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Relationships between the ant-thrushes *Neocossyphus* and the flycatcher-thrushes *Stizorhina*, and their position relative to *Myadestes*, *Entomodestes* and some other Turdidae (Passeriformes)

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Abstract

This paper discusses the relationships of a peculiar group of Turdine birds, the ant-thrushes (genus *Neocossyphus*, terrestrial-adapted birds) and the flycatcher-thrushes (genus *Stizorhina*, flycatching-adapted birds), based on cytochrome-*b* and 16S mitochondrial DNA analyses. Although these genera do not share the typical characters of Turdine birds (juvenile spotted plumage and 'turdine thumb' pattern of the syrinx), they are generally considered members of the Turdidae family. The present study has confirmed the formerly expressed hypotheses that: (1) *Neocossyphus* and *Stizhorma* form a monophyletic group; (2) they are related to *Myadestes*, another peculiar genus also lacking both diagnostic Turdine characters, hence justifying the subfamily Myadestinae; and (3) these three genera are related to other large typical Turdine birds. It has also confirmed that *Entomodestes* is not immediately related to *Myadestes*, but is a true large Turdine bird, and that the classically known ensemble Turdidae–Muscicapidae should be divided as proposed by Sibley and Ahlquist (*Phylogeny and Classification of Birds. A Study in Molecular Evolution*, New Haven: Yale University Press, 1990). The detailed analysis of relationships between species of the genera *Neocossyphus* and *Stizorhina* failed to support a strict dichotomous evolutionary pattern but showed that the species of *Stizorhina* are very closely related and of much more recent origin than the species of *Neocossyphus*. The most probable scenario is that of a basal trichotomy of the two *Neocossyphus* species and *Stizorhina* which fragmented later.

Key words: Key words: Turdidae – *Myadestes* – *Stizorhina* – *Neocossyphus* – flycatchers – mitochondrial DNA – phylogeny

Introduction

Most Turdidae are ground-dwelling birds, with rather long and strong tarsus. They form a natural group, related to the Muscicapine flycatchers, and defined by (1) spotted juvenile plumage and (2) thumb-like turdine pattern of the syrinx (Ames 1975). Some genera, because of their general appearance, are placed in the Turdidae even though they lack both of these characteristics: three from Africa, *Modulatrix*, *Neocossyphus* and *Stizorhina*, and the New World *Myadestes*, including *Phaeornis obscurus*, the Hawaiian thrush.

The case of *Neocossyphus* (*Neocossyphus poensis* and *Neocossyphus rufus*) and *Stizorhina* (*Stizorhina finschi* and *Stizorhina fraseri*) is puzzling. The two genera have very different morphological characteristics and eco-ethological adaptations: the thin-billed *Neocossyphus* species are ground-foraging birds, named ant-thrushes because they follow and depend on army ants; the broad-billed *Stizorhina* behave like true flycatchers, hence their name flycatcher-thrushes (Brosset and Erard 1986; Erard 1987, 1990, 1992). Nevertheless, the four species have very similar rufous plumage pattern, which is considered to be taxonomically significant by some authors (Chapin 1953). The two genera are often merged in *Neocossyphus* (Hall and Moreau 1970; Erard 1987). The remarkable thing is that the two species in each genus have similar differences in plumage pattern: West African *N. poensis and S. finschi* have dark upper-parts and white spots on two to three external tail feathers, whereas Central-Eastern *N. rufus* and *S. fraseri* are almost uniformly rufous and lack white outer-tail patches. Two alternative scenarios which could support this pattern have been proposed by Erard (1987): both suppose an event with a morphologically based separation of ecological forms and another one based on the evolution of two distinct colour patterns, the scenarios differing in the sequence of both events. Furthermore, a relation between *Stizorhina* and *Myadestes* (Solitaires) has been proposed (Sharpe 1881; Ripley 1952) and, since they both lack Turdidae–Muscicapidae characteristics (Ames 1975), Olson (1989) proposed merging them in the subfamily Myadestinae. However, the supposedly related genus, *Entomodestes* (comprising the two Solitaire species *Entomodestes leucotis* and *Entomodestes coracinus*), is unquestionably in the Turdidae (Ames 1975). Sibley and Ahlquist (1980, 1990) showed that *Myadestes* is related to *Entomodestes*, and, more distantly, to the true thrushes, but they did not take into account *Neocossyphus* or *Stizorhina*. Here we offer the results of a molecular analysis, based on two partial mitochondrial genes [cytochrome-*b* (cyt-*b*) and 16S], which addresses the question of relationships of *Neocossyphus*, *Stizorhina*, *Mydestes*, *Entomodestes* and the true thrushes.

Materials and methods

Species and source of DNA

Our samples (Table 1) include all the species of genera *Stizorhina* and *Neocossyphus*, as well as *Myadestes ralloides*, *Entomodestes leucotis*, and eight species in genera of the Turdi-Muscicapid complex. In addition, we sequenced representatives of the closely related groups (included in Muscicapoidea *sensu* Sibley and Ahlquist 1990): one Cinclid, one Bombycillid, two Sturnids and one Mimid. We also included representatives of several families of the Corvoidea, *sensu* Sibley and Ahlquist (1990) (five genera), of the Sylvii–Timalii–Pycnonotidae clade (five genera), one Sittidae, one Passeridae, one Motacillidae and one Tyrannidae; all these sequences were done by the first and second authors for other studies (see Table 1). Total genomic DNA was extracted from either frozen or alcohol-preserved tissues (muscle, liver, blood) or small pieces (0.5–1 cm^2) of museum skins (labelled MNHN, CG in Table 1), with the same CTAB buffer containing proteinase K (0.1 mg/ml) (Doyle and Doyle 1987; Winnepenninckx *et al.* 1993). In the case of museum skins, the time of protein digestion was increased from 2 h to 1 night.

DNA amplification and sequencing

Polymerase chain reactions (PCR) were carried on for 35–40 cycles. In each cycle, denaturation was carried out at 93° C for 30 s, annealing at

Table 1. List of taxa studied, geographic origin, number of the samples used and Genbank accession numbers

Family[1]	Species	Origin	Number and Collection[4]	Genbank accession numbers	
				Cyt-*b*	16S
Muscicapidae	*Muscicapa striata*	France	MNHN, no. 13–1A	AF096458	AF096480
	Ficedula hypoleuca	France	MNHN, no. 21–26	**AF151409**[5]	**AF151426**
	Cyornis banyumas	Thailand	MNHN, no. 4–9F	**AF151408**	**AF151425**
Turdidae	*Phoenicurus phoenicurus*	France	MNHN, no. 22–43	AF135050	AF135057
	Saxicola ferrea	China	MNHN, no. 14–10	**AF151407**	**AF151424**
	Stiphrornis erythrothorax	Cameroon	MNHN, no. 1–01	**AF151406**	**AF151423**
	Geokichla[2] *princei*	Cameroon	MNHN, no. 1–12	**AF151405**	**AF151422**
	Turdus philomelos	France	MNHN, no. 22–22	**AF151404**	**AF151421**
	Entomodestes leucotis	Peru	MNHN, C.G. 1967–1269	**AF151403**	**AF151420**
	Myadestes ralloides	Peru	MNHN, C.G. 1966–1471	**AF151402**	**AF151419**
	Stizorhina[3] *finschi*	Ivory Coast	McM. Univ. no. BO90	**AF151401**	**AF151418**
	Stizorhina fraseri	Cameroon	MNHN, no. E20	**AF151400**	**AF151417**
	Neocossyphus poensis	Cameroon	MNHN, no. 1–62	**AF151399**	**AF151416**
	Neocossyphus rufus	Kenya	MNHN, C.G. 1968–1067	**AF151398**	**AF151415**
Cinclidae	*Cinclus cinclus*	France	MNHN, no. C11	**AF151393**	**AF151410**
Bombycillidae	*Bombycilla japonica*	unknown	MNHN, no. 23–1G	**AF151394**	**AF151411**
Mimidae	*Dumetella carolinensis*	North America	MNHN, no. C24	**AF151395**	**AF151412**
Sturnidae	*Sturnus vulgaris*	France	MNHN, no. 22–17	**AF151396**	**AF151413**
	Leucopsar rothschildi	unknown	MNHN, no. C23	**AF151397**	**AF151414**
Dicruridae	*Dicrurus paradiseus*	Laos	MNHN, no. 5–57	AF096473	AF096475
Corvidae	*Corvus corone*	France	MNHN, no. 13–16	AF094613	AF094643
Monarchidae	*Terpsiphone viridis*	Cameroon	MNHN, no. 2–23	AF094616	AF094646
Laniidae	*Lanius collaris*	Thailand	MNHN, no. 2–26	AF094614	AF094644
Oriolidae	*Oriolus xanthornus*	Thailand	MNHN, no. 4–10D	AF094615	AF094645
Sittidae	*Sitta europaea*	France	MNHN, no. 9–15	AF135049	AF135055
Sylviidae	*Camaroptera brevicaudata*	Cameroon	MNHN, no. 2–15	AF094626	AF094654
	Acrocephalus aedon	Thailand	MNHN, no. 4–8D	AF094623	AF094653
	Sylvia melanocephala	France	MNHN, no. S4	AF135052	AF135056
Timaliidae	*Garrulax leucolophus*	Thailand	MNHN, no. 4–6E	AF094627	AF094655
	Pellorneum ruficeps	Thailand	MNHN, no. 4–6F	AF094632	AF094660
Pycnonotidae	*Andropadus latirostris*	Cameroon	MNHN, no. 2–52	AF096457	AF096477
Motacillidae	*Anthus pratensis*	France	MNHN, no. 13–5A	AF096460	AF096479
Passeridae	*Passer domesticus*	France	MNHN, no. 13–5C	AF094639	AF094667
Tyrannidae	*Tyrannus melancholicus*	South America	MNHN, no. 12–33	AF135051	AF135058

[1] Taxonomy presented here mainly follows Howard and Moore (1991)
[2] Often placed in *Zoothera*
[3] Placed in *Neocossyphus* by Howard & Moore 1991
[4] MNHN: National Museum of Natural History, Paris, France. McM University of McMaster University, Ontario, Canada
[5] Genbank accession numbers in bold represent the new sequences done for the present study. Other numbers represent sequences done by Cibois and Pasquet for other studies, Cibois *et al.* (1999), Pasquet et al. (submitted)

50–55° C for 40 s, and extension at 72 C for 40 s. Cyt-*b* amplifications were done with primers L15383 (5′ GGA CAA ACA CTA GTA GAA TG 3′, designed at our laboratory), and H15916 (5′ ATG AAG GGA TGT TCT ACT GGT TG 3′, Edwards et al. 1991), which delimit a portion of 484 DNA bases; 16S amplifications were done with primers L3214 (5′ CGC CTG TTT ATC AAA AAC AT 3′, Hedges 1994) and H3783 (5′ CCG GTC TGA ACT CAG ATC ACG T 3′ Hedges and Sibley 1994) which delimit a portion of 513 aligned bases. All primers are numbered with reference to the chicken complete mitochondrial genome (Desjardin and Morais 1990). Sequencing reactions were performed by direct cycling PCR with the Thermo Sequenase Cycle Sequencing kit (Amersham Pharmacia Biotech); migrations were carried out on polyacrylamid gels with manual sequencers. Sequences were read twice independently and managed with the MUST package (Philippe 1993). The alignment of the 16S sequences were made by hand, minimizing the number of gap positions needed in the homologous sequences.

Phylogenetic analyses

We first analysed cyt-*b* and 16S separately [both neighbour-joining (NJ) and maximum-parsimony (MP)], and then combined both data sets into a single analysis. The NJ topologies were obtained using the MUST package (Philippe 1993), with row distances calculated on all variable sites for both separate and common analyses (see Table 3). The MP analyses were performed using PAUP 3.1.1 (Swofford 1991), all using the heuristic algorithm, with 10 random addition-sequence replicates. The cyt-*b* data were treated without and with weighting scheme (see Table 3) built with respect to saturation analysis (Mindell and Honeycutt 1990; Irwin et al. 1991). Weight was applied to the data set using a step matrix in PAUP. We also carried out the analysis taking out all the transitions at the third codon position. No weighting was used with 16S data because the analysis did not give evidence for saturation (Fig. 1b). Gaps in 16S sequences were treated as a fifth character. Combined MP analyses were conducted on the two data-sets together, first with all sites, second without transitions at third codon position of the cyt-*b*

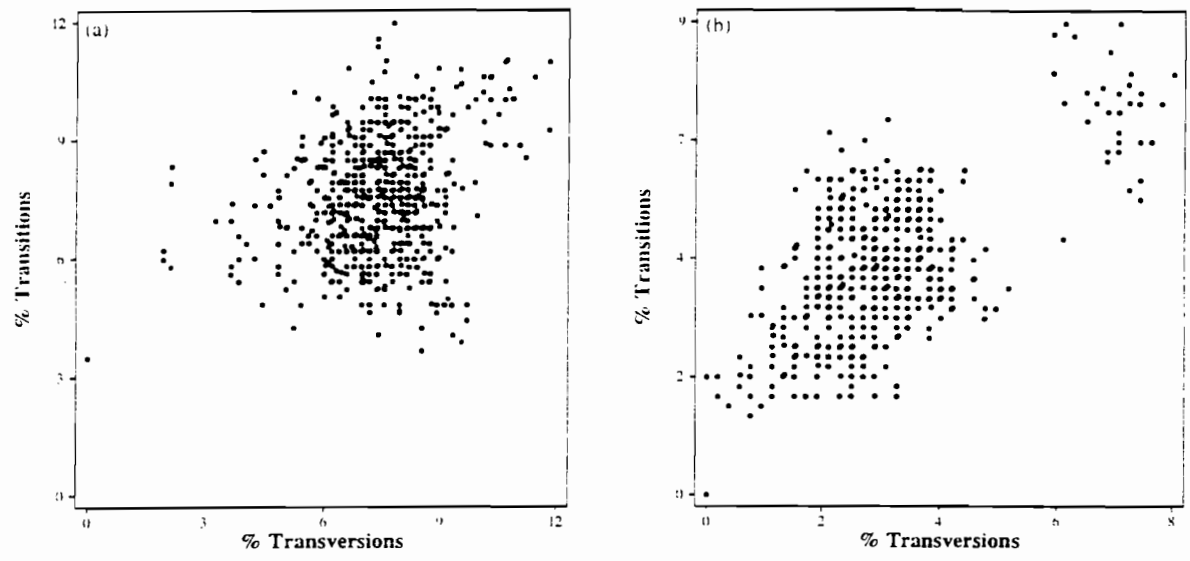

Fig. 1. Row percentages of differences, calculated in all studied molecular sites, and plotted by transitions and transversions for each pair of species. (a) partial cyt-*b* gene (b) partial 16S gene.

sequences: this solution was chosen instead of the weighting of transversions because, in this way, the problem of the compensatory weighting of the 16S versus the cyt-*b* can be avoided. The robustness of the trees was tested by bootstrap analysis with 1000 (NJ) or 100 (MP) iterative resampling (Felsenstein 1985). In all analyses, *Tyrannus melancholicus* was used as the outgroup.

Results

Sequences variation and saturation

The sequences have been deposited in Genbank (Table 1). Among the 484 sites of cyt-*b* analysed, 250 sites (51.6%) were variable and 204 (42.1%) were phylogenetically informative. For each pair of species, separate percentages of transitions and transversions, in the total number of sites, were plotted against each other (Fig. 1a); this figure shows evidence of the transition saturation phenomena. With regard to Fig. 1a, we estimated the initial ratio of transition : transversion as 4 : 1: this value was used as a compensatory weight which was applied to the transversions in the separate cyt-*b* analysis. In the 16S sequences, a few gaps were introduced for the alignment of sequences; among the 513 homologous sites, 175 (34.1%) were variables and 124 (24.2%) were phylogenetically informative. There was no evidence of transition versus transversion saturation phenomena (Fig. 1b).

General phylogenetic results

We present the results of the common NJ analysis (Fig. 2), and the corrected MP analysis, discarding transitions at the third codon position (Fig. 3). Other trees are not shown, but are compatible with both these trees; the detailed bootstrap proportions of all analyses (NJ and MP) are presented in Table 3. Both separate (NJ and MP) and common analyses appear very weakly resolved for many parts of the topologies, which shows the limit of the interest of both these mitochondrial genes. However, they show the following:

(1) Both *Stizorhina* are always grouped with high support (node no. 1) but *Neocossyphus* species are in paraphyletic position in some analyses (nodes no. 2 or no. 2 bis) (see the detailed analysis below);

(2) The four species of *Stizorhina* and *Neocossyphus* form a well supported clade (node no. 3);

(3) *Stizorhina*, *Neocossyphus* and *Myadestes* form another clade (node no. 4);

(4) *Entomodestes* and *Turdus* are sister taxa (node no. 5), and form with *Geokichla* a clade which corresponds to the large true Turdidae (node no. 6);

(5) Small Turdidae are mixed with Muscicapidae (nodes no. 8,9,10), and no link appears between all these taxa and the Turdidae as defined by clade no. 6 or by clade no. 7 (if we include clade no. 4 in the Turdidae);

(6) Finally, *Sturnus* and *Leucopsar*, both in the Sturnidae, are close together (node no. 11) and linked to *Dumetella* (Mimidae) (node no. 12).

Relationships in and between *Neocossyphus* and *Stizorhina*

A detailed look at the matrices of distances (Table 3, Fig. 4) shows that the relation between 16S and cyt-*b* transversion distances is linear: this reflects the similarity of information. The relation between 16S and cyt-*b* transitions (as between cyt-*b* transversions and transitions) is saturated, so the distances decline with the *Myadestes* points. There are no differences between the DNA sequences of the *Stizorhina* species both for the cyt-*b* transversions and the 16S, which explains the 100% bootstrap value for the *Stizorhina* clade (node no. 1); on the contrary, the distance between both *Neocossyphus* species (2.56% for 16S, 2.27% for cyt-*b* transversions) is as great as that between *Stizorhina* and *Neocossyphus* (respectively 2.76–2.95% and 2.07–2.29%); this makes the resolution of a strictly dichotomous tree impossible. The grouping of both *Neocossyphus* species (node no. 2) is therefore not supported (Table 3).

Discussion

On the Muscicapoidea general phylogeny

Sibley and Ahlquist (1990), in their enormous phylogenetic work based on DNA hybridization, proposed numerous very different and sometimes provocative views of the taxonomy of

Table 2. Muscicapoidea nodes, and their bootstrap proportions (only values > 50%) obtained with various analyses

	Gene	Cyt-*b*				16S		Both genes		
	Sites	All		Tv*4	−Ts3	All		All		Cytb-Ts3
Node	Method	NJ	MP	MP	MP	NJ	MP	NJ	MP	MP
1	*Stizorhina finschi* − *fraseri*	100	100	100	100	100	99	100	100	100
2	*Neocossyphus poensis* − *rufus*	−	−	−	−	62		67	−	
2 bis	1 − *Neocossyphus rufus*	54	53	50		−	−	−	51	−
3	1 − 2 = *Stizorhina* − *Neocossyphus*	66	51	75	67	81	76	95	80	97
4	3 − *Myadestes*	61		55				92	79	72
5	*Entomodestes* − *Turdus*	66	53	55		80	72	96	75	69
6	5 − *Geokichla*							79	63	63
7	4 − 6 = large Turdidae					90	78	91	68	72
8	*Stiphrornis* − *Muscicapa*					63				63
9	*Saxicola* − *Cyornis*					75	68		50	
10	Small Turdi-Muscicapidae				50	53		93	76	75
11	*Leucopsar* − *Sturnus*	95	76	97	98	75		98	80	88
12	11 − *Dumetella*					52		68		
13	*Garrulax* − *Pellorneum*					65	61	58	54	50
14	13 − *Sylvia*							58		
15	Sylvii-Timalii-Pycnonotidae clade					76	72	89	79	90
16	*Passer* + *Anthus*	65	54	59	65	67	57	95	93	93
17	Passerida (*sensu* Sibley and Ahlquist 1990)					55		68		
18	*Corvus* + *Terpsiphone*					64	51	51		
19	13 − *Dicrurus*					57				
	Number of nodes with bootstrap > 50%	7	6	7	5	16	9	16	13	12

Tv*4, indicates that a weight of 4 is given to transversions; Ts3, indicates that transitions at third position are discarded

birds. Around the thrushes, they defined a superfamily Muscicapoidea (including the classical families Dulidae, Bombycillidae, Cinclidae, Turdidae, Muscicapidae, Sturnidae and Mimidae) and discussed their relationships. But, because the robustness of their molecular results had not been evaluated, any new robust information brought, whether congruent or not with them, is of great value.

The following results are well supported and in very good agreement with those of Sibley and Ahlquist (1990): (1) the proximity of Mimidae and Sturnidae, largely discussed by them, is herein confirmed; (2) the new partition of the Turdi–Muscicapine birds, proposed by Sibley and Ahlquist (1990), followed by Sibley and Monroe (1990), finds here new evidence. Formerly the distinction between Turdine and Muscicapine birds was mainly based on etho-ecological adaptation: non-flycatcher group one versus flycatcher group two. We confirm that Turdinae can be restricted to the 'large' thrushes and that the Muscicapinae should include the small Turdine birds, as well as the Flycatchers. Nevertheless, inside this latter group (connected in our topologies at node no. 10), we did not obtain a partition between the small terrestrial Turdids (*Phoenicurus*, *Stiphrornis*, *Saxicola*) and the flycatchers (*Muscicapa*, *Ficedula*, *Cyornis*). Their relative positions require further studies.

The place of *Entomodestes* and *Myadestes*

Myadestes and *Entomodestes* are related to the Turdinae (restricted to the large thrushes) as Sibley and Ahlquist (1980) also showed, but our results do not suggest a close relationship between *Myadestes* and *Entomodestes*. No other nodes corresponding to Sibley and Ahlquist's work on Muscicapoidea could be defined by our results. In particular, we could not confirm the relative basal position of *Cinclus* or *Bombycilla*. In our molecular study, *Entomodestes* appears related to *Turdus*, but not to *Myadestes*. This result is congruent with the morphological studies because, like *Turdus* and many other Turdids, *Entomodestes* has the two diagnostic turdine characters (Ames 1975; Olson 1989). This confirms that *Entomodestes* must be considered a true thrush. On the other hand, *Myadestes* is clearly related to the *Stizorhina–Neocossyphus* clade. This relation is not a complete surprise, since it had already been suspected because of their very similar shape (Sharpe 1881; Ripley 1952; Olson 1989) and the absence of the two typical turdine characters (Ames 1975). Nevertheless, the lack of these characters alone should not be sufficient to group these species, considered as primitive. However, the present results provide a new argument for the validity of this group and further support to the Myadestinae subfamily erected by Olson (1989) for these birds. In the present results, Myadestinae are the sister-group of the large true Turdinae and are not at the basal position of the large group of the Turdi-Muscicapine birds, defined as a whole by spotted juvenile plumage and the 'turdine thumb' pattern of the syrinx (Ames 1975). If the monophyly of this assemblage is accepted, then the absence of the diagnostic turdine characters in Myadestinae is a secondary loss.

Stizorhina–Neocossyphus relationships

Stizorhina and *Neocossyphus* raise a puzzling and interesting problem. Puzzling because, as already stated, we found in each of both large Afrotropical forest-blocks (i.e. Upper versus Lower Guinean) a pair of syntopic species, almost sibling in

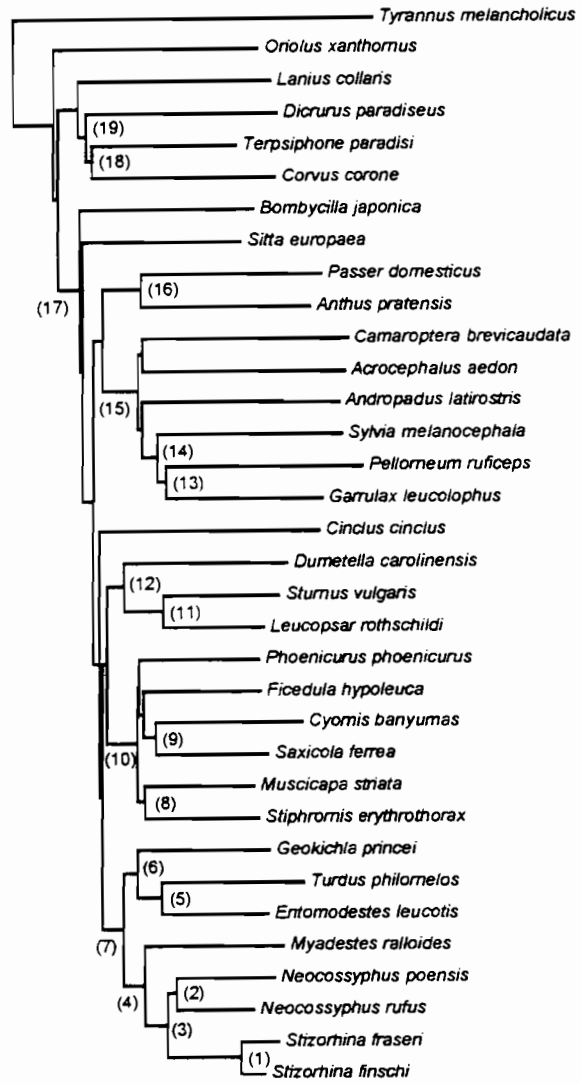

Fig. 2. Tree obtained with common neighbour-joining analysis with both cyt-*b* and 16S, unweighted. Nodes are numbered for use in Table 3; all numbered nodes appear in the various analyses, at least once with a bootstrap proportion more than 50%.

their coloration pattern, but different in their proportions, in relation to their location in the forest, and in their foraging behavior (see Erard 1987, 1990). This is interesting because this case involves the significance of morphological traits (here both coloration patterns and structural proportions) for relationship studies and how to distinguish phylogenetic relationships from convergence or parallel evolution.

From our results, the very close relationship of *Stizorhina* species is unquestionable. This is in good agreement with the near specific taxonomic level given to the taxa: mere subspecies because of their almost allopatric distributions (White 1970), or species because of their different coloration patterns, and tempo/pitch differences in their songs which playback experiments in Gabon have shown to be distinctive and species-specific (Hall and Moreau 1970; Erard 1990, 1992). However, *fraseri* and *finschi* hybrids in south-east Nigeria, and resulting hybrids have intermediate song (Dowsett and Dowsett-Lemaire 1993).

The case of *Neocossyphus* is clearly different and both species were separated much longer ago; their specific level is evident and is confirmed by their significantly, though not completely, sympatric distribution (see maps in Erard 1992).

As it seems impossible to detect a clear symmetrical dichotomous structure for the relationships between *Neocossyphus* and *Stizorhina*, such as the two scenarios given by Erard 1987, an alternative scenario could be a basal trichotomy with both *Neocossyphus* species and *Stizorhina*, and an ulterior fragmentation of *Stizorhina*. A scenario where, during glacial episodes, tropical forest remnants were restricted in western, central and eastern Africa (see, for example, maps in Petit-Maire 1999), permitting speciation with emergence of *N. poensis* in the west and *N. rufus* in the east, from a central ancestor that gave also rise to *Stizorhina*. Of course, we cannot build the true story of the evolution of this group. What is clear is the very recent divergence of *Stizorhina* species and the ancient radiation for the whole group. In our scenario, the flycatcher etho-ecological adaptation of *Stizorhina* is probably derived from an arboreal ancestor, as are most of the large Turdids. The striking white patches in phenotypes of *finshi* and *poensis* are very probably a small event included in the genetic variability of the ancestor taxa.

Hall and Moreau (1970), followed by Erard (1992), made the taxonomic decision to place all the species of the *Stizorhina–Neocossyphus* group in a single genus *Neocossyphus*. Our phylogenetic result and the evolutionary scenario we propose are in agreement with this nomenclatural decision.

This example shows also that the so-called Old World flycatchers (in which *Stizorhina* was formerly placed) are not a natural group of related species (particularly when we consider also recent results obtained on Monarchs, see Pasquet et al. submitted) but rather an assemblage of species with similar ecology and behaviour patterns and convergent morphologies. The same could be true for chats as suggested here by the position of *Muscicapa* among small Turdids.

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Zusammenfassung

Verwandtschaftsbeziehungen zwischen den Fuchsdrosseln Neocossyphus und den Finsch-und Kurzlaufdrosseln Stizorhina und ihre Stellung zu Myadestes, Entomodestes und einigen anderen Turdiden (Passeriformes)

In dieser Arbeit werden die Verwandtschaftsverhältnisse einer besonderen Gruppe der drosselartigen Vögel, die Fuchsdrosseln (Gattung *Neocossyphus*, bodenadaptierte Vögel) und die Finsch-und Kurzlaufdrosseln (Gattung *Stizorhina*, fliegenfangende Vögel) mit Hilfe von Cytochrom-*b*-und mitochondrialen 16S-DNA Analysen besprochen. Obgleich diese Gattungen die typischen Merkmale der drosselartigen Vögel (juvenile Gefiederfleckung und drosselartige Syrinx) nicht besitzen, werden sie im allgemeinen doch in die Familie der Turdidae gestellt. Wir können die bereits früher aufgestellten Hypothesen bestätigen: (1) *Neocossyphus* und *Stizorhina* bilden eine monophyletische Gruppe; (2) sie sind verwandt mit *Myadestes*, einer anderen, besonderen Gattung, der auch die beiden diagnostischen Merkmale der Drosselartigen fehlen, so daß eine Unterfamilie Myadestinae gerechtfertigt erscheint; (3) diese

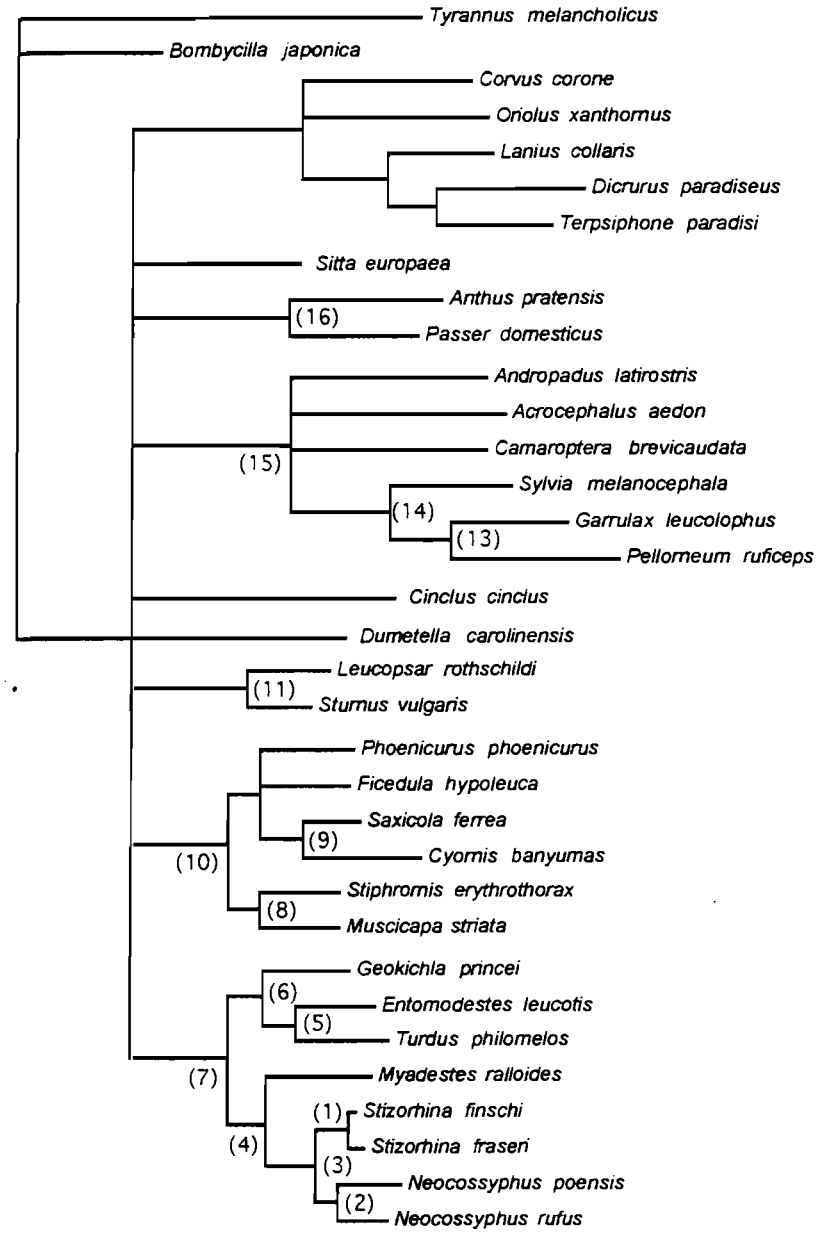

Fig. 3. Strict consensus of the four maximum-parsimony (MP) trees obtained with the common MP analysis with cyt-*b*, discarding transitions at third position, and 16S, unweighted. Nodes are numbered as in Fig. 2.

Table 3. Pairwise distances (in percentage of variation) between *Myadestes*, *Neocossyphus* and *Stizorhina* species, detailed for 16S, all mutations, cyt-*b*, transitions and transversions separately

		16S, all mutations				Cyt-*b*, transitions				Cyt-*b*, transversions			
		1	2	3	4	1	2	3	4	1	2	3	4
1	*Myadestes ralloides*												
2	*Stizorhina finschi*	4.92				7.44				3.93			
3	*Stizorhina fraseri*	4.92	0.00			7.90	3.74			3.95	0.00		
4	*Neocossyphus poensis*	5.31	2.76	2.76		7.02	8.47	8.94		4.13	2.27	2.29	
5	*Neocossyphus rufus*	5.91	2.95	2.95	2.56	5.99	6.40	6.65	6.20	3.93	2.07	2.08	2.27

drei Gattungen sind mit den anderen großen drosselartigen Vögeln verwandt. Wir können ebenso bestätigen, daß *Endomestes* mit *Myadestes* nicht direkt verwandt, aber doch große drosselartige Gattungen sind, und daß die klassische Zusammenstellung Turdidae-Muscicapidae entsprechend Sibley and Ahlquist (*Phylogeny and Classification of Birds. A Study in Molecular Evolution*. New Haven: Yale University Press, 1990) unterteilt werden sollte. Eine detaillierte Analyse der Verwandtschaftsbeziehungen zwischen den Arten der Gattungen *Neocossyphus* und *Stizorhina* war nicht imstande ein strikt dichotones Evolutionsmuster aufzudecken, aber es zeigte sich, daß die Arten von *Stizorhina* näher miteinander verwandt und jüngeren Ursprungs sind als die Arten von *Neocossyphus*. Das wahrscheinlichste Szenario ist eine

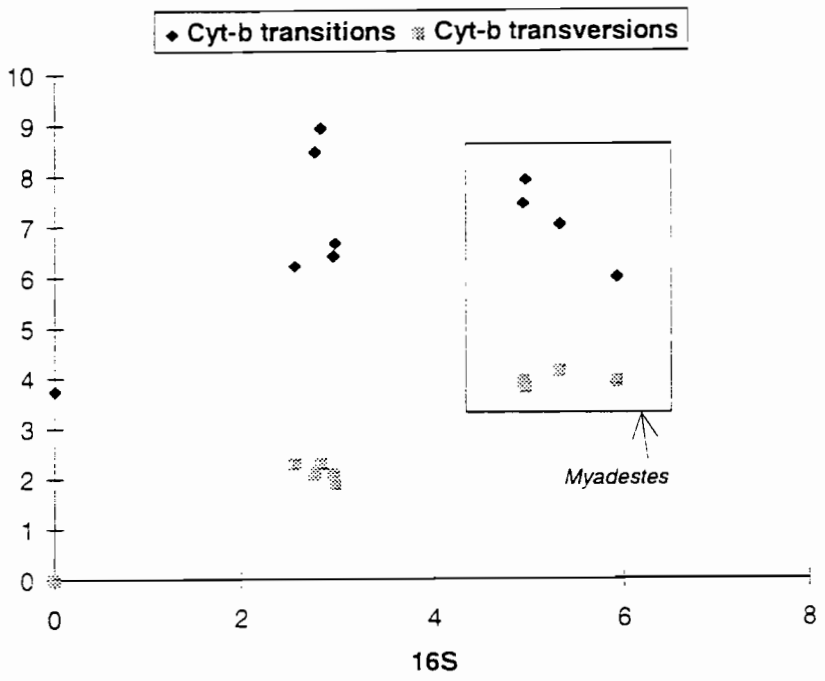

Fig. 4. Plot of pairwise distances shown in Table 3. Horizontal axis: 16S distances; vertical axes cyt-*b* transitions and cyt-*b* transversions.

ursprüngliche Trichotomie von zwei *Neocossyphus*-Arten und *Stizorhina*, welche etwas später abzweigt.

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