolved trichotomy, with one Eurasian (*Muscicapa striata*–*M. muttui*) and two African (*Bradornis* and the remaining species) clades. This leads to two opposite biogeographic scenarios, suggesting that the Eurasian lineage either evolved from or is sister to the African species. The genus *Muscicapa* is apparently polyphyletic, but some nodes in the flycatcher clade are not supported and the SH test failed to reject a monophyletic *Muscicapa*. The evidences are conflicting and resolving these relationships needs a denser sampling and/or additional loci. Contrary to the common assumptions (e.g. Urban *et al.* 1997 and references therein), we recovered *Bradornis* not closely related to the other large African flycatchers (*Melaenornis*, *Sigelus* and *Empidonax*). Here belongs also the genus *Myioparus*, including two small grey species long placed in the warbler genus *Parisoma*. Their

reclassification among the Muscicapidae based on the discovery of their spotted juvenile plumage (Vaurie 1957) proves to be correct. Unfortunately we were not able to obtain a sample of *N. herero*. For this species, Beresford *et al.* (2005) sequenced different genes (exons RAG-1 and RAG-2) from those we selected, and it has been impossible to incorporate their data in the present dataset. Beresford *et al.* recovered *Namibornis* sister to *Muscicapaa ferruginea*, the only Muscicapidae included. A re-analysis of their data with a larger selection of Muscicapidae indicates that *Namibornis* belong to the African flycatcher clade (D. Zuccon, unpublished data), but more data are needed to fully resolve its relationships.

The African flycatchers are sister to a clade that includes scrub robins (*Cercotrichas* and *Erythroprogyia*), magpie-robins and shamas (*Copsychus* and *Trichixos*) and *Saxicoloides* (clade 3). It is a rather heterogeneous assemblage, with marked differences in habitat choice. Scrub robins, as their name suggest, prefer thick vegetation in various arid habitats, from tropical deciduous forest and savannas to Mediterranean maquis (Keith *et al.* 1992). *Saxicoloides* occurs in various open or semi-open habitats over most of India, from dry forests to ravines, while *Copsychus* and *Trichixos* are forest species (Rasmussen & Anderton 2005). Despite these differences, all species share a peculiar cocking and fanning of their long tails. *Cercotrichas* has a uniform black plumage that keeps it apart from *Erythroprogyia*, but they share similar structure and *Erythroprogyia* is often merged in *Cercotrichas* (e.g. Dickinson 2003). The genus *Copsychus* is polyphyletic, with *Copsychus malabaricus* sister to *Trichixos* and *Copsychus saularis* sister to *Saxicoloides*. This topology is congruent with the ecological division between magpie-robins and shamas. The magpie-robins (here represented by *C. saularis*) inhabit open woodlands in lowland areas, not so different from those used by *Saxicoloides*, which are only drier. Shamas (here *C. malabaricus*) are old forest specialist like *Trichixos*. It would be more appropriate to merge all species in a single genus, or use two genera to emphasize their ecological differences, although taxonomic changes should await a more comprehensive phylogenetic analysis.

Beresford (2003) recovered *Alethe castanea* and *Alethe diademata* far apart from the other alethes and the African forest robins, but their position remained unresolved due to the reduced taxon sampling. Here, we show that *Alethe* is basal to the African flycatchers and to magpie- and shrub robins (clade 1).

The majority of the Asian flycatchers cluster in another clade (clade 4). It includes the blue flycatchers (*Niltava*, *Cyanoptila*, *Eumyias* and *Cyornis*), the *Rhinomyias* jungle flycatchers and *F. moniliger*. The drab-coloured *Rhinomyias* are fairly similar to *Muscicapaa* in structure and appearance,

differing only in a longer bill. However, *Rhinomyias ruficauda* is here recovered as sister to the colourful *Cyornis* and thus not related to *Muscicapaa*. Our results seemingly do not agree with those of Cibois & Cracraft (2004) who recovered *Rhinomyias goodfellowi* as sister to *Meleanornis*, i.e. in the clade including the African flycatchers and *Muscicapaa*. However, the *Rhinomyias* jungle flycatchers are not a particularly uniform group. Ten of the species in the genus are rather similar, with rufous tail and, often, rufous underpart. *Rhinomyias goodfellowi* stands out in being larger and having a greyish plumage without rufous tail. Our results may not necessarily contradict Cibois & Cracraft (2004), but instead might indicate polyphyly of the genus *Rhinomyias*. The blue flycatchers do not group together and in particular *Niltava* and *Cyornis*, despite their remarkably similar plumage, belong to different lineages.

Although our results strongly support a single origin of the African forest robins (clade 5), they agree only in part with the taxonomy suggested by Irwin & Clancey (1974) and Jensen (1990) for this group. Beside the true forest species like *Cosypha*, *Pogonocichla*, *Pseudaethe*, *Sheppardia* and *Stiphornis*, this clade includes also the African genus *Cicbladusa*, occurring instead in palm savannas and thickets, and the Palearctic *E. rubecula*, that prefer temperate woodlands. Beresford (2003) investigated the relationships in the same group, but in most cases she failed to recover a monophyletic African forest robins clade and the trees suffer from a generally poor resolution and/or weak support of the basal nodes. Only the β -fibrinogen intron 5 data recover a monophyletic assemblage, albeit with no support. However, we feel that Beresford's lack of monophyly is possibly due to a suboptimal choice of molecular markers (cytochrome *b* and β -fibrinogen intron 5) and to the use of parsimony as the only optimality criterion. On the other hand, we found that splitting *Pseudaethe* from the true *Alethe* was appropriate (Beresford 2003), with only the former being part of the forest robins assemblage.

The presence of the Eurasian *E. rubecula* in the African forest robins clade is surprising. The hypothesis of close relationships among *Erithacus*, *Luscinia* and *Tarsiger* (Ripley 1952 and Vaurie 1955) is thus refuted. The two Japanese species *Luscinia komadori* and *L. akabige* have a plumage remarkably similar to *E. rubecula*, prompting some authors to include them in *Erithacus* (e.g. Voous 1977; Clements 2008). However, using molecular data Seki (2006) showed that *L. komadori* and *L. akabige* are closer to another Eastern Asian species, *L. cyane*, while *E. rubecula* is removed from that clade. Yet, Seki's sampling was inadequate for fully resolving their relationships. The remaining species form a large radiation composed mostly by Asian taxa. In this clade, several previous hypotheses about relationships could not be confirmed, suggesting that morphology has

been a poor predictor of phylogenetic relationships in this group. At the base are three clades of skulking, terrestrial, long legged birds (clades 6–8). The monotypic *Heinrichia calligyna* is the most basal branch. It is often merged with *Brachypteryx* (e.g. Ripley 1952), but it is larger, with stouter bill and different plumage pattern (White & Bruce 1986). The shortwings *Brachypteryx* instead belong to the next branch, together with *L. sibilans*. The third branch comprises another *Luscinia* and the monotypic *Irania* and *Hodgsonius*.

Brachypteryx and *Heinrichia* have had complex taxonomic histories. At first placed among the Timaliidae (Gray 1869; Sharpe 1883, 1903), they were later reclassified among the Turdidae in their subfamily Brachypteryginae (Stuart Baker 1921, 1924). Ripley (1952) did not recognize internal subdivision in his family Turdidae and he placed *Brachypteryx* (including *Heinrichia*) at the beginning of the sequence as the ‘most primitive’ of chats. Later *Brachypteryx* was removed from the chats (Saxicolini) and included among the true thrushes (Turdinae) following DNA hybridization data (Sibley & Ahlquist 1990), while Rasmussen & Anderton (2005) and Collar (2005) returned *Brachypteryx* to the beginning of the chats. Our results indicate that although *Brachypteryx* and *Heinrichia* are correctly allocated to the chats clade, they are not basal to this radiation nor are they its sister taxa. The genus *Luscinia* is another surprising case of polyphyly. Despite the plumage similarities between *L. sibilans* and *L. luscinia*, they end up in different clades with *L. luscinia* associated with more patterned birds. *Irania* in particular has similar size and structure to *Luscinia* but reminds of *Coscypha* in its plumage (Cramp 1988), whereas *Hodgsonius* has a deep blue plumage similar to other Asian blue chats like *Cinclidium* and *Myiomela*.

The blue robins *Cinclidium* and *Myiomela* are so similar that they are usually merged into a single genus (e.g. Ripley 1964; Sibley & Monroe 1990), but the molecular evidence separates them. *Myiomela* and *Tarsiger* are recovered sister taxa in the combined and nuclear only datasets, although only in the latter topology the node is supported (clade 9). Instead *Cinclidium* is sister to another group of blue birds, the large *Myiophonus* whistling thrushes (clade 10). The structure, habitat occupation and behaviour were the main reasons for classifying *Myiophonus* in the family Turdidae (Delacour 1942; Ripley 1952) and the DNA hybridization supported this view (Sibley & Ahlquist 1990). Our data indicate that a relationship of *Myiophonus* with Turdidae is unwarranted. Some species in *Myiophonus* are sexually dimorphic as *Cinclidium*, with blue males and brownish females, and both genera inhabit thick forests near running water. *Enicurus* are sister to the *Cinclidium* + *Myiophonus* clade, and like these they occur along

fast-flowing rivers and streams in wet mountain forests. Although characterized by their distinct black and white plumage and long tails, *Enicurus* is deeply nested within the Muscicapidae and any treatment as a separate subfamily or tribe is unjustified.

Close to these chats is the last flycatcher clade that includes the large genus *Ficedula* (except *F. moniliger*) and the monotypic *Muscicapella* (clade 11). Although, *Muscicapella* strongly resembles a diminutive *Niltava*, and is often treated as such (e.g. Vaurie 1953), Ripley (1955) pointed out several differences in morphology (size, bill, tarsus) and foraging habits that suggested either the retention of a monotypic genus or merging it within *Ficedula*. Outlaw & Voelker (2006) reconstructed a well-sampled phylogenetic hypothesis for *Ficedula* using mitochondrial data. In their tree *Muscicapella* was nested in the *Ficedula* clade, confirming Ripley’s hypothesis.

The redstarts (*Phoenicurus*, *Chaimarrornis* and *Rhyacornis*) form a well supported clade. The suggested split of the group, with the transfer of *Rhyacornis* close to *Oenanthe* and of *Chaimarrornis* near or in *Thamnolaea* is invalidated (Goodwin 1957; Deshayes 1969). The redstarts form the basal branch of a large radiation (79 species) of chats adapted to various arid ecosystems (clade 12). The redstarts are the only exclusively Eurasian group, with a maximum diversity in the Sino-Himalayan region. Some species of *Oenanthe* and *Saxicola* occur also in Africa, while the majority of *Monticola* and *Cercomela* and all the remaining genera (*Campicoloides*, *Myrmecocicbla*, *Pentholaea*, *Pinarochroa* and *Thamnolaea*) are African. The phylogenetic hypotheses for *Monticola* (Goodman & Weigt 2002; Outlaw *et al.* 2007; Zuccon & Ericson in press), *Oenanthe* (Aliabadian *et al.* 2007) and *Saxicola* (Illera *et al.* 2008) recovered complex biogeographic scenarios, suggesting that transcontinental dispersal have occurred several times. A complete species-level sampling will provide a better picture of the African-Asian faunal interchange and its role in the diversification of this clade.

There is a lack of agreement in the taxonomy of some of the species adapted to arid ecosystems. The genus *Cercomela* comprises small chats with plain colour occurring in India and over most of Africa. The monotypic *Pinarochroa sordida* is usually merged in the same genus (e.g. Keith *et al.* 1992; Dickinson 2003), but its split from *Cercomela* has been justified by the longer tarsi and the shorter tail (Collar 2005). The molecular data corroborate its reclassification.

We have already showed that *Thamnolaea* is polyphyletic and that *Thamnolaea semirufa* should be transferred to *Monticola* (Zuccon & Ericson in press). Furthermore, *Thamnolaea cinnamomeiventris* forms a clade with the genera *Pentholaea* and *Myrmecocicbla*, and all these species are sometimes merged into the latter genus (e.g. Keith *et al.* 1992).

Hall & Moreau (1970) considered the monotypic *Campicoloides bifasciatus* to have 'uncertain affinities'. In fact it has been either merged with *Saxicola* (e.g. Tye 1989; Keith *et al.* 1992) or *Oenanthe* (e.g. Ripley 1964), but our topology indicates that it belongs to a distinct lineage between *Saxicola* and *Oenanthe*, in agreement with the taxonomic treatment advocated by Clancey (1990).

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Supporting Information

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

Fig. S1 The majority rule consensus tree obtained from the mixed-model Bayesian analysis of the concatenated dataset without ND2. Posterior probability values are indicated at the node.

Fig. S2 The majority rule consensus tree obtained from the Bayesian analysis of the ND2 genes. Posterior probability values are indicated at the node.

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