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Early *Xanthochorema* (Trichoptera, Insecta) radiations in New Caledonia originated on ultrabasic rocks

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ABSTRACT

The toxic and nutrient poor ultrabasic rock substrate covering one-third of New Caledonia greatly influenced on the biogeography and diversity of plants in the island. Studies on the effect of ultrabasic substrate on fauna are almost entirely absent. In this paper we examine whether the diversification of Trichoptera of the New Caledonian endemic genus *Xanthochorema* Kimmins, 1953 was related to the presence of ultrabasic substrate. The analysis is based on data from a phylogeny derived from DNA sequences of mitochondrial COX1, COX2 and 16S, and nuclear EF1a genes. The study of the relationships between ancestral species and substrate was carried out using dispersal–vicariance analysis and tracing the history of substrate association with ultrabasic and non-ultrabasic distributions representing the terminals in the fully resolved phylogenetic tree. Our results show that (1) the ancestor of all *Xanthochorema* species was present on ultrabasic substrate, (2) early speciation events were restricted to ultrabasic substrate, (3) younger ancestral species dispersed into non-ultrabasic substrates, and (4) late speciation events were restricted to non-ultrabasic substrate. These results correspond to the hypothesis that New Caledonia once was more extensively covered by ultrabasic rocks than at present.

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1. Introduction

Ultrabasic or ultramafic rocks typically have high concentrations of Mg, Fe, Cr, Co and Ni, and low content of the nutrients P, K and Ca. These rocks are scattered on many tropical islands, i.e. on Sulawesi, Papua New Guinea, Solomon Islands and New Caledonia (Hamilton, 1979; Proctor, 2003). The layers of ultrabasic rocks on New Caledonia formed during the tertiary when the island underwent a series of submersions. By the late Eocene nearly all of the main island Grande Terre and smaller islands nearby were covered by a layer of ultrabasic rocks resulting from ocean floor being pushed upwards and over the basement rocks due to the collision of the Indo-Australian and Pacific plates (Guillon, 1975; Moores, 1973; Paris et al., 1979). Much of the ultramafic cover has since been reduced by erosion (Guillon, 1969, 1975; Guillon and Routhier, 1971; Trescases, 1969, 1975) and now covers around 1/3 of the terrestrial land surface (Jaffré et al., 1987) (Fig. 1). High level of heavy metals combined with low level of nutrients in these soils gives specialized edaphic conditions which have had a great influence on New Caledonian phytogeography and diversity (Brousemiche, 1884; Jaffré, 1980; Jaffré and Latham, 1974; Jaffré and Veillon, 1990; Lee et al., 1977; Lowry, 1991, 1998; Morat, 1993; Morat et al., 1984; Proctor, 1992, 2003). In total 98% of the plant species occurring only on ultramafic rocks are endemic to New Caledonia, indicating strong adaptation (Lowry, 1998).

New Caledonia is considered a natural laboratory by naturalists ever since its discovery by James Cook in 1774. And as the knowledge about the biota of islands has increased, its originality has been confirmed (Morat, 1993). About 90 percent of all plant and animal species are endemic, indicating a high within-island speciation frequency and local adaptation to the many different microhabitats (Chazeau, 1993; Jaffré, 1992; Lowry, 1998).

The New Caledonian fauna has been far less studied than the flora and in 1993 more than 3200 phanerogam species had been recorded, and less than 4500 animal species, including everything from sponges to vertebrates, a clear underrepresentation compared to the situation in the rest of the world (Chazeau, 1993). The edaphic conditions together with spatial and temporary isolation have, however, also played a role in the composition of the fauna, with high endemism at the species and generic level for many arthropods, molluscs and reptiles (Bauer and Sadlier, 1993).

Previous studies on the effect of ultramafic rocks on faunal diversity and radiation have been almost entirely absent. A study on Lepidoptera, however, demonstrated that the species diversity is low in ultrabasic areas with high floral endemicity (Holloway, 1993). Haase and Bouchet (1998) found a species radiation of hydrobiid snails in a variety of habitats on ultrabasic rocks, and also observed that representatives of one clade avoid waters emerging from ultrabasic rocks. Murienne et al. (2008) in one of

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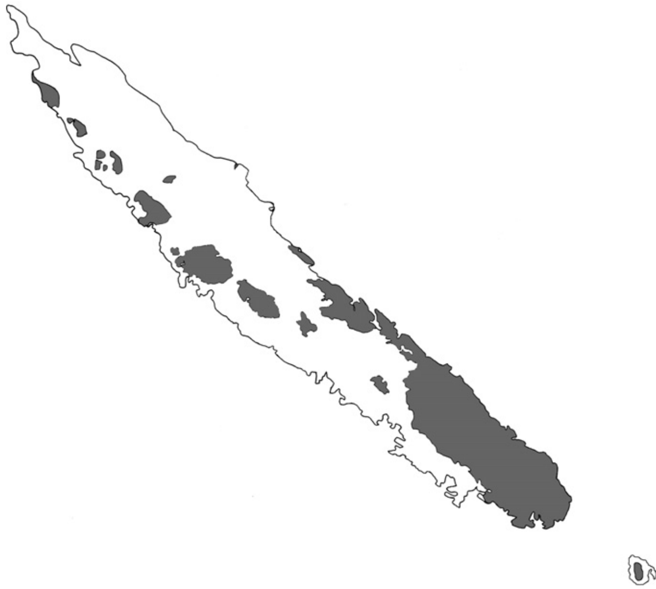

Fig. 1. The current distribution of ultrabasic rock (gray areas) on New Caledonia.

the few molecular phylogenetic studies of the New Caledonian fauna found no relationships between diversification in the genus and distribution on ultrabasic rocks when studying a genus of cockroaches.

Streams and rivers draining ultramafic rocks have high concentrations of heavy metals and water with a pH around 7.5 or higher is not uncommon (Trescases, 1974). These specialized conditions potentially affect the freshwater fauna, like caddisflies (Trichoptera). This order forms a moderately species-diverse group of holometabolous insects with around 13,000 described species in 45 families (Morse, 1999). So far 132 species are recorded from New Caledonia, all but two endemic. Fifty-eight more species are presently being described (Espeland and Johanson, 2007; Espeland and Johanson, in press; Johanson and Keijsner, 2008; Johanson and Ward, submitted; Malm and Johanson, 2007, 2008a,b; Oláh and Johanson, 2008) and more than 200 so far undescribed species are present in the collections at the Swedish Museum of Natural History. On the generic level, seven out of the 23 present genera are endemic. Trichoptera are integral parts of almost all fresh water communities (Resh and Rosenberg, 1984), and are diverse in terms of the microhabitats and trophic niches the species occupy (Mackay and Wiggins, 1979). Ecological diversity and general intolerance to pollution is argued to make the group excellent biological indicators of water quality (Rosenberg and Resh, 1993).

In this paper we test whether the diversification of Trichoptera on New Caledonia took place on ultrabasic or non-ultrabasic substrates. The organisms under study are the species of the genus *Xanthochorema* Kimmins, 1953 (Hydrobiosidae) which is endemic to New Caledonia and represented by nine described and one currently undescribed species, all of which the larvae are free-living predators. For this analysis we use information provided by a molecular phylogeny inferred from both mitochondrial and a nuclear marker, and historical biogeographic methods. The broad goal of our study of New Caledonian caddis flies is to develop a well-resolved phylogeny to allow us to address our specific biogeographical/ecological questions. Therefore, a critical step is to identify stable monophyletic groups. Using the monophyletic *Xanthochorema* clade, estimated scenarios of radiation are evaluated according to distributions.

2. Materials and methods

2.1. Sampling and specimens

All included taxa were collected in the years 2000–2006, except a few which were borrowed from the Illinois Natural History Survey (Table 1). Trichoptera were collected from 156 localities on New Caledonia and *Xanthochorema* was found on 40 of these. Maps of the distributions of the species are given in Fig. 2a–f. A central element for our analysis was the sampling along and on both sides of the ultramafic and non-ultramafic substrate border. Collecting methods were Malaise traps, light traps and sweep nets for adults and handpicking for larvae and pupae.

Specimens were stored in 80% alcohol and preserved at −20 °C. Vouchers and DNA extractions are deposited at the Entomology Department, Swedish Museum of Natural History. DNA was extracted from the abdomen in adult specimens or the right hind leg in larvae, using the Qiagen DNeasy Tissue Extraction kit (Qiagen Inc., Valencia, California) and gene regions were amplified with a polymerase chain reaction (PCR).

2.2. Molecular methods

Samples from all described species of *Xanthochorema* and of one undescribed species were included in the analysis. The closely related genera *Synchorema* (represented by *S. zygoneurum*), *Psilochorema* (represented by *P. leptoharpax)* and *Neurochorema* (Ward et al., 2004) were chosen as outgroups.

Four genes were sequenced for all taxa: the mitochondrial genes cytochrome oxidase I (COX1) (658 bp) and cytochrome oxidase II (COX2) (524 bp), the ribosomal gene 16S (480–520 bp) and the nuclear elongation factor-1a (EF1a) (1099 bp). These genes have successfully been used for phylogenetic analyses of Trichoptera (Johanson, 2007; Kjer et al., 2001, 2002; Malm and Johanson, 2008a). Some of the COX1 and 16S sequences are taken from Johanson (2007). The primers are listed in Table 2. COX1 primers are given in Folmer et al. (1994), the COX2 in Malm and Johanson (2008a), the 16S in Palumbi et al. (1991) and the EF1a primers are modified from Kjer et al. (2001) and from Whiting (2002). Sequences were complete for all taxa except for a few having between 1 and 20 missing bases at the 3′ end of EF1a, so all EF1a sequences were shortened to 1085 bp to avoid most missing data in the sequences.

In a separate analysis only COX1 and COX2 sequences from all available specimens of each species of *Xanthochorema* were included to determine the within species relationships. Only *Psilochorema leptoharpax* and *Neurochorema* sp. were used as outgroups in this analysis.

Loci were amplified using Ready-To-Go™ PCR Beads (Amersham Pharmacia Biotech, Piscataway, NJ). Reaction mixtures were heated to 95 °C for 5 min, followed by 40 cycles of 30 s at 95 °C, 30 s at a specific annealing temperature and 50 s at 72 °C, and then a final extension of 8 min at 72 °C. Annealing temperature was set to 54 °C for EF1a and to 50 °C for COX1, COX2 and 16S.

PCR products were visualized by ultraviolet light on an 0.8% agarose gel after electrophoresis and were purified using EZNA Cycle-Pure Kit (Omega Biotek). Gene regions were sequenced with the same primers as in the PCR's using the BigDye™ Terminator ver. 3.1 Cycle Sequencing Kit (Applied Biosystems). Each sequencing reaction ran for 96 °C (1 min) and then 25 cycles of 96 °C (30 s), 50 °C (15 s) and 60 °C (4 min). Sequencing reactions were purified using the DyeEx 96 kit (QIAGEN) and cycle sequencing reactions were run on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems).

Table 1
List of specimens with voucher codes, locality information and GenBank accession number

Species	Voucher	Coordinates, degrees south/east	Genbank Accession Nos.			
			16s	COI	COII	EF1α
Xanthochorema caledon	DR4	22.58633/167.47245	–	**AM902811**	**AM902913**	–
Xanthochorema caledon	DR9	22.58633/167.47245	–	**AM902816**	**AM902918**	–
Xanthochorema caledon	DR8	22.58633/167.47245	–	**AM902815**	**AM902917**	–
Xanthochorema caledon	DR7	22.58633/167.47245	–	**AM902814**	**AM902916**	–
Xanthochorema caledon	DR6	22.58633/167.47245	–	**AM902813**	**AM902915**	–
Xanthochorema caledon	DQ6	22.58633/167.47245	–	**AM902804**	**AM902906**	–
Xanthochorema caledon	DR5	22.58633/167.47245	–	**AM902812**	**AM902914**	–
Xanthochorema caledon	DR3	22.58633/167.47245	–	**AM902810**	**AM902912**	–
Xanthochorema caledon	DR2	22.58633/167.47245	–	**AM902808**	**AM902910**	–
Xanthochorema caledon	DR1	22.58633/167.47245	–	**AM902807**	**AM902909**	–
Xanthochorema caledon	DQ9	22.58633/167.47245	–	**AM902806**	**AM902908**	–
Xanthochorema caledon	DQ7	22.58633/167.47245	–	**AM902805**	**AM902907**	–
Xanthochorema caledon	S1	22.18288/166.50073	–	DQ485492	**AM902857**	–
Xanthochorema caledon	T8	22.18288/166.50490	–	DQ485506	**AM902872**	–
Xanthochorema caledon	S4	22.18365/166.50451	–	DQ485495	**AM902860**	–
Xanthochorema caledon	S6	22.18288/166.50245	–	DQ485497	**AM902862**	–
Xanthochorema caledon	AV6	22.18288/166.50490	–	**AM902794**	**AM902896**	–
Xanthochorema caledon	R2	22.18406/166.50383	–	DQ485484	**AM902849**	–
Xanthochorema caledon	R9	22.18288/166.50073	–	DQ485491	**AM902856**	–
Xanthochorema caledon	J8	22.18198/166.48637	–	DQ485488	**AM902825**	–
Xanthochorema caledon	O8	22.18288/166.50167	DQ480652	DQ485463	**AM902828**	**AM902753**
Xanthochorema caledon	P5	22.20593/166.67996	–	DQ485469	**AM902834**	–
Xanthochorema caledon	AI3	22.18447/166.50315	–	**AM902785**	**AM902821**	–
Xanthochorema caledon	DQ8	22.14158/166.67993	–	**AM902809**	**AM902911**	–
Xanthochorema caledon	U8	22.07473/166.33167	–	DQ485514	**AM902880**	–
Xanthochorema caledon	U4	22.18100/166.49220	–	DQ485511	**AM902877**	–
Xanthochorema caledon	U2	22.20593/166.67996	–	DQ485509	**AM902875**	–
Xanthochorema caledon	T9	21.64890/165.78075	–	DQ485507	**AM902873**	–
Xanthochorema caledon	T3	22.07473/166.33183	–	DQ485502	**AM902867**	–
Xanthochorema caledon	S2	22.18288/166.50073	–	DQ485493	**AM902858**	–
Xanthochorema caledon	R5	22.07473/166.33167	–	DQ485528	**AM902852**	–
Xanthochorema caledon	Q4	20.81739/165.22585	–	DQ485477	**AM902842**	–
Xanthochorema caledon	P8	22.18447/166.50315	–	DQ485472	**AM902837**	–
Xanthochorema caledon	P6	21.63863/165.85970	–	DQ485470	**AM902835**	–
Xanthochorema caledon	P4	20.71808/164.83213	–	DQ485468	**AM902833**	–
Xanthochorema caledon	P3	20.71808/164.83213	–	DQ485467	**AM902832**	–
Xanthochorema caledon	P2	22.03697/166.47610	DQ480670	DQ485466	**AM902831**	**AM902755**
Xanthochorema caledon	P1	22.18311/166.50564	–	DQ485465	**AM902830**	–
Xanthochorema caledon	O9	22.18288/166.50167	DQ480653	DQ485464	**AM902829**	**AM902754**
Xanthochorema caledon	AI4	22.18406/166.50383	–	**AM902786**	**AM902822**	–
Xanthochorema calcaratum	V8	22.03883/166.47675	–	DQ485519	**AM902884**	–
Xanthochorema calcaratum	W5	22.03455/166.47433	–	DQ485524	**AM902888**	–
Xanthochorema calcaratum	R3	22.03697/166.47610	DQ480667	DQ485485	**AM902850**	**AM902766**
Xanthochorema calcaratum	T5	22.03455/166.47433	–	DQ485504	**AM902869**	–
Xanthochorema calcaratum	W6	22.18365/166.50451	–	DQ485525	**AM902889**	–
Xanthochorema calcaratum	DQ3	22.20593/166.67996	–	**AM902802**	**AM902904**	–
Xanthochorema calcaratum	AV8	22.18288/166.50490	–	**AM902796**	**AM902898**	–
Xanthochorema calcaratum	AV9	22.18288/166.50490	–	**AM902797**	**AM902899**	–
Xanthochorema calcaratum	DQ4	22.20593/166.67996	–	**AM902803**	**AM902905**	–
Xanthochorema calcaratum	O7	22.18365/166.50451	DQ480669	DQ485462	**AM902827**	**AM902752**
Xanthochorema calcaratum	R4	22.03697/166.47610	DQ480668	DQ485486	**AM902851**	**AM902767**
Xanthochorema calcaratum	S3	22.03455/166.47433	–	DQ485494	**AM902859**	–
Xanthochorema calcaratum	V6	21.72688/166.10945	–	DQ485518	**AM902883**	–
Xanthochorema calcaratum	AU8	20.40000/164.53333	–	**AM902793**	**AM902895**	–
Xanthochorema celadon	J7	22.14158/166.67993	–	DQ485487	**AM902824**	–
Xanthochorema celadon	S5	22.26611/166.82483	–	DQ485496	**AM902861**	–
Xanthochorema celadon	P7	22.18447/166.50315	DQ480657	DQ485471	**AM902835**	**AM902756**
Xanthochorema celadon	R8	22.19045/166.71447	–	DQ485490	**AM902855**	–
Xanthochorema celadon	S9	22.26611/166.82483	–	DQ485500	**AM902865**	–
Xanthochorema celadon	U3	22.18100/166.49220	–	DQ485510	**AM902876**	–
Xanthochorema celadon	S7	21.73931/166.10015	–	DQ485498	**AM902863**	–
Xanthochorema celadon	U5	22.18100/166.49220	–	DQ485512	**AM902878**	–
Xanthochorema celadon	AI2	22.20593/166.67996	–	**AM902784**	**AM902820**	–
Xanthochorema celadon	Q9	22.20593/166.67996	DQ480664	DQ485482	**AM902847**	**AM902764**
Xanthochorema celadon	Q2	22.18103/166.84275	DQ480674	DQ485475	**AM902840**	**AM902759**
Xanthochorema celadon	S8	21.73931/166.10015	–	DQ485499	**AM902864**	–
Xanthochorema celadon	U7	22.07473/166.33167	–	**AM904698**	**AM902879**	–
Xanthochorema christinae	P9	22.03455/166.47433	DQ480672	DQ485483	**AM902838**	**AM902757**
Xanthochorema christinae	R1	22.12505/166.49832	DQ480665	DQ485473	**AM902848**	**AM902765**
Xanthochorema bifurcatum	Q6	22.20593/166.67996	DQ480661	DQ485479	**AM902844**	**AM902762**
Xanthochorema bifurcatum	T4	22.18311/166.50564	–	DQ485503	**AM902868**	–
Xanthochorema bifurcatum	U9	22.20593/166.67996	–	DQ485515	**AM902881**	–
Xanthochorema bifurcatum	W2	22.18288/166.50073	–	DQ485522	**AM902886**	–
Xanthochorema bifurcatum	J6	22.14158/166.67993	–	DQ485460	**AM902823**	–

Table 1 (*continued*)

Species	Voucher	Coordinates, degrees south/east	Genbank Accession Nos.			
			16s	COI	COII	EF1α
Xanthochorema bifurcatum	AW1	22.18288/166.50490	–	**AM902798**	**AM902900**	–
Xanthochorema bifurcatum	AV7	22.18288/166.50490	–	**AM902795**	**AM902897**	–
Xanthochorema bifurcatum	V1	22.17212/166.50873	–	DQ485516	**AM902882**	–
Xanthochorema bifurcatum	U1	22.18365/166.50451	–	DQ485508	**AM902874**	–
Xanthochorema bifurcatum	R7	22.07473/166.33183	DQ480677	DQ485489	**AM902854**	**AM902769**
Xanthochorema bifurcatum	AP2	21.62067/165.88290	–	**AM902791**	**AM902893**	–
Xanthochorema bifurcatum	AU7	20.40000/164.53333	–	**AM902792**	**AM902894**	–
Xanthochorema paniensis	DF6	20.58167/164.76472	**AM902782**	**AM902800**	**AM902902**	**AM902775**
Xanthochorema paniensis	DS3	20.58167/164.76472	–	**AM902819**	**AM902921**	–
Xanthochorema paniensis	DS2	20.58167/164.76472	–	**AM902818**	**AM902920**	–
Xanthochorema paniensis	DS1	20.58167/164.76472	–	**AM902817**	**AM902919**	–
Xanthochorema paniensis	DF7	20.58167/164.76472	**AM902783**	**AM902801**	**AM902903**	**AM902776**
Xanthochorema neocaledonia	O1	21.61635/165.85257	**AM902777**	**AM902787**	**AM902826**	**AM902751**
Xanthochorema nathaliae	Q1	22.12480/166.46723	**AM904700**	**AM904699**	**AM902839**	**AM902758**
Xanthochorema nathaliae	W7	22.07530/166.27653	–	DQ485526	**AM902890**	–
Xanthochorema nathaliae	T1	22.07530/166.27653	DQ480689	DQ485501	**AM902866**	**AM902770**
Xanthochorema nathaliae	V9	22.18198/166.48637	–	DQ485520	**AM902885**	–
Xanthochorema nathaliae	Q7	22.20908/166.67076	–	DQ485480	**AM902846**	–
Xanthochorema nathaliae	R6	21.12457/165.11302	DQ480676	DQ485527	**AM902853**	**AM902768**
Xanthochorema johnwardi	Q3	21.92097/166.33158	DQ480675	DQ485476	**AM902841**	**AM902760**
Xanthochorema johnwardi	Q8	22.12505/166.49832	DQ480663	DQ485481	**AM902846**	**AM902763**
Xanthochorema johnwardi	Q5	22.12505/166.49832	DQ480660	DQ485478	**AM902843**	**AM902761**
Xanthochorema johnwardi	T6	22.13907/166.50245	–	DQ485595	**AM902870**	–
Xanthochorema sp.n.	T7	22.16552/166.87558	**AM902778**	**AM902788**	**AM902871**	**AM902771**
Psilochorema leptoharpax	AO1	39.20000/176.61667	**AM902780**	**AM902790**	**AM902892**	**AM902773**
Neurochorema sp.	AN9	38.61667/176.23333	**AM902779**	**AM902789**	**AM902891**	**AM902772**
Synchorema zygoneurum	BY5	42.48333/172.56667	**AM902781**	**AM902799**	**AM902901**	**AM902774**

New sequences in the present study in bold.

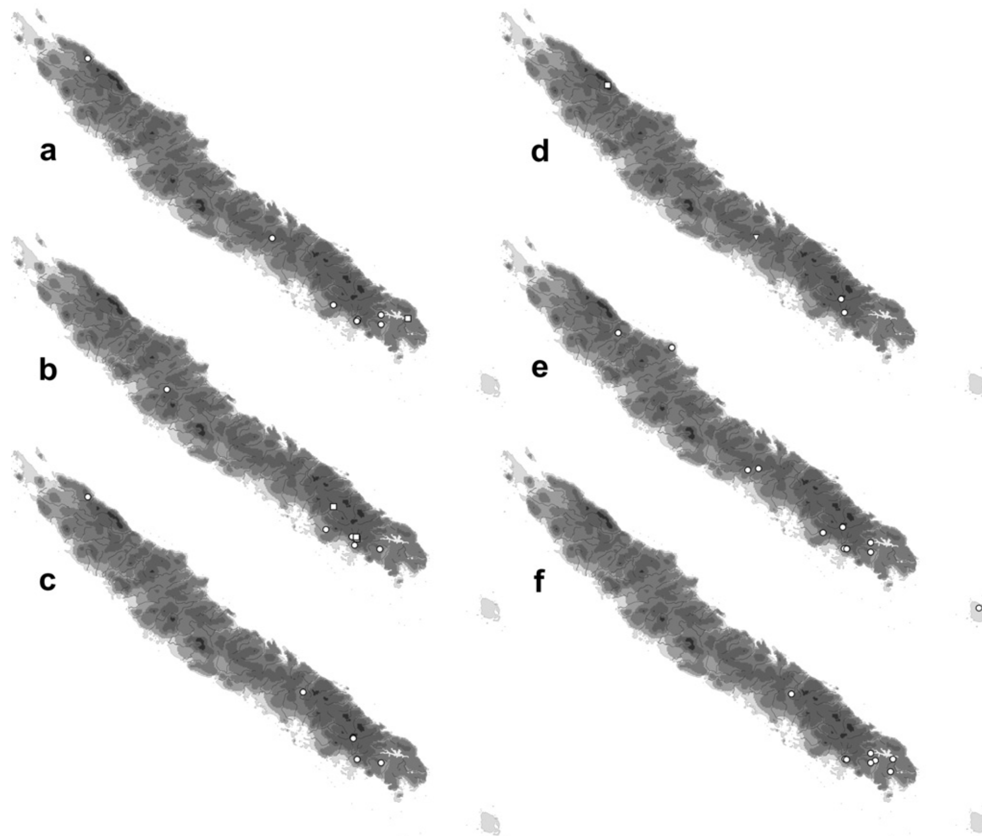

Fig. 2. Distribution maps of the New Caledonian endemic *Xanthochorema*: (a) *X. bifurcatum* (circles), *X.* sp.n. (square), (b) *X. nathaliae* (circles), *X. johnwardi* (squares), (c) *X. calcaratum*, (d) *X. christinae* (circles), *X. paniensis* (squares), *X. neocaledonia* (triangle), (e) *X. caledon*, (f) *X. celadon*.

Table 2
Primers used in this study

Gene	Primer	Reference
16s	ARL (f) 5′-CGC CTG TTT ATC AAA AAC AT-3′	Palumbi et al. (1991)
	BRH (r) 5′-CCG GTC TGA ACT CAG ATC ACG T-3′	Palumbi et al. (1991)
COI	LCO1490 (f) 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′	Folmer et al. (1994)
	HCO2198 (r) 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′	Folmer et al. (1994)
COII	LeptoF (f) 5′-AGA TCN TCY CCW ATW ATA GAA C-3′	Malm and Johanson (2008a)
	LeptoR (r) 5′-CCA CAA ATT TCW GAR CAT TGN CC-3′	Malm and Johanson (2008a)
EF1a	Ef1aF (f) 5′-ATC GAG AAG TTC GAG AAR GAR GC-3′	Kjer et al. (2001)
	Ef1a IntR (r) 5′-CCA YCC CTT GAA CCA NGG CAT-3′	Kjer et al. (2001) (modified)
	EF M46-1 (f) 5′-GAG GAA ATY AAR AAG GAA G-3′	Whiting (2002)
	Ef1aR (r) 5′-GGG AAY TCC TGG AAR GAY TC-3′	Kjer et al. (2001)

Raw sequence data and contigs were viewed and assembled using the Pregap4 and Gap4 modules of the Staden package (Staden et al., 1998). Forward and reverse primers were used to sequence each region in both directions, and EF1a was amplified in two overlapping regions. Primer sequences were removed from the beginning of each sequence and sequence data were checked for accuracy by matching forward and reverse sequences for each gene region. The 16S sequences were aligned using in the L-INS-I strategy in MAFFT v. 6 (Katoh et al., 2005). The alignment of COX1, COX2 and EF1a were trivial since they were length invariant.

2.3. Phylogenetic reconstruction

The datasets for the four separate genes were analyzed separate and combined. An equally weighted parsimony analysis was performed with TNT (Goloboff et al., 2004). Heuristic searches were performed using 2000 random addition sequence replicates with tree bisection–reconnection (TBR) branch swapping, 10 trees held at each step during stepwise addition, gaps treated as missing, and branches collapsed if maximum branch length was zero. Jackknifing (Farris et al., 1996) with 2000 replicates and a deletion

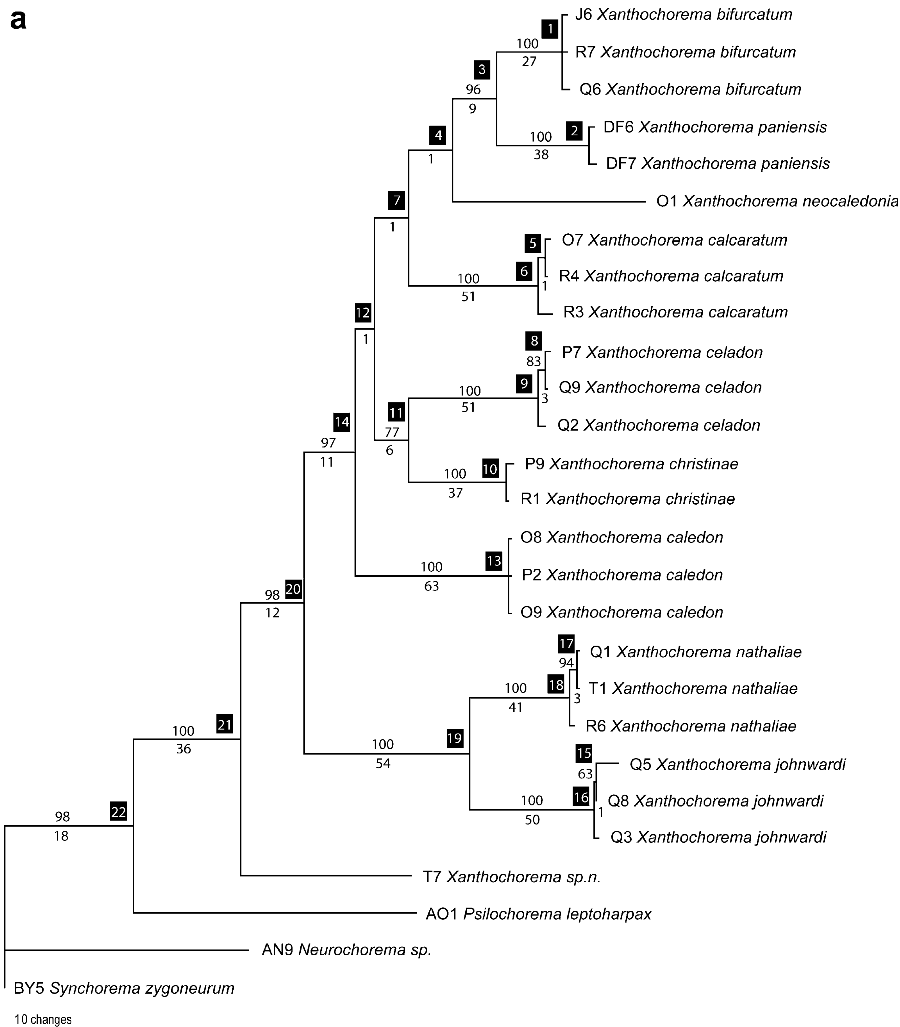

Fig. 3. Phylogenies obtained when combining all genes. (a) Strict consensus of the two most parsimonious trees. Jackknife support values are shown above the branches and Bremer support below. Numbers in black squares are node numbers used for the partitioned Bremer support in Table 3. (b) Fifty percent majority rule tree representing the trees obtained in the Bayesian analysis with posterior probabilities above the branches.

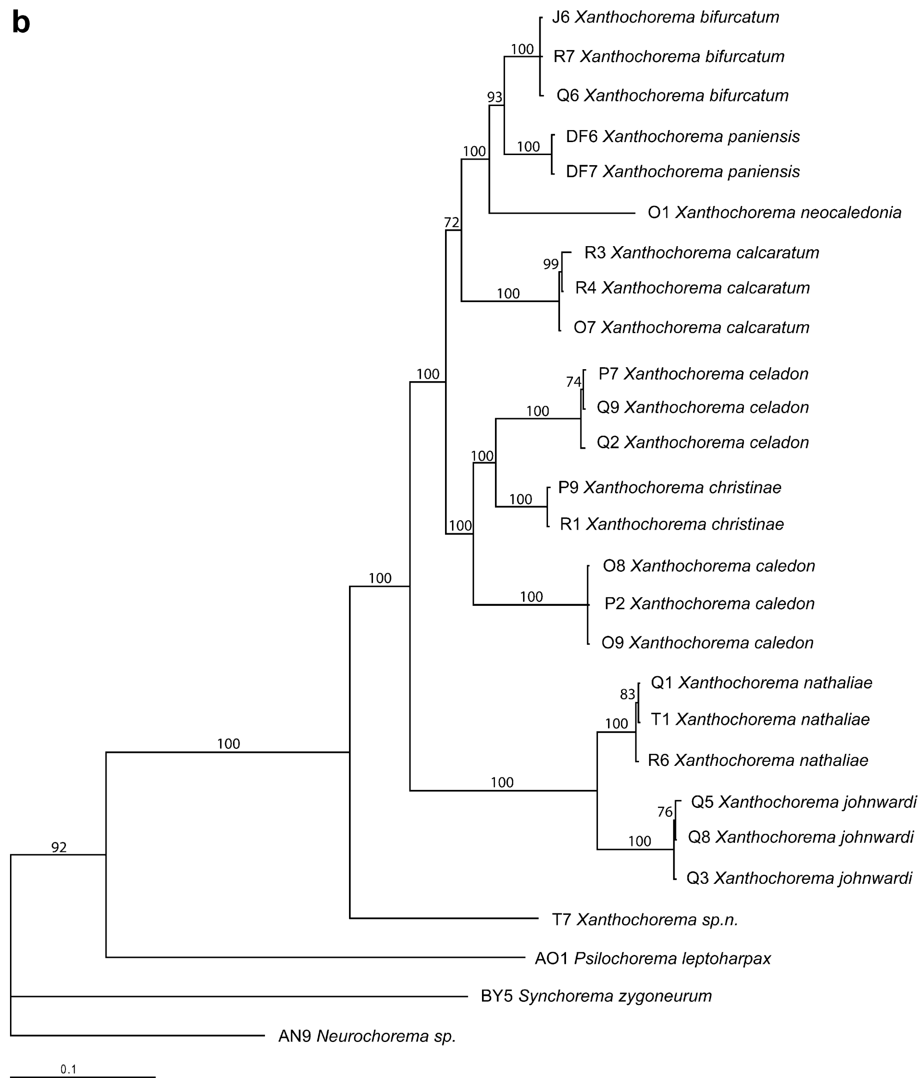

Fig. 3 (*continued*)

probability for each character of 36% and with results shown as GC values, and Bremer support, BS, (Bremer, 1988) were used for evaluating nodal support. In addition partitioned Bremer support, PBS (Baker and De Salle, 1997) was implemented as a support measurement, and also as a measurement of character conflicts between the partitions (genes) for each clade. PBS values for each partition were standardized by dividing them by the number of parsimony informative sites for each partition. All support statistics were calculated with TNT.

To further evaluate group stability, a Bayesian analysis was performed using MrBayes2.2 (Huelsenbeck and Ronquist, 2001) for both the combined dataset and separate datasets. The best model of substitution for all separate partitions (genes) was determined using the AIC criterion (Akaike information criterion, Akaike, 1974) in MrModeltest v. 2 (Nylander, 2004) and this model was incorporated in the Bayesian analysis. When analyzing the combined dataset the partitions were unlinked allowing each partition to have its own set of parameters and each partition was allowed to evolve with different rates under a flat Dirichlet prior. All analyses were performed with random starting trees without constraints. Four Markov chains were run simultaneously for 2,000,000 generations with sampling every 1000 generations to ensure independence of samples. The first 25% of sampled trees were discarded as burnin. The analysis was repeated three times to ensure that final trees converged on the same topology. Groups

Table 3
Partitioned Bremer support (PBS) for the phylogenetic tree in Fig. 4a

Node No.	16s	COX1	COX2	EF1a	Total PBS	Total BS
1	1.0	14.0	8.0	4.0	27	27
2	2.0	16.0	16.0	4.0	38	38
3	3.0	3.0	2.0	1.0	9	8
4	−1.0	3.0	−2.0	1.0	1	1
5	0.0	2.0	0.0	−1.0	1	1
6	5.0	27.0	13.5	5.5	51	52
7	−1.0	3.0	−2.0	1.0	1	1
8	0.0	1.0	1.0	0.0	2	2
9	6.5	26.0	8.5	10.0	51	50
10	0.0	24.0	7.0	5.0	36	36
11	−1.3	7.7	−2.7	2.3	6	5
12	−1.0	3.0	−2.0	1.0	1	1
13	6.0	28.0	15.5	13.5	63	62
14	0.0	6.0	−2.0	7.0	11	11
15	0.0	0.0	0.0	1.0	1	1
16	5.0	31.0	7.0	7.0	50	50
17	0.0	2.0	1.0	0.0	3	3
18	4.5	19.5	14.0	3.0	41	40
19	7.0	8.0	12.0	27.0	54	56
20	3.0	−4.0	4.0	9.0	12	12
21	7.0	6.0	5.0	18.0	36	34
22	7.0	4.0	1.0	6.0	18	19
Sum	52.7	230.2	104.8	125.3	510	510
Standardized	0.64	1.17	0.72	0.85		

Total BS is Bremer support calculated without partitioning the data.

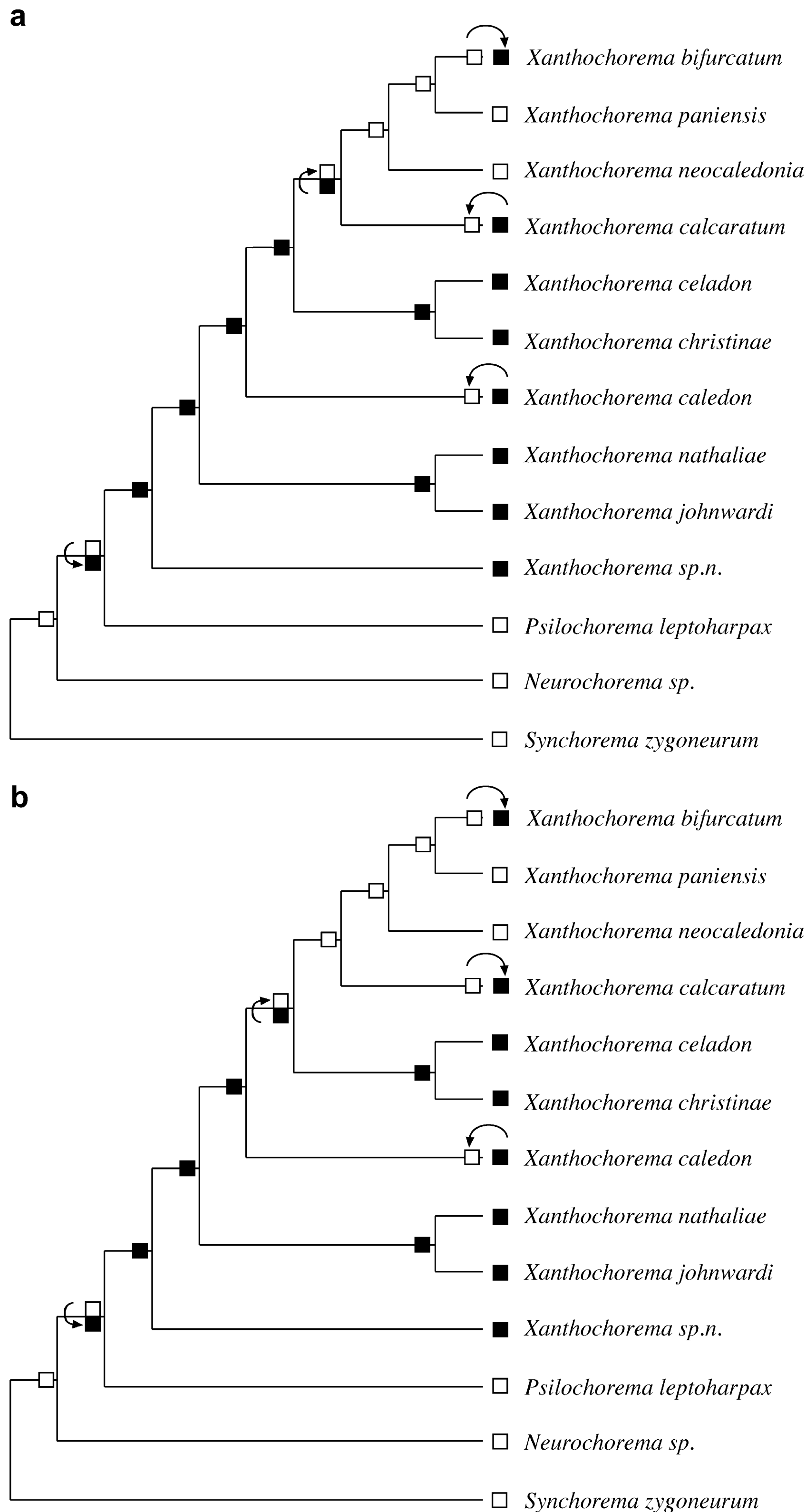

Fig. 4. Two most parsimonious reconstructions (models) of the association of ancestral species of *Xanthochorema* to ultrabasic or non-ultrabasic substrates on New Caledonia. The reconstructions are based on results given by dispersal–vicariance analyses in DIVA 1.1 (Ronquist, 1996) with all species being considered unique, separate units. Black and white boxes indicate presence on ultrabasic and non-ultrabasic substrate, respectively. Arrows indicate dispersal routes within species.

receiving high support in both the parsimony and Bayesian analyses were considered stable.

To associate specimens to species and study internal relationships within the *Xanthochorma* species an equally weighted parsimony analysis combining COX1 and COX2 for all available specimens of all species was performed, including the two most closely related genera *Psilochorema* and *Neurochorema* as outgroups. The analysis was constrained to use the topology obtained

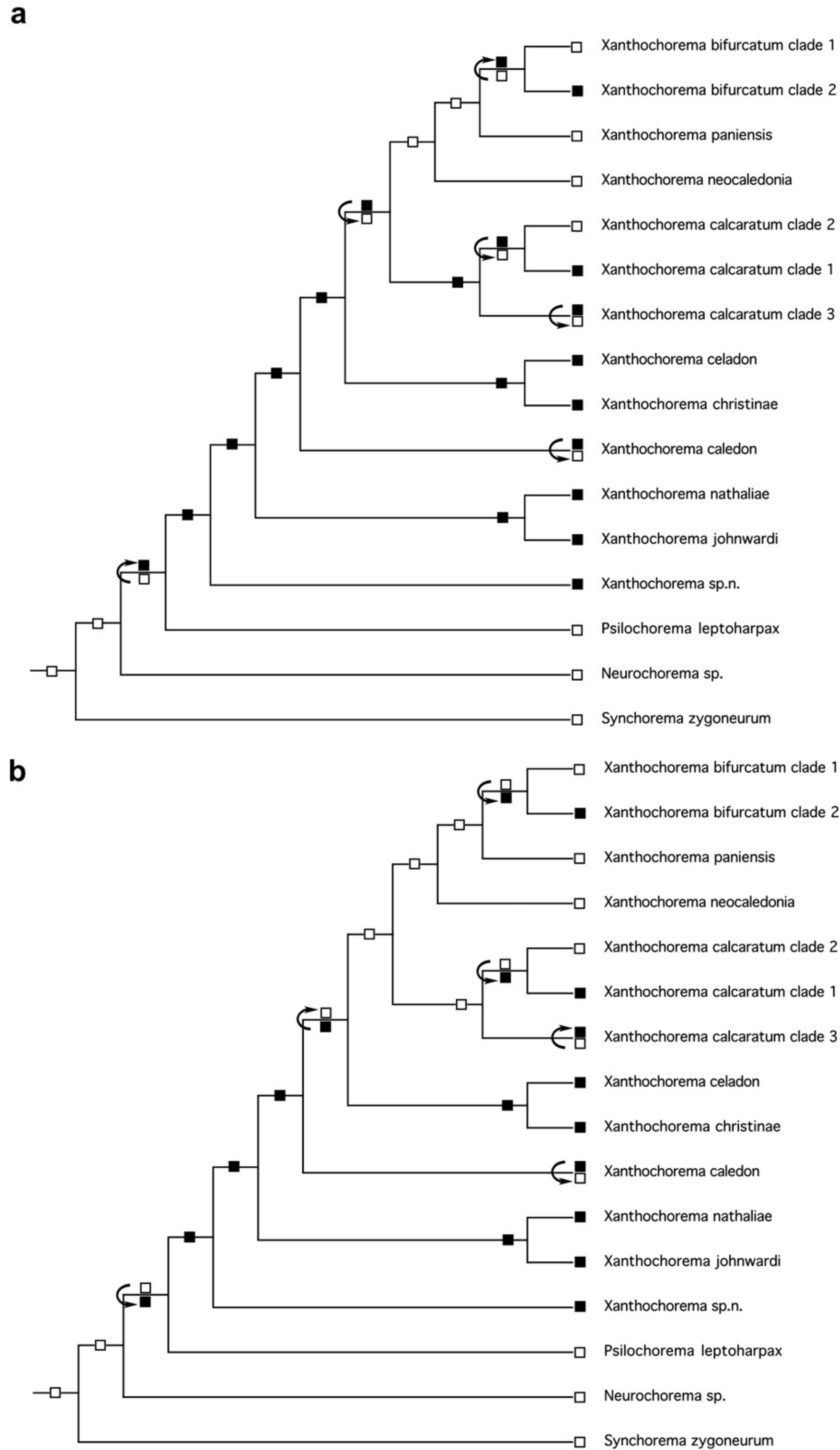

Fig. 5. Two most parsimonious reconstructions (models) of the association of ancestral species of *Xanthochorema* to ultrabasic or non-ultrabasic substrates on New Caledonia. The reconstructions are based on results given by dispersal–vicariance analyses in DIVA 1.1 (Ronquist, 1996) with all intraspecific monophyletic groups having unique substrate association considered unique, separate units. Black and white boxes indicate presence on ultrabasic and non-ultrabasic substrate, respectively. Arrows indicate dispersal routes within species.

in the parsimony and Bayesian analyses with all four genes (above), since COX1 and COX2 have too high levels of homoplasy to alone give a credible between-species phylogeny (Lin and Danforth, 2004).

Because of the short branches between individuals within species, the Bayesian runs never converged sufficiently and the Bayesian analysis was not used for internal relationships.

2.4. Analyzing distribution patterns

Analysis of the historical distribution of *Xanthochorema* on ultrabasic and non-ultrabasic substrates was executed in two different ways. First, a cost-matrix optimization to reconstruct the history of associations (Ronquist and Nylin, 1990) is implemented in DIVA 1.1 (Ronquist, 1996) and was used for hypothesizing ancestral distributions. Second, tracing the history of substrate association, 'tracing distributions', was performed with ultrabasic and non-ultrabasic distributions mapped on the terminal taxa in a fully resolved phylogenetic tree in MacClade 4.08 (Maddison and Maddison, 2005).

A commonly applied method for analyzing biogeographical patterns is event-based methods first adopted for co-evolutionary studies (Page, 1995). The four typical elements in event-based biogeographical and co-evolutionary analyses are vicariance, dispersal, extinction, and sympatric/allopatric speciation. A cost-matrix, as originally developed for host–parasite associations and event-based biogeographical analyses, implements different costs to the four events: 1, allopatric/sympatric speciation (cost 0); 2, dispersal (cost 1); 3, extinction (cost 1); and 4, vicariance (cost 0) (Ronquist, 1996). In this analysis, dispersal to new types of substrate and extinction from a particular substrate has a cost of 1 and sympatric speciation and vicariance associated with a particular substrate has no cost. The default software setting was applied, involving maxareas = 2 due to a presence of only two available areas in the distribution block. A model for the association of *Xanthochorema* species ancestors' to ultrabasic or non-ultrabasic substrate was generated from the results of the dispersal–vicariance analysis in DIVA with 'substrates' instead of 'areas' or 'host'.

The 'tracing distributions' approach has methodological limitations, i.e. the analysis rejects widespread ancestors and requires speciation subsequent to dispersal (Ronquist, 1996). Equivocal internal distributions can be resolved by applying either accelerated (ACCTRAN) or delayed (DELTRAN) transformations of characters, but at present there are no available criteria for choosing between these two transformation options. Rejecting widespread ancestors is a serious weakness because widespread distributions are initial steps of vicariance. Despite the drawbacks of the 'tracing distributions' approach the method has relevance in the analysis of *Xanthochorema* biogeography because ultrabasic and non-ultrabasic substrates are not strictly biogeographical entities, but rather adaptive ecological traits like those of morphological characteristics, which are frequently examined using identical methods.

3. Results

3.1. Phylogenetic analyses

MAFFT inserted between 13 and 19 gaps into the ingroup 16s sequences and between 6 and 15 in the outgroup sequences. Eight of the gaps in the ingroup sequences were caused by an unambiguous insertion in one of the outgroups (AN9 *Neurochorema* sp.).

The combined dataset yields 2801 characters of which 564 (20%) are parsimony informative. The parsimony analysis gives two most parsimonious trees (L = 1674) which differs only internally within *X. bifurcatum*. The strict consensus tree is given in Fig. 3a. The result is principally identical to the result from the Bayesian analysis (Fig. 3b, GTR + I + G model for all partitions), except for the placement of *X. caledon*, and both trees are very well supported for most nodes. *Xanthochorema* is monophyletic in all analyses, except in the separate parsimony analysis of COX2 where the outgroup *Psilochorema leptoharpax* appears within *Xanthochorema*. All *Xanthochorema* species are monophyletic in all analyses.

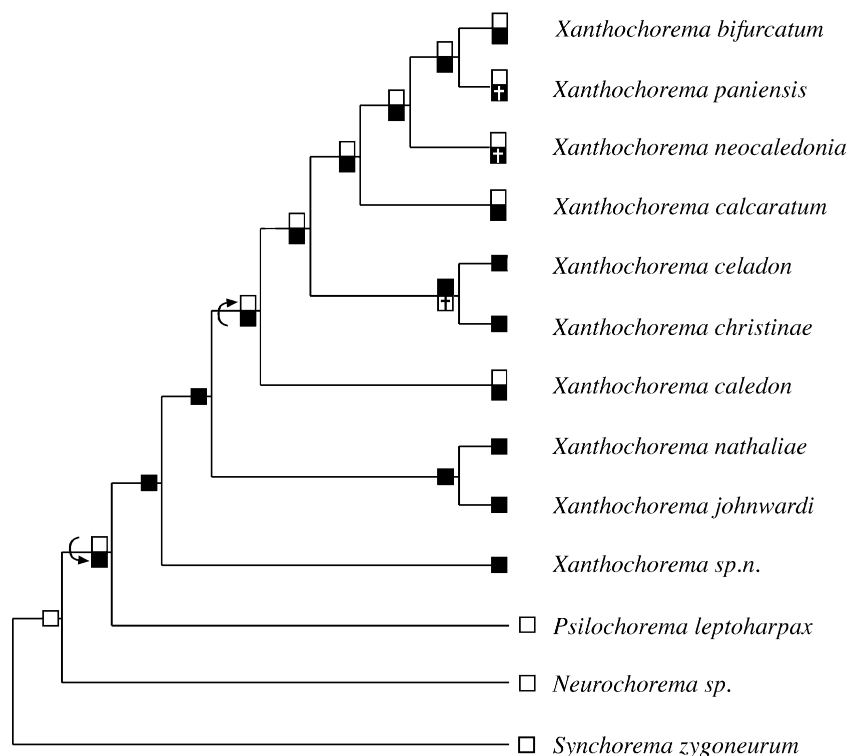

Fig. 6. One out of multiple possible most parsimonious reconstructions (models) of the ancestral association of *Xanthochorema* species to ultrabasic or non-ultrabasic substrates on New Caledonia, with extinctions considered equally parsimonious as dispersals. The cladogram is based on findings in DIVA 1.1 (Ronquist, 1996), except with extinctions added and dispersals removed manually. Black and white boxes indicate presence on ultrabasic and non-ultrabasic substrate, respectively, and white crosses on black background indicate extinction from ultrabasic substrates and black cross on white background indicates extinction from non-ultrabasic substrate. Arrows indicate dispersal routes within species.

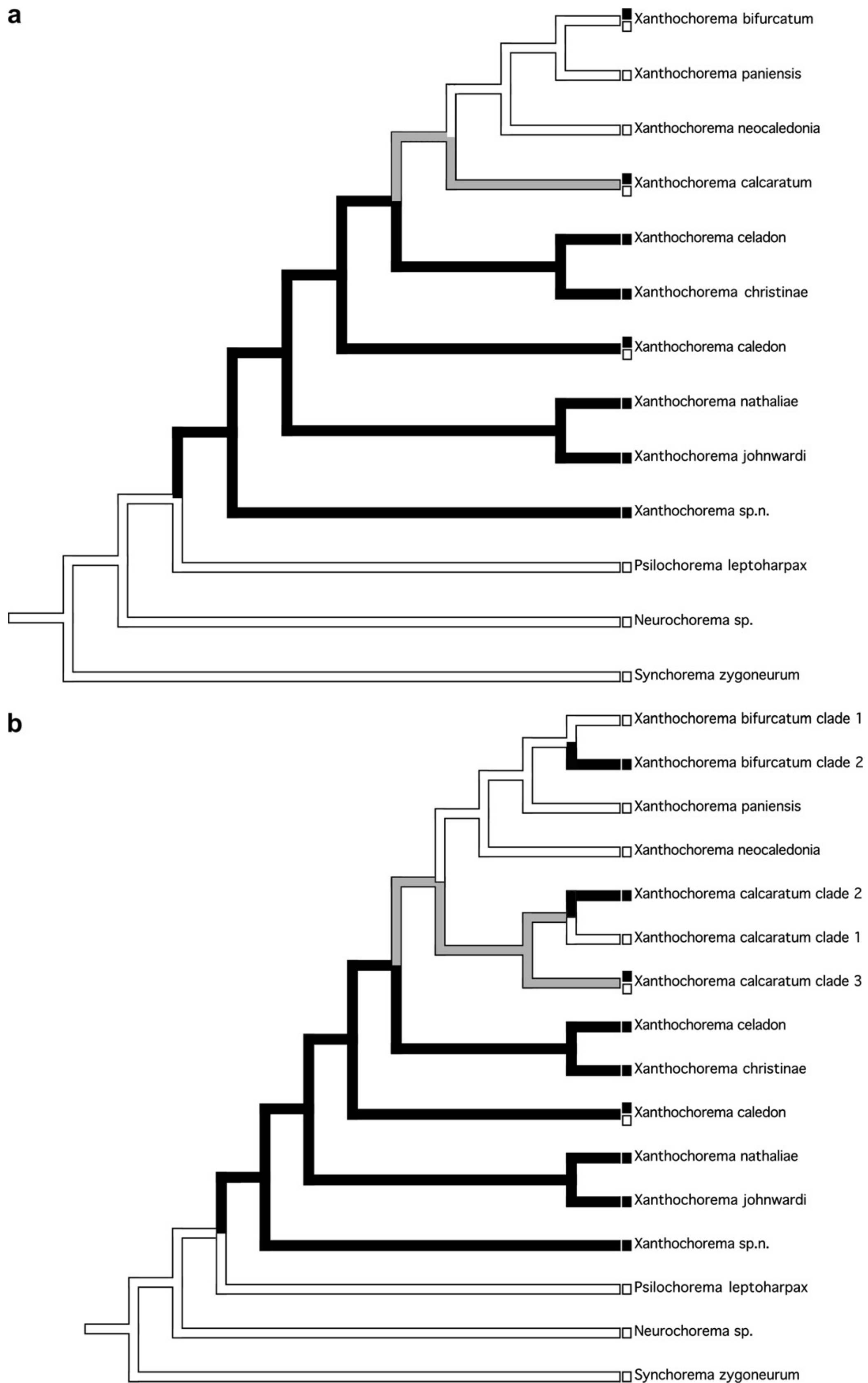

Fig. 7. Tracing ancestral distributions of New Caledonian *Xanthochorema* generated by the 'tracing characters' option in MacClade 4.08 (Maddison and Maddison, 2005). Black branches and boxes indicate presence on ultrabasic substrate and white branches and boxes indicate presence on non-ultrabasic substrate. Gray branches indicate equivocal distributions that can be resolved by applying either accelerated (ACCTRAN) or delayed (DELTRAN) transformations of the distribution changes: (a) shows widespread descendants as species, (b) shows most of the widespread descendants divided into monophyletic populations.

The tree topology resulting from separate analysis of EF1a is broadly congruent with the tree topology from the combined analysis. Separate analysis of 16S and COX2 gives quite unresolved trees and COX1 results in a resolved tree that to some extent differ from the combined result (not shown). The PBS (Table 3) values for all partitions give positive support for most nodes in the combined analysis, that is, the individual genes support the clades in the combined topology when combined with each other (Table 3). The tree obtained from analyzing the combined dataset (maximum parsimony) is used in further analyses.

The analysis of combined COX1 and COX2 on all individuals was constrained to the topology obtained in the combined analysis, and gave 501 most parsimonious trees with (L = 971) (not shown), which is ten steps longer than the unconstrained trees. It is mainly unresolved within species relationships, but some clades are discernable, e.g. two clades; one entirely ultrabasic and one entirely non-ultrabasic clade, where found in both *X. bifurcatum* and *X. calcaratum*.

3.2. Ancestral substrate association

3.2.1. DIVA

Based on the trees from the phylogenetic analysis (Fig. 3a and b) the association of species to a particular substrate is indicated in Figs. 4–7 where open squares represent presence on non-ultrabasic substrate, and black squares represent presence on ultrabasic substrate. In Fig. 6 extinctions from ultrabasic or non-ultrabasic substrates are shown as white cross on black background and black cross on white background, respectively. A combination of the squares indicates presence on both substrate types. Arrows indicate dispersal routes. When treating each species as a single unit the DIVA analysis resulted in 2 equally parsimonious ancestral reconstructions, both characterized by 5 independent dispersals (Fig. 4a and b; Table 4). The only differences between the two most parsimonious histories are the position of a widespread ancestor within *Xanthochorema*, and the single following dispersal due to the position of that widespread ancestor.

In both alternative models the ancestor to all *Xanthochorema* species was restricted to ultrabasic substrates. The earliest speciations within *Xanthochorema* were confined to ultrabasic substrate and resulted in 6 or 7 extant species, the exact number varying between the two resulting models. Of these speciations, and varying between the two resulting models, one or two extant species dispersed to non-ultrabasic substrates after speciation. The ancestor to *X. bifurcatum*–*X. christinae* or the ancestor to *X. bifurcatum*–*X. calcaratum* also dispersed to non-ultrabasic substrates. This dispersal was followed by speciation on non-ultrabasic substrates, with one or two subsequent dispersals of extant species to ultrabasic substrates after speciation.

The two models (Fig. 4a and b) differ in minor elements. In the first model (4a) the ancestor to *X. bifurcatum*–*X. calcaratum* is present on both substrates. This species separated into the ancestor to *X. bifurcatum*–*neocaledonia* present on non-ultrabasic substrate, and *X. calcaratum* present on ultrabasic substrate but which dispersed into non-ultrabasic substrate after speciation. A second species, *X. bifurcatum*, also dispersed into ultrabasic substrate after speciation. *Xanthochorema calcaratum*, oppositely, dispersed into non-ultrabasic substrate subsequent to speciation.

In the second model (4b) the ancestor to *X. bifurcatum*–*X. christinae* is present on both substrates. This species subsequently split into the ancestor of *X. celadon* + *X. christinae* restricted to ultrabasic substrate, and into the ancestor to *X. bifurcatum*–*X. calcaratum* present on non-ultrabasic substrates. In this model, both extant species *X. bifurcatum* and *X. calcaratum* dispersed into ultrabasic substrates after speciation.

We tested the effect of applying maximally resolved phylogenies within species instead of consider each species a single unit by expanding the input tree for DIVA to a level where as many as possible of the terminal taxa have resolved distributions, i.e. minimum number of widespread terminal taxa. The widespread *X. bifurcatum* was divided into two monophyletic groups, one present on ultrabasic and the other present on non-ultrabasic substrate. The widespread *X. calcaratum* was divided into three monophyletic groups, one group confined to ultrabasic, one group to non-ultrabasic and a third group widespread on both substrates. *Xanthochorema caledon* has a basally unresolved phylogeny, and was impossible to divide further, and was kept as widespread in the analysis. The analysis left two equally most parsimonious ancestral distribution patterns (Fig. 5a and b; Table 5) involving six independent dispersals due to an extra dispersal event within *X. calcaratum* in both results. Except for this, the ancestral distribution patterns are identical with those from the reduced cladogram

Table 4

Number of ancestors and terminal taxa exclusively on ultrabasic and non-ultrabasic substrate, and number of dispersals from ultrabasic to non-ultrabasic substrates, and *vice versa*

Model No.	Ancestral taxa on ultrabasic	Ancestral taxa on non-ultrabasic	Terminal taxa initially on ultrabasic substrate	Terminal taxa initially on non-ultrabasic substrate	No. dispersals from ultrabasic to non-ultrabasic	No. dispersals from non-ultrabasic to ultrabasic
Model 1 (Fig. 4a)	**7**	3	**7**	3	**3**	1
Model 2 (Fig. 4b)	**6**	4	**6**	4	**2**	**2**

The figures are from the result of the dispersal–vicariance analysis when each terminal taxa represent a species.
The bold figures symbolize the most frequent alternative of two competing patterns.
The table illustrates that there are more ancestral and terminal taxa confined to ultrabasic substrate.
It is also demonstrated that in model 1 there are three dispersals from ultrabasic to non-ultrabasic substrates and only one dispersal from non-ultrabasic to ultrabasic substrate; in model to the dispersals from ultrabasic 2 non-ultrabasic substrates and *vice versa* are equally frequent.

Table 5

Number of ancestors and terminal taxa exclusively on ultrabasic and non-ultrabasic substrate, and number of dispersals from ultrabasic to non-ultrabasic substrates, and *vice versa*

Model No.	Ancestral taxa on ultrabasic	Ancestral taxa on non-ultrabasic	Terminal taxa initially on ultrabasic substrate	Terminal taxa initially on non-ultrabasic substrate	No. dispersals from ultrabasic to non-ultrabasic	No. dispersals from non-ultrabasic to ultrabasic
Model 1 (Fig. 5a)	**10**	5	**9**	4	**4**	1
Model 2 (Fig. 5b)	**8**	7	**8**	5	2	**3**

The figures are from the result of the dispersal–vicariance analysis when each widespread terminal taxa are divided into monophyletic clades when possible.
The bold figures symbolize the most frequent alternative of two competing patterns.
The table illustrates that there are more ancestral and terminal taxa confined to ultrabasic substrate.
It is also demonstrated that in model 1 there are four dispersals from ultrabasic to non-ultrabasic substrates and only one dispersal from non-ultrabasic to ultrabasic substrate; in model 2 there are more dispersals from non-ultrabasic to ultrabasic substrates than the opposite way.

in Fig. 4a and b. The identical results between the expanded and simple ancestral area trees are probably due to the small number of clades actually available for resolving the species' ancestral state of the widespread species.

Several additional equally most parsimonious solutions are found by manual examination of the distribution pattern after sympatric speciation of widespread species followed by extinction from one of the two substrates were considered. Extinctions are not given by the DIVA program as alternatives to dispersal–vicariance events (Ronquist, 1996) even when present in the cost-matrix. The tree models of sympatric/allopatric speciation followed by extinctions are equally parsimonious as trees based on dispersal and vicariance alone, with a total cost of 5 when applied to the simple ancestral area trees (Fig. 6). One of the additional equally most parsimonious solutions (Fig. 6) involves two dispersals identical with the dispersals near the root of the tree as in Fig. 4b. Maximum three extinctions are observed, one within the ancestor to *X. celadon* and *X. christinae* that became extinct from non-ultrabasic substrates; and one extinction from ultrabasic substrates within the extant *X. paniensis* and *X. neocaledonia*.

3.3. Tracing distributions

The two different resolutions of the phylogeny of *Xanthochorema*, *sensu* Figs. 4 and 5, form the basis for tracing distributions analysis and are shown in Fig. 7a and b where presence on non-ultrabasic substrate is indicated as white branches and boxes, ultrabasic substrate as black branches and boxes, and uncertain (equivocal) substrate as gray branches. The equivocal branches become black or white if the DELTRAN or ACCTRAN is applied, respectively. The resulting trees clearly demonstrate that the ancestral *Xanthochorema* was adapted to and was present exclusively on ultrabasic substrate. The six most basal species evolved within the ultrabasic substrate, with a subsequent dispersal into non-ultrabasic substrate only in *X. caledon*. The ancestor to *X. calcaratum* developed either on ultrabasic or non-ultrabasic substrate. The ancestor to *X. bifurcatum*–*X. neocaledonia* was able to disperse into non-ultrabasic areas before further speciation took place exclusively on non-ultrabasic substrate. Finally, a single clade of *X. bifurcatum* irreversibly dispersed back into ultrabasic substrate.

4. Discussion

4.1. Phylogeny

The phylogeny obtained when using the combined dataset is mostly well supported and congruent between methods (i.e. parsimony and Bayesian). The PBS shows that even though the different genes alone produce different phylogenies, when analyzed together they support the combined phylogeny. The mitochondrial genes have too high heterogeneity in among-site rate variation and thus higher saturation rate, to be able to give a trustworthy lower level relationship on their own (Lin and Danforth, 2004), but are very good in assigning the different specimens to species. COX1, as expected contributes much to the total BS in the combined analysis, even though high homoplasy is indicated when COX1 is analyzed alone. The nuclear gene, EF1a, does well when determining the relationships between species, and is also quite applicable in delimiting the species, but the individual species receive slightly lower BS when using EF1a than when using mitochondrial genes. This reflects the slower mutation rate within EF1a than within mitochondrial genes, and corresponds to the findings of e.g. Lin and Danforth (2004) that nuclear genes generally do better than mitochondrial genes when inferring phylogenetic relationships on a deeper level in insects.

4.2. Distributions and ultrabasic rocks

Six, alternatively seven ancestral species of *Xanthochorema* were confined to ultrabasic substrates (Tables 4 and 5). In addition, six alternatively seven of the ten extant species developed on ultrabasic substrate (Tables 4 and 5). All of the species confined to ultrabasic substrates were found to represent the earlier part of the *Xanthochorema* history, while the species also or exclusively found on non-ultrabasic substrate developed later. The ability to survive on both substrate types was retained throughout the evolution of the clade, involving two extinctions from ultrabasic substrates in *X. paniensis* and *X. neocaledonia*, and one extinction from non-ultrabasic substrates in the ancestor to *X. celadon* + *X. christinae*.

It has been demonstrated that the closest sistergroups to *Xanthochorema* are *Neurochorema* and *Psilochorema* (Ward et al., 2004), both endemic to New Zealand. In DIVA a premise is that speciations are associated with vicariance and not dispersal. For New Caledonia this might be a reasonable premise as the island is of Gondwanan origin and might have shared faunas with other Gondwana fragments previous to final isolation from New Zealand 30-40 MYA (Walley and Ross, 1991). However, as the age of *Xanthochorema* is unknown, ancestral *Xanthochorema* might have become isolated from its New Zealand sister population's dispersal after New Caledonia and New Zealand separated.

Adaptation to ultrabasic substrates can have developed instantly after dispersal from New Zealand as indicated in the results from the 'tracing distributions' analyses. However, ultrabasic deposits are also present in a narrow band along the northern part of the Alpine fault, at the northernmost part of New Zealand South Island (Molnar et al., 1999), but the closest relatives to *Xanthochorema* are widely distributed across New Zealand (Ward, personal communication), and nothing indicates that the ultrabasic deposits had anything to do with the adaption of the ancestor of *Xanthochorema* to this kind of substrate.

Our findings demonstrate that radiation on non-ultrabasic substrate took place later than the radiation on ultrabasic substrate. This corresponds to the findings by Guillon (1969, 1975), Guillon and Routhier (1971) and Trescases (1969, 1975) that ultrabasic substrate once covered extensive areas on Grande Terre before gradually eroded to its present distribution. Early speciation apparently took place on this widely distributed ultrabasic substrate before exposed non-ultrabasic substrate allowed subsequent radiation. This hypothesis has also been proposed by De Kok (2002) for some plant genera.

Trichoptera has often been used as biological indicators for water quality because of their ecological diversity and intolerance to pollution (Rosenberg and Resh, 1993). The water in streams and rivers on ultrabasic rock substrate with its high heavy metal concentration can be seen as naturally polluted. This study shows that the ancestor of *Xanthochorema* has adapted quickly to these conditions, questioning the use of caddisflies as bio indicators for water quality at genus level, at least when it comes to inorganic pollution. On species level, however, our findings strongly demonstrate that certain species tolerate toxic conditions while others do not.

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