Supporting Information

Hao and Palmer 10.1073/pnas.0908766106

SI Text

Analysis of Chloroplast Donor Sequences. Following upon the second paragraph of *Discussion*, we elaborate on potential false-negative (this paragraph) and false-positive (next paragraph) results that may stem from the use of the angiosperm chloroplast consensus sequence in the recombination-detection method developed for and used in this study. The chloroplast region embedded within the *Apodanthes* mitochondrial *atp1* gene shows a noteworthy pattern of variation relative to this consensus sequence. Excluding its historically ambiguous 5′-most 15 NTs, the 79-bp conversion tract breaks down rather neatly into 3 regions with respect to the chloroplast consensus. Two regions, the 14-NT tract at positions 957–970 and the 34-NT tract at 987-1020, each with all 7 chloroplast signatures for the region, are separated by a 10-NT tract (at 975–984) that lacks 3 of the 4 chloroplast consensus signatures and instead possesses the mitochondrial consensus sequence at these 3 positions. There are a variety of possible explanations for this pattern, some involving additional transfer events (from either chloroplast or mitochondrial genes). Most likely, however, is some combination of nucleotide sequence divergence in this region in both the donor chloroplast gene and, following the conversion event, in the *Apodanthes* mitochondrial gene. With respect to the latter, note that *Apodanthes* mitochondrial genes have highly elevated rates of synonymous substitutions (1). It is thus not unlikely that 1 or more of the 3 sites may have mutated/converged to the mitochondrial consensus sequence following chloroplast conversion. With respect to the former, note that these 3 aberrant NTs are, as shown in Fig. S2*C*, located at *the* most poorly conserved 3 positions among the 120 positions included in Fig. 2*B*. Moreover, *atpA* genes from a large and disparate number of chloroplast lineages have the angiosperm mitochondrial consensus sequence at 2 of these 3 sites. Thus, it is not unlikely that the ultimate chloroplast donor to *Apodanthes atp1* carried with it the mitochondrial rather than chloroplast consensus at 1 or more of the 3 sites in question. If such a donor engaged in a more typically short-patch conversion event that were centered on the 3 NTs in question, then such a conversion would probably go undetected using the approach used in this study.

As noted obliquely in the first section of *Discussion* (paragraph 2, sentence 3), the use of the angiosperm *atpA* chloroplast consensus sequence to fix 1 of the 3 sequences used in all comparisons also poses the risk of yielding false positives. This would occur if a particular mitochondrial *atp1* sequence happened by chance to somehow "converge" on the chloroplast consensus sequence despite the donor *atpA* sequence being somewhat divergent from that consensus. We do not, however, see any evidence for such behavior in our data. More importantly, this possibility can be effectively ruled out for those 4 putative conversion lineages for which chloroplast sequences are available from the same or relatively closely related plants. This is because in all 4 cases, the listed *atpA* gene is identical to the putative recombinant *atp1* gene throughout the region in question. The 4 cases are *Passiflora suberosa* (for which an *atpA* sequence is available from *P. biflora*), *Ranunculus* sp. (*R. macranthus*), the large Lamiales group (*Jasminum nudiflorum*), and *Myrtus communis* (*Oenothera biennis*).

Alternative Explanations for the Findings of This Study. Here we consider potential alternative molecular mechanisms, experimental artefacts, or selective pressures that could theoretically produce some or all of the 9 cases of putative chloroplast/mitochondrial gene conversion inferred in this study. First, we consider RNA editing and retroprocessing. Six of the 8 putative conversion sites shown in Fig. 2*A* for the Lamiales represent C-to-T changes, while a significant number of the sites highlighted in the figure for the other 4 lineages of putatively chimeric genes are also C-to-T changes. Primary transcripts from angiosperm mitochondrial protein genes typically undergo high levels of C-to-U RNA editing (i.e., a significant fraction of sites that are C in the gene and primary transcript are converted to U in the functional mRNA; refs. 2 and 3). It is thus formally possible that the suite of changes highlighted in Fig. 2*A* results from recurrent mitochondrial retroprocessing (i.e., gene conversion of the mitochondrial *atp1* gene by its edited mRNA) rather than chloroplast conversion. Retroprocessing can, however, be ruled out because none of the 10 diverse angiosperms for which *atp1* cDNA sequences are known are edited at any but the last of the 6 relevant C residues (4, 5).

In vitro recombination between mitochondrial and chloroplast copies of *atp1* in the course of PCR amplification could also, in theory, produce the types of putatively chimeric sequences uncovered in this study. This possibility can be ruled out for 2 reasons. First, for 8 of the 9 chimeric lineages (all but *Apodanthes*), mitochondrial *atp1* was sequenced directly from uncloned PCR product; it is extraordinarily unlikely that an inevitably rare chloroplast/mitochondrial recombinant could somehow rise to such dominance in PCR product that it would be the major if not sole sequence detected in the sequence traces resulting from direct DNA sequencing of the PCR product. Second, for 3 of the 9 chimeric lineages the chimeric sequence has been reproducibly obtained from 2 or more members of the lineage (i.e., Lamiales, *Empetrum*/*Rhododendron*/*Vaccinium* from the Ericales, and *Clethra* from the Ericales; see Fig. 2), while for *Cynomorium* the same sequence was obtained from 2 different amplifications of the same template DNA (T. Barkman, personal communication).

DNA contamination or misidentification—a constant source of worry in those cases of putative horizontal gene transfer in which an additional, nonchimeric copy of a gene is apparently acquired by the recipient genome—cannot be a *primary* issue in the present study. This is because contamination alone could not produce these findings, i.e., some *additional* factor, either biological such as the 2 discussed in this section or artefactual such as PCR recombination (see preceding paragraph), would also have to be involved. Contamination is potentially an issue only secondarily—and only for the 6 cases where the chimeric sequence has not yet been validated by amplification from an independent DNA sample (either identical or closely related to the one examined thus far)—in the sense that 1 or more of these single-DNA cases could reflect contamination with DNA from some other plant, which itself has a mitochondrial *atp1* gene of chloroplast chimeric origin. Note, however, that any such cases of contamination are unlikely to reduce the number of inferred cases of chloroplast conversion (and/or mitochondrial horizontal transfer), because no pair of the 6 cases shown in Fig. 2*A* (or of the 3 shown in Fig. 2*B*) have identical conversion tracts.

Finally, intense, highly directional purifying selection could in theory lead to convergent, independent evolution of short motifs within homologous, but distantly related genes toward similar or even identical sequences. For 3 reasons, this formal possibility can be entirely dismissed in the present case. First, such unusual, convergent selective pressures in the case of a gene pair such as *atp1*/*atpA* that has long since saturated at the level of synony-

mous substitutions should lead to similarity/identity at the amino acid but not nucleotide level. Exactly the opposite pattern is seen here (compare Figs. 2*A* and 2*B* with Fig. S5*A* and *B*, respectively). Second, it is hard to imagine why such acute, convergent selective pressures should be felt only sporadically across the phylogeny of angiosperm mitochondrial *atp1* genes. Third, and related, such convergent point-mutational pressures should produce a phylogenetic record in which lineages experiencing this hard-to-imagine sporadic pressure exhibit a more-or-less gradual accumulation of directional substitutions toward the chloroplast sequence in the region in question. Instead, however, within the limits of current taxon sampling, all 9 converted groups show a sharp, entirely or nearly all-or-nothing pattern; by and large, mitochondrial *atp1* genes either have the chloroplast conversion tract or they do not. Only minor traces (i.e., involving but a single NT in all but 1 case) of possible intermediates are apparent for some of the 9 converted lineages (these are all evident in Fig. 2*A*).

Possible Spread of the Chloroplast Conversion Tract in Parasitic Angiosperms via Mitochondrial Horizontal Gene Transfer. Most relevant, for 2 reasons, to the possibility (see second section of *Discussion*) of a chloroplast-derived conversion tract spreading via mitochondrial-to-mitochondrial horizontal gene transfer are the 2 cases reported here involving nonphotosynthetic, parasitic angiosperms, i.e., *Apodanthes* and *Cynomorium*. First, the mitochondrial genomes of parasitic angiosperms have an apparent propensity for acquiring (often from their host plants) foreign mitochondrial genes by horizontal transfer (4, 6, 7). Second, although no studies have yet examined these 2 parasitic lineages to see whether they still possess plastid *atpA* genes, or even plastid genomes at all, what is known about plastid genomes in other nonphosynthetic, parasitic angiosperms (8–10) strongly suggests that the *Apodanthes* and *Cynomorium* plastids no longer harbor *atpA*. These 2 observations emphasize the possibility (especially for *Apodanthes*, whose close relative *Pilostyles* lacks a chloroplast conversion tract; Fig. 2*B*) that one or both parasitic genera acquired their chloroplast conversion tract indirectly, via mitochondrial horizontal transfer. On the other hand, it is still entirely possible that the mitochondrial lineages of these parasites acquired *atpA* directly, via intracellular transfer, in a photosynthetic ancestor of the parasites. If so, the conversion event in *Apodanthes* must have happened millions of years after the transfer event, following the loss of photosynthesis and the divergence of *Apodanthes* and *Pilostyles* from a common ancestor.

Mitochondrial Provenance and Copy Number of Chimeric *atp1* Genes. The strongest evidence for a mitochondrial provenance of the chimeric *atp1* genes comes from the only complete mitochondrial genome sequence available for any members of the 9 chimeric clades. The sequence of *atp1* from the mitochondrial genome sequence of *Digitalis purpurea* (J. P. Mower and J. D. Palmer, unpublished results), in the Lamiales (Fig. 2*A*), is identical to the published, PCR-generated sequence of *Digitalis* used in this study. Indirect evidence for a mitochondrial location of the other chimeric *atp1* genes is of 2 types. First, apart from the chimeric region itself, these genes generally show the highly conserved properties expected for genes located in the generally low-mutation-rate environment of the mitochondrial genome, as opposed to genes transferred to the plant nuclear genome, where the synonymous substitution rate is usually 10–100 times higher [refs. 1 and 11–13; the only exception relevant to this study is *Apodanthes* (see ref. 1 and *SI Text Analysis of Chloroplast Donor Sequences*, whose apparently mitochondrial-genomewide elevation in synonymous substitutions rates is evident throughout its mitochondrial *atp1* gene)]. Second, all of the abundant evidence available indicates that *atp1* belongs to that class of plant mitochondrial genes that are very rarely, if ever, functionally transferred to the nucleus (14). Given all of the above, and the absolute essentiality of the gene, it is highly likely both that *atp1* is functional in all these plants and that the functional *atp1* gene resides in the mitochondrial genome. Furthermore, the possibility that the putatively chimeric and mitochondrial copy of *atp1* in these plants is not itself functional, and that instead there is a second, functional copy of the gene in the mitochondrial genome, is very unlikely for multiple reasons. First, if a second, different copy of *atp1* were present in the high-copy-number environment of the mitochondrial genome, then it should have been PCR amplified just as readily as the chimeric copy, yet there is no indication that any of the PCR-product sequencing traces were suggestive of such evenly mixed products (only for *Citrus* do we know that the PCR product gave a mixed sequence, of chimeric and nonchimeric *atp1* read, but with the dominant signal in the sequencing traces being the chimeric type; T. Barkman, personal communication). Second, taxa representing 6 of the 9 chimeric lineages (all but *Apodanthes*, *Cynomorium*, and *Myrtus*) were included in the Southern blot survey of ref. 14; recent reinspection of the original X-ray films indicates that there is very likely to be only a single, full-length, conserved *atp1* gene in the mitochondrial genome for most of these 6 lineages. And for those cases where the blotting patterns are consistent with 2 "copies" of *atp1* being present in the mitochondrial genome, the 2 copies could readily be identical (plant mitochondrial genomes almost always possess large, often gene-containing, identical repeats; ref. 15), or, if there is a second, nonchimeric copy, it could be a pseudogene. Furthermore, the sequenced mitochondrial genome of *Digitalis* (Lamiales) indisputably contains only a single intact copy of *atp1*, with this gene identical, as noted above, to the PCR sequence for *Digitalis atp1* used in this study.

Functionality of Chimeric *atp1* Genes—Evidence of Transcription. To our knowledge, none of the putatively chimeric mitochondrial *atp1* genes have been deliberately assayed (e.g., by sequencing RT-PCR products or by Northern blots) for evidence of in vivo transcriptional activity. However, for 2 members (*Mimulus guttatus* and *Salvia fruticosa*) of the Lamiales clade of chimeric genes (see Fig. 2*A*), multiple (6 and 9) *atp1* EST clones were recovered. The existence of such multiple EST clones and their preferential location at the 3′ end of the gene (Fig. S6) are consistent with the clones being derived from bona fide transcripts. In addition, 28 *atp1* EST clones are present among libraries made from 3 species of *Citrus*, while 64 *atp1* clones were identified in an EST library from *Vaccinium corymbosum*.

Sources of the Topologies Shown in Fig. 2. For Fig. 2*A*, the Lamiales et al. topology is from ref. 16 (relationships among the species with the chloroplast-derived segment are deliberately shown unresolved), the Ericales topology is from ref. 17, the *Passiflora* et al. topology is from ref. 18, and the *Cynomorium* et al. topology is from ref. 19. For Fig. 2*B*, the *Apodanthes* et al. topology is from ref. 7, the *Ranunculus* et al. topology is from ref. 20, and the *Myrtus* et al. topology is from ref. 21.

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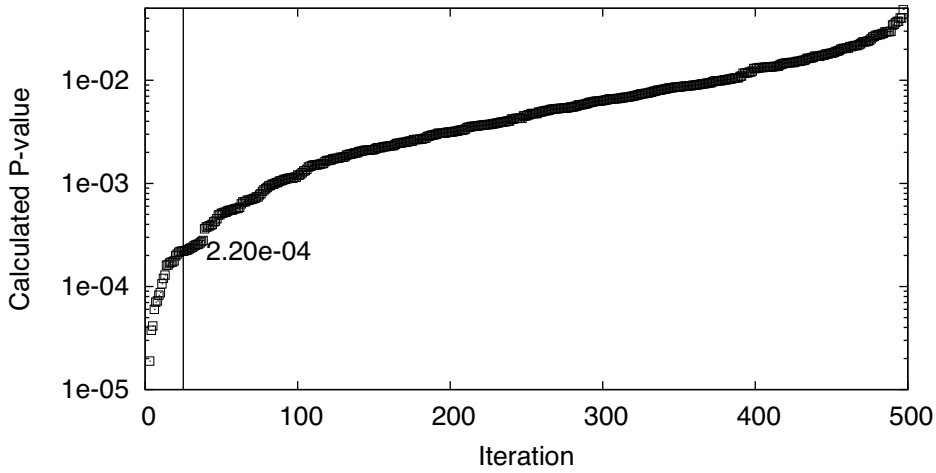

Fig. S1. Simulated distribution of calculated *P*-values using the consensus of angiosperm mitochondrial *atp1* genes in the analysis. The 5% critical value (2.2×10^{-4}) of the calculated *P*-values was used to determine significance (Table 2).

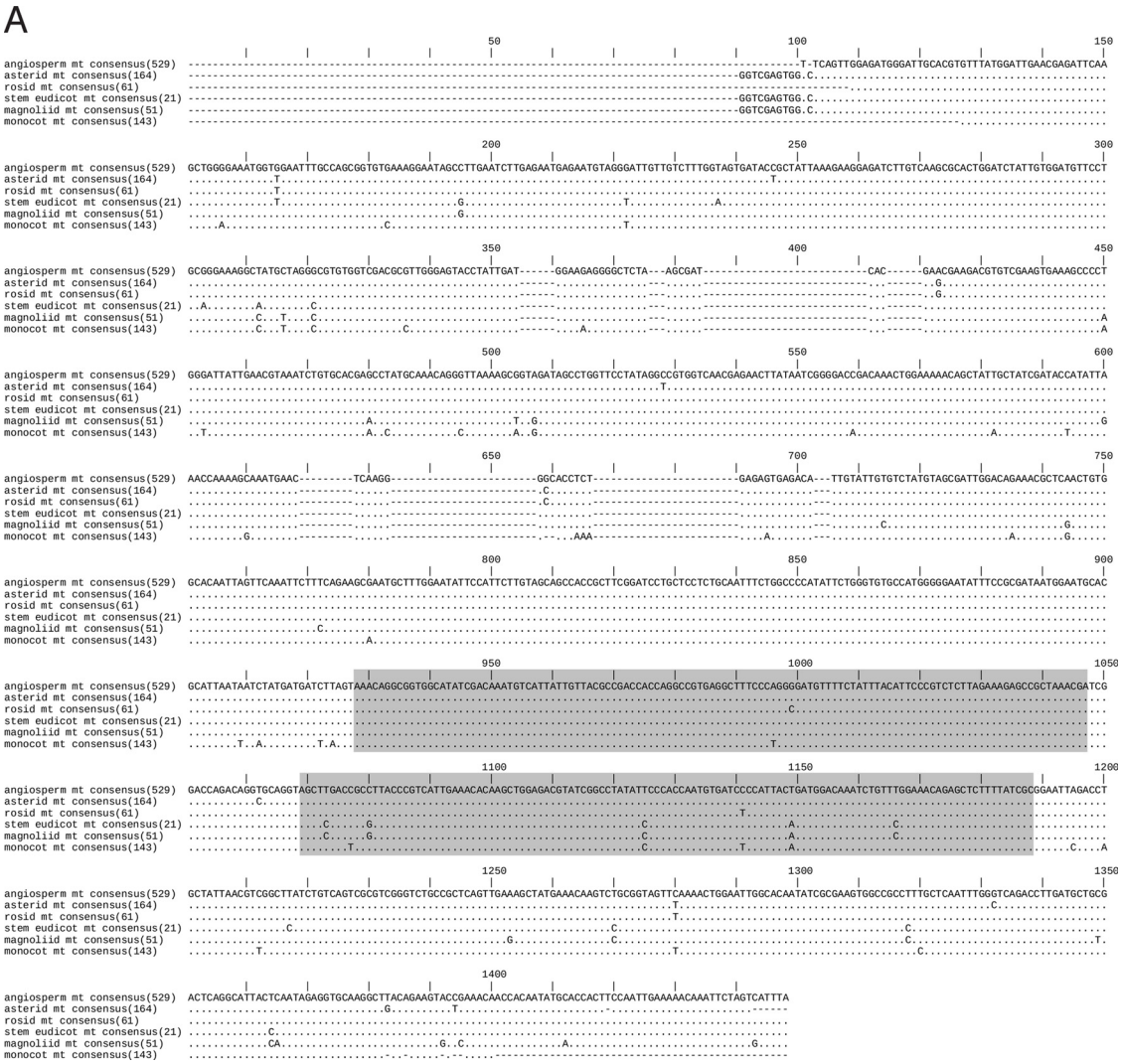

Fig. S2. Consensus sequences used in this study. Fig. S2 *A* and *B* are the full-length consensus sequences for mitochondrial *atp1* and chloroplast *atpA*, respectively, for all angiosperms and for 5 subgroups of angiosperms. The number of sequences used to generate each consensus is shown in parentheses. Gaps at the end of the alignment were removed, while internal gaps and gaps at the beginning of the alignment were retained to keep the NT coordinates consistent across all relevant figures. Regions shown in Fig. 2 are shaded in gray. Fig. S2C shows histograms displaying the frequency with which the predominant NT occurs at each position for both the angiosperm chloroplast and mitochondrial consensus sequences across the regions shown in Fig. 2 (the *Top* and *Bottom* figures correspond to the regions shown in Figs. 2*B* and 2*A*, respectively). The NTs given below each histogram correspond to deviations in the angiosperm chloroplast consensus sequence from the angiosperm mitochondrial consensus (see Fig. 2).

B

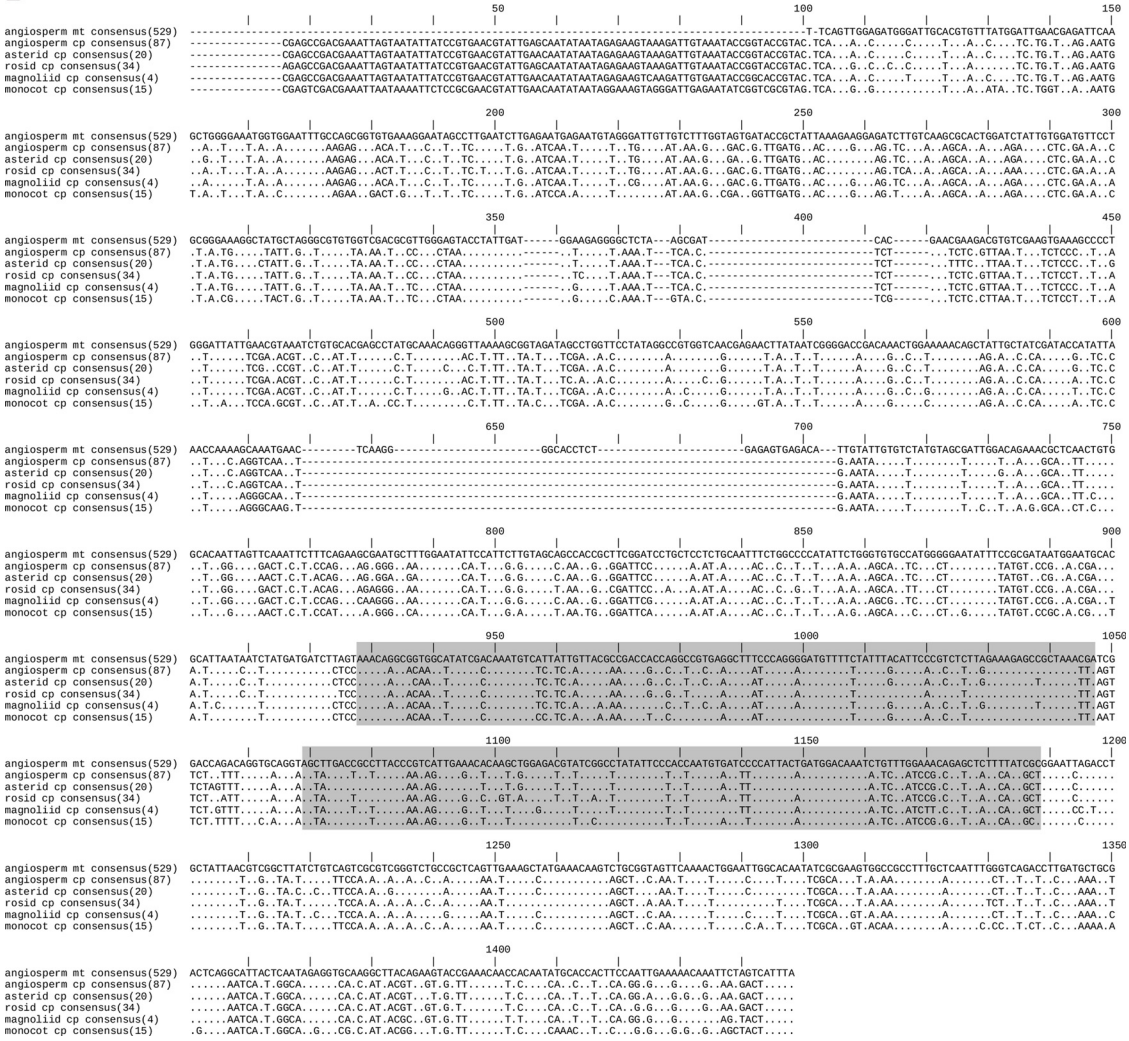

Fig. S2 (continued).

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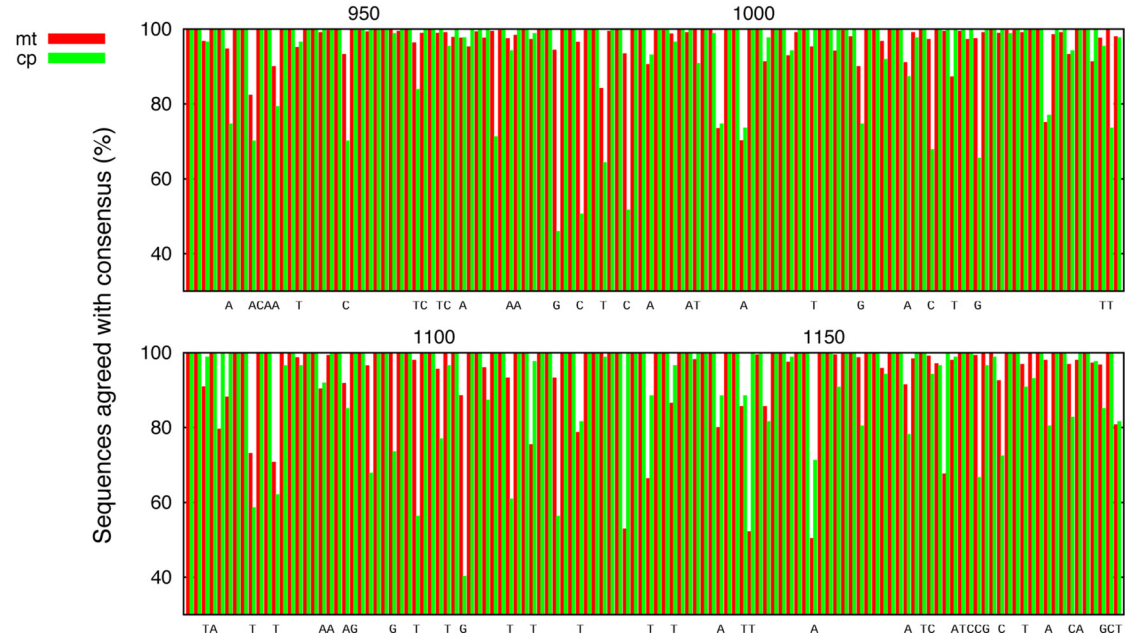

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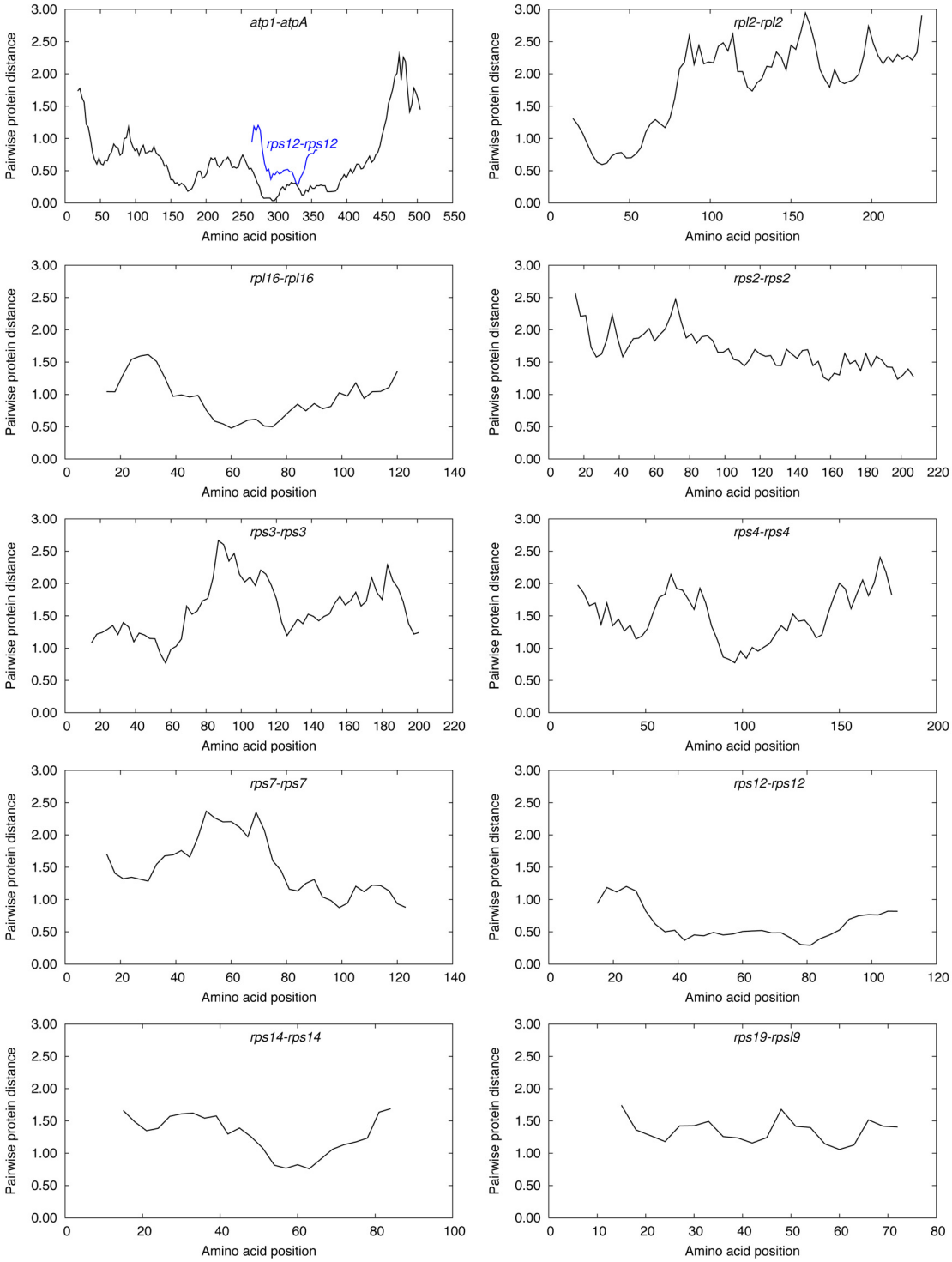


Fig. S3. Protein conservation in 20 protein-coding genes present in both mitochondria and chloroplasts. The plots used a sliding window of 30 aa, slid 3 aa at a time, and with each window labeled according to the amino acid falling in the middle. The *y* axis corresponds to the estimated number of substitutions/changes per site, with protein distance measured using the JTT matrix. All gaps were removed before analysis.

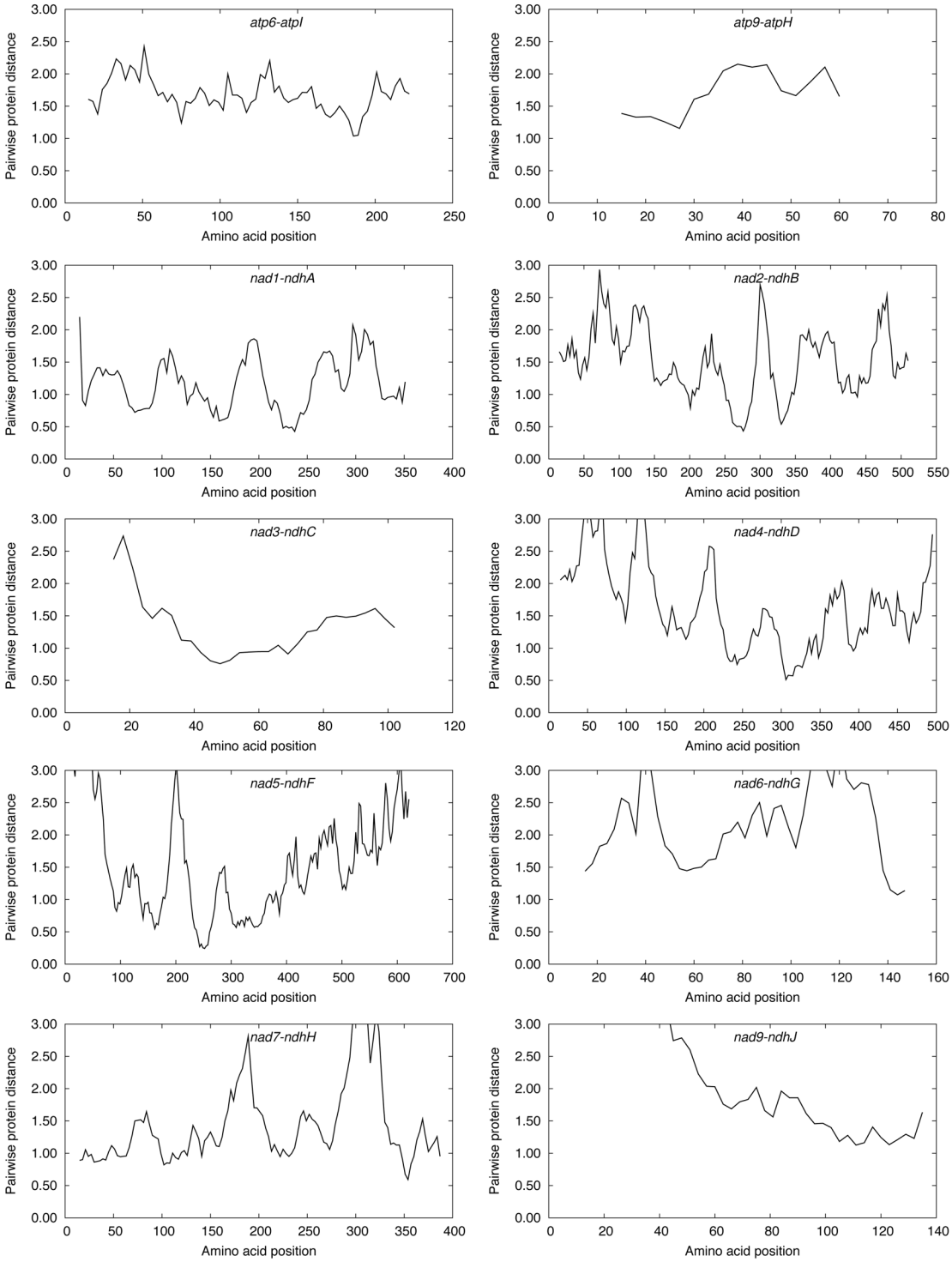


Fig. S3 (continued).

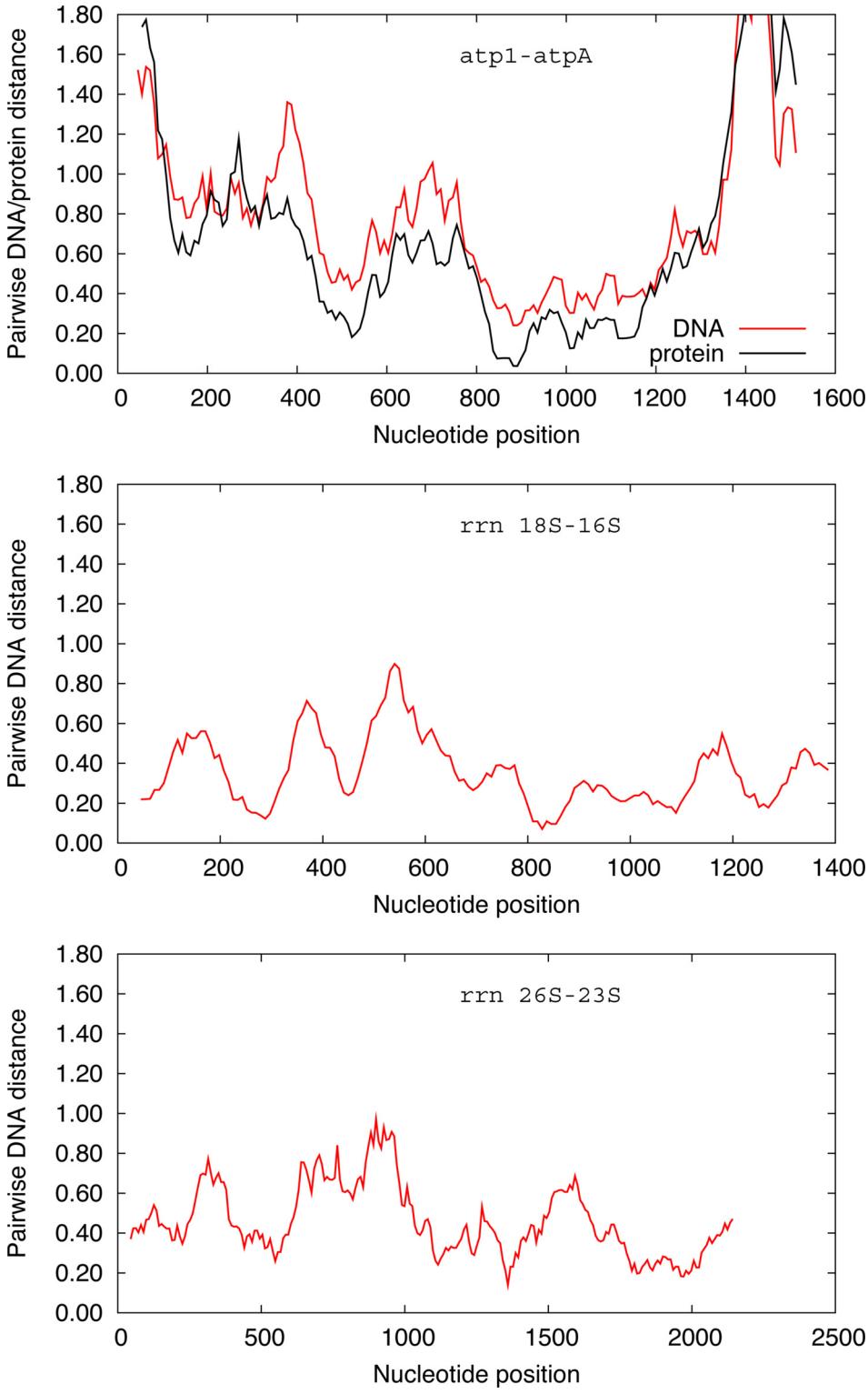


Fig. S4. Sequence conservation between 3 pairs of mitochondrial and chloroplast ribosomal RNA and protein genes. The NT plots used a sliding window of 90 NTs, slid 9 NTs at a time, and with each window labeled according to the NT falling in the middle. The amino acid plot used a sliding window of 30 aa, slid 3 aa at a time, and with each window labeled according to the amino acid falling in the middle. The *y* axis corresponds to the estimated number of substitutions/changes per site, with DNA distance measured using the F84 matrix and protein distance using the JTT matrix. All gaps were removed before analysis. Unlike *atp1/atpA*, the rRNA alignments contain many gaps (compare these plots to the % identity and % gap columns in Table 1)

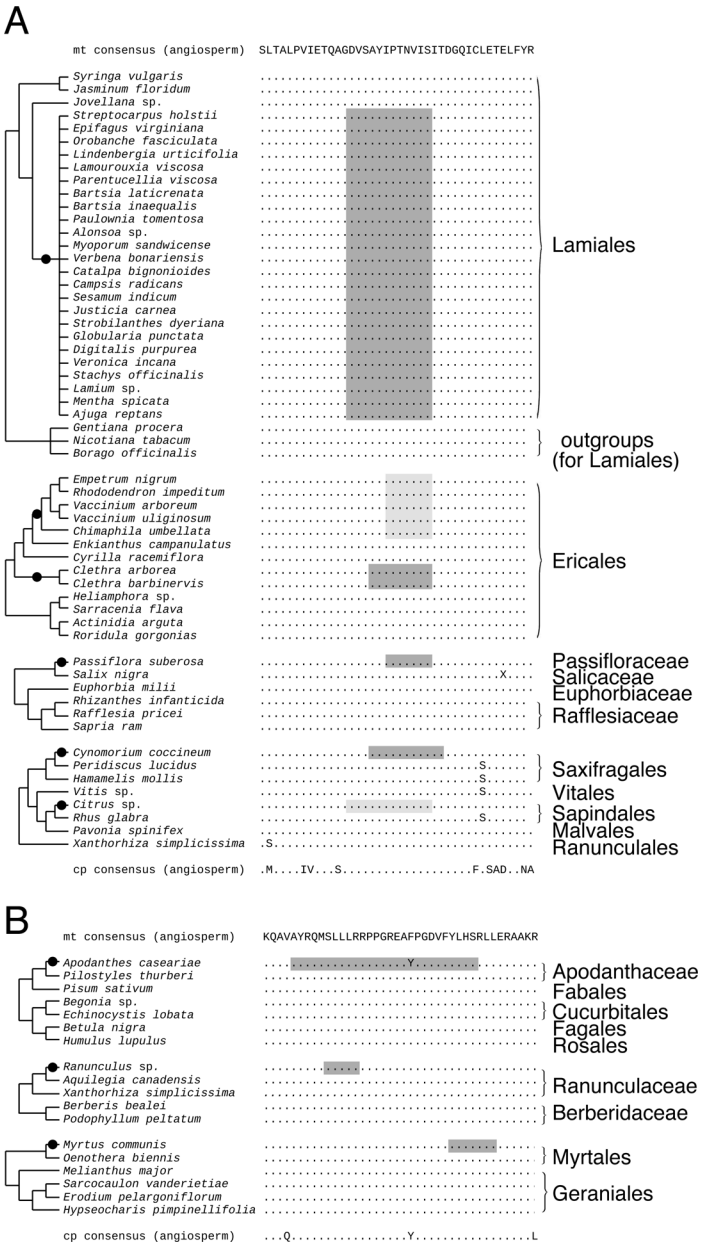


Fig. S5. Alignments of amino acid sequences corresponding to the region shown in Fig. 2*A* (*A*) and in Fig. 2*B* (*B*), with gray shading as in these figures. Note that NT 73 in Fig. 2*A* is a conserved, C-to-U RNA editing site in angiosperms; the corresponding amino acid (the last one shaded in the *Top* 4 groups of shaded sequence blocks) is therefore shown as the ''edited'' S, rather than the ''unedited'' P.

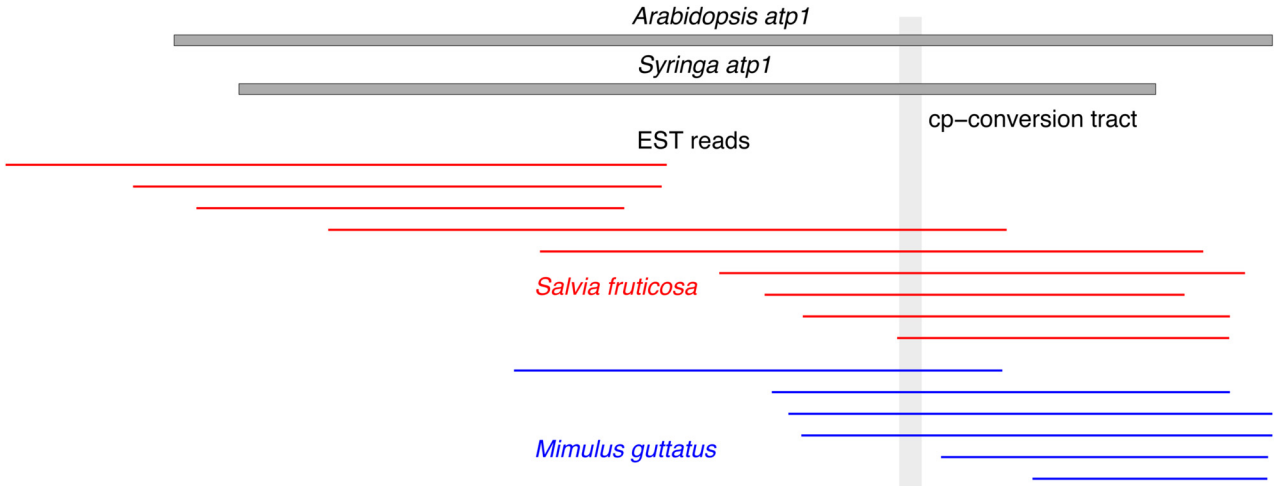


Fig. S6. Available EST reads for 2 taxa that have the chloroplast conversion tract (*Mimulus* and *Salvia* both belong to the Lamiales group of converted taxa shown in Fig. 2A). Numerous EST reads are also available for 4 other taxa that have the chloroplast conversion tract (see *SI Text Functionality of Chimeric* atp1 *Genes—Evidence of Transcription*).

A

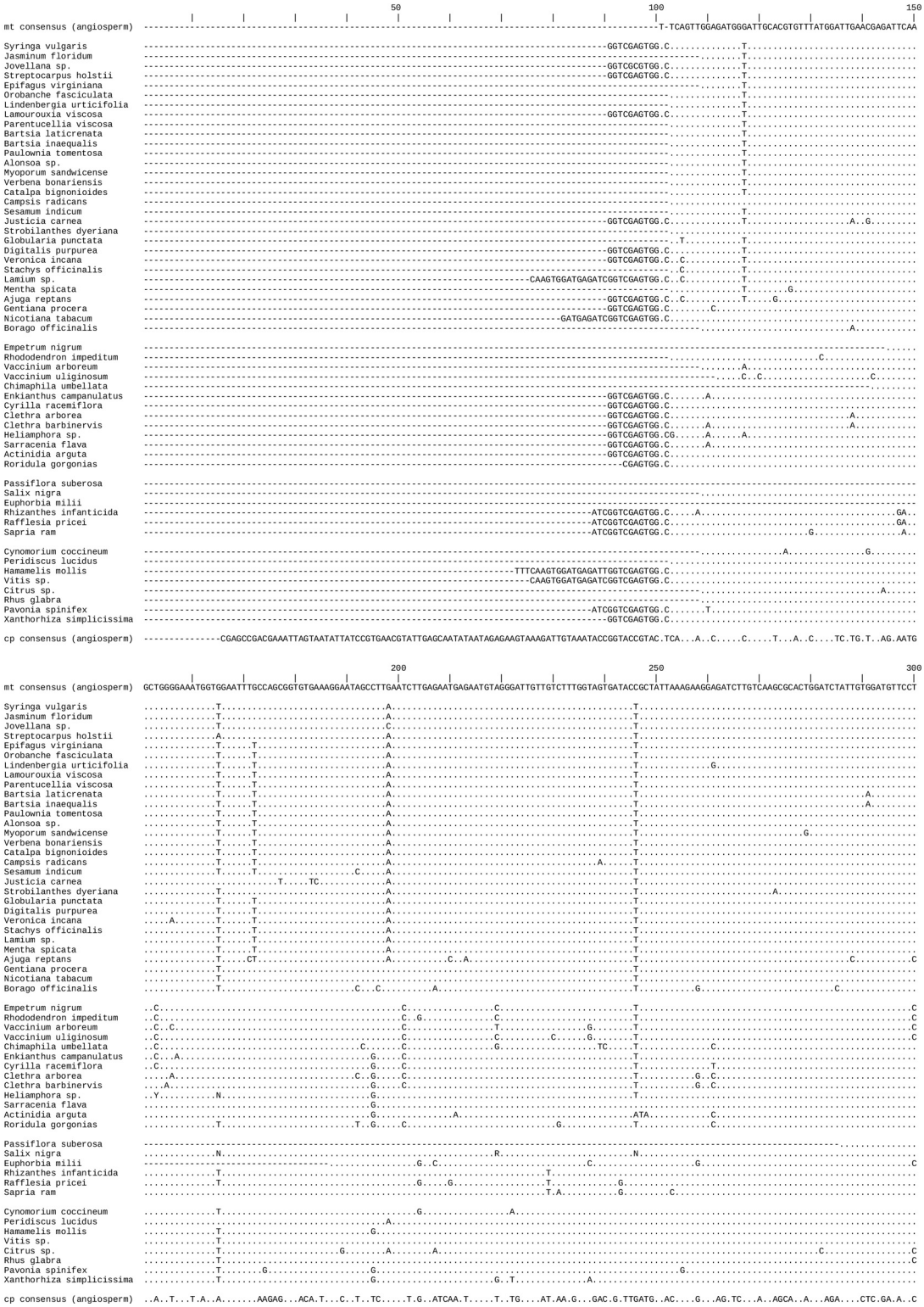
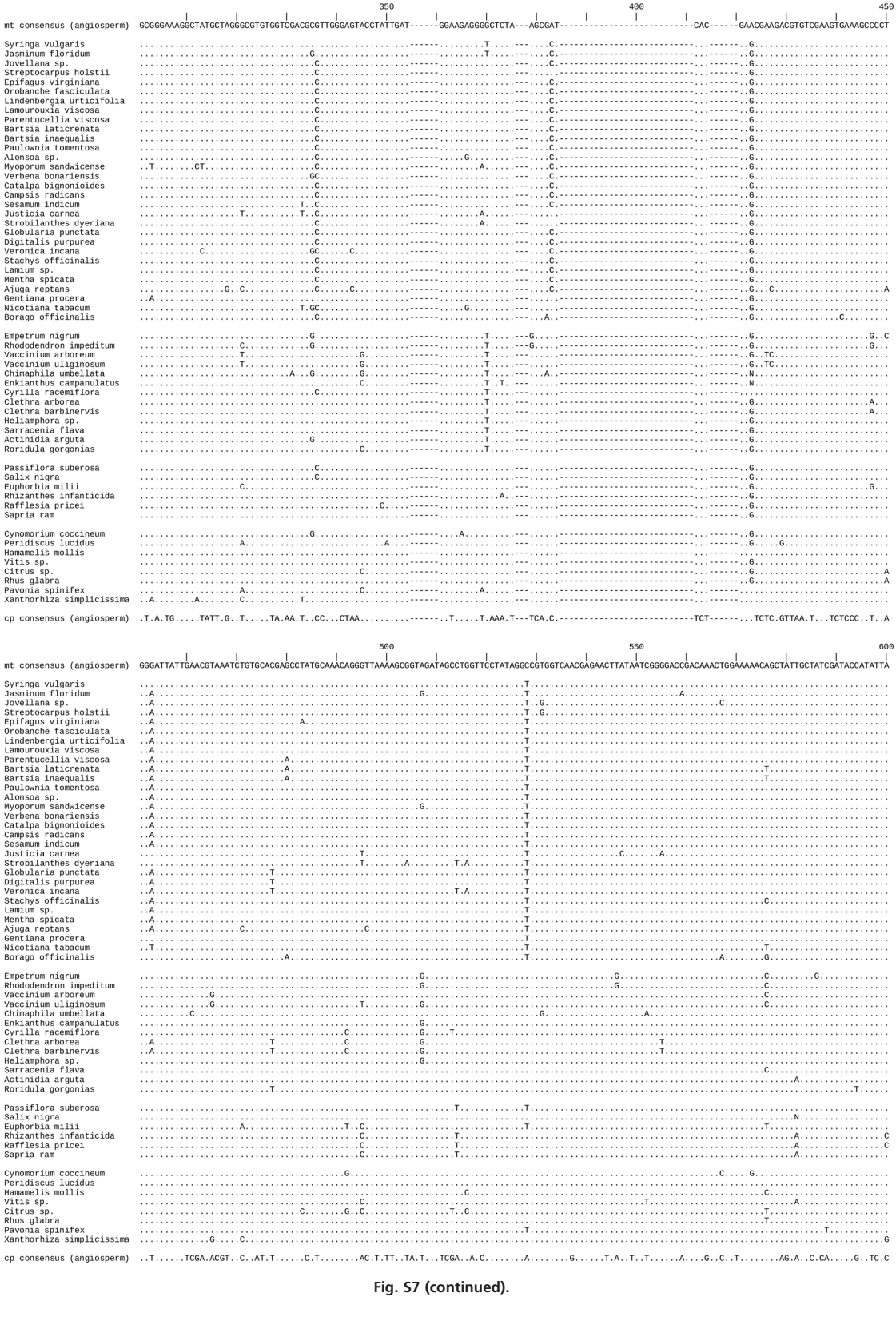


Fig. S7. Complete NT alignments of the mitochondrial *atp1* genes for which partial alignments (shaded in gray) are shown in Fig. 2*A* (*A*) and in Fig. 2*B* (*B*). Gaps at the end of the alignment were removed, whereas internal gaps and gaps at the beginning of the alignment were retained to keep the NT coordinates consistent across all relevant figures. Regions shown in Fig. 2 are shaded in gray.



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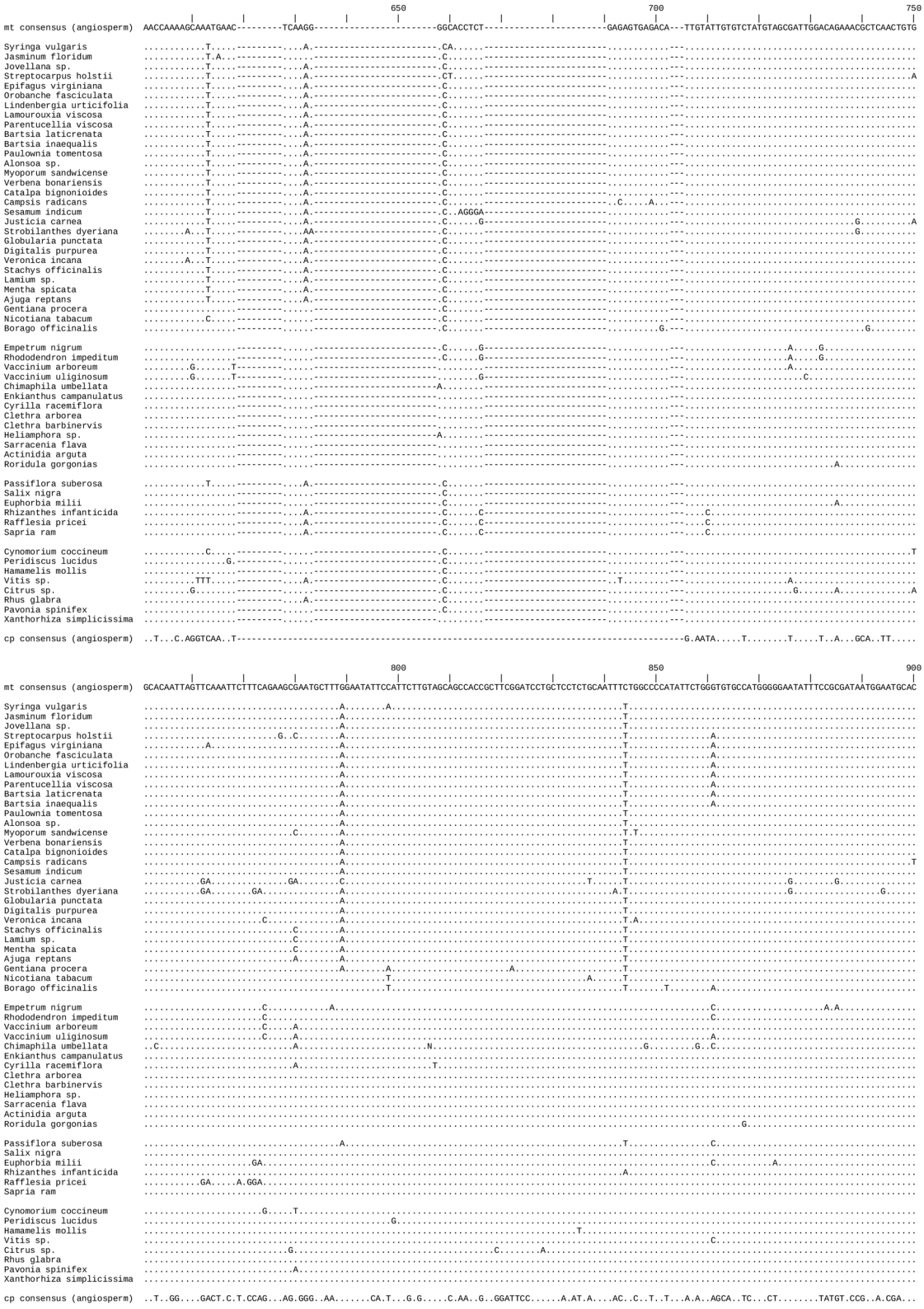

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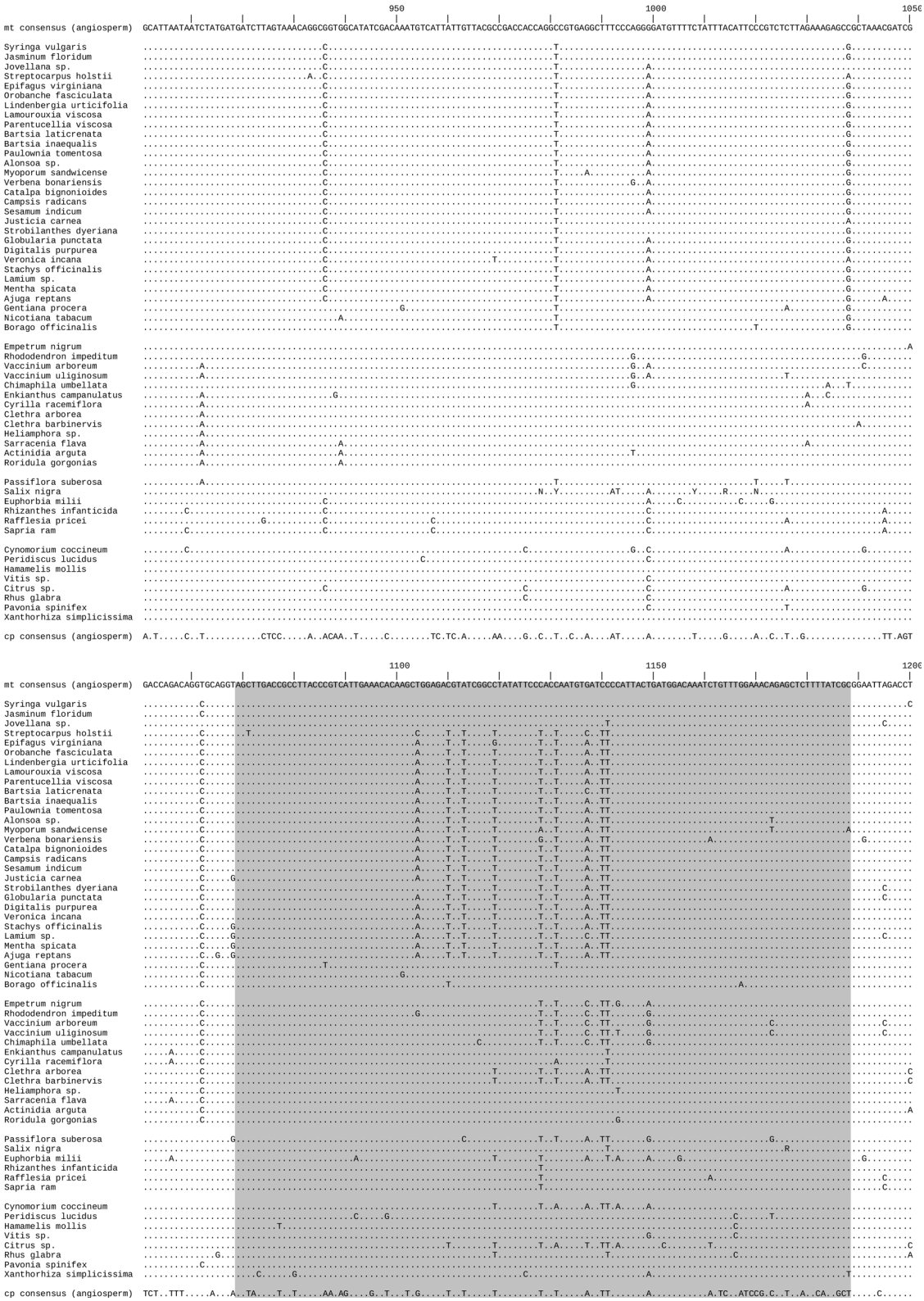

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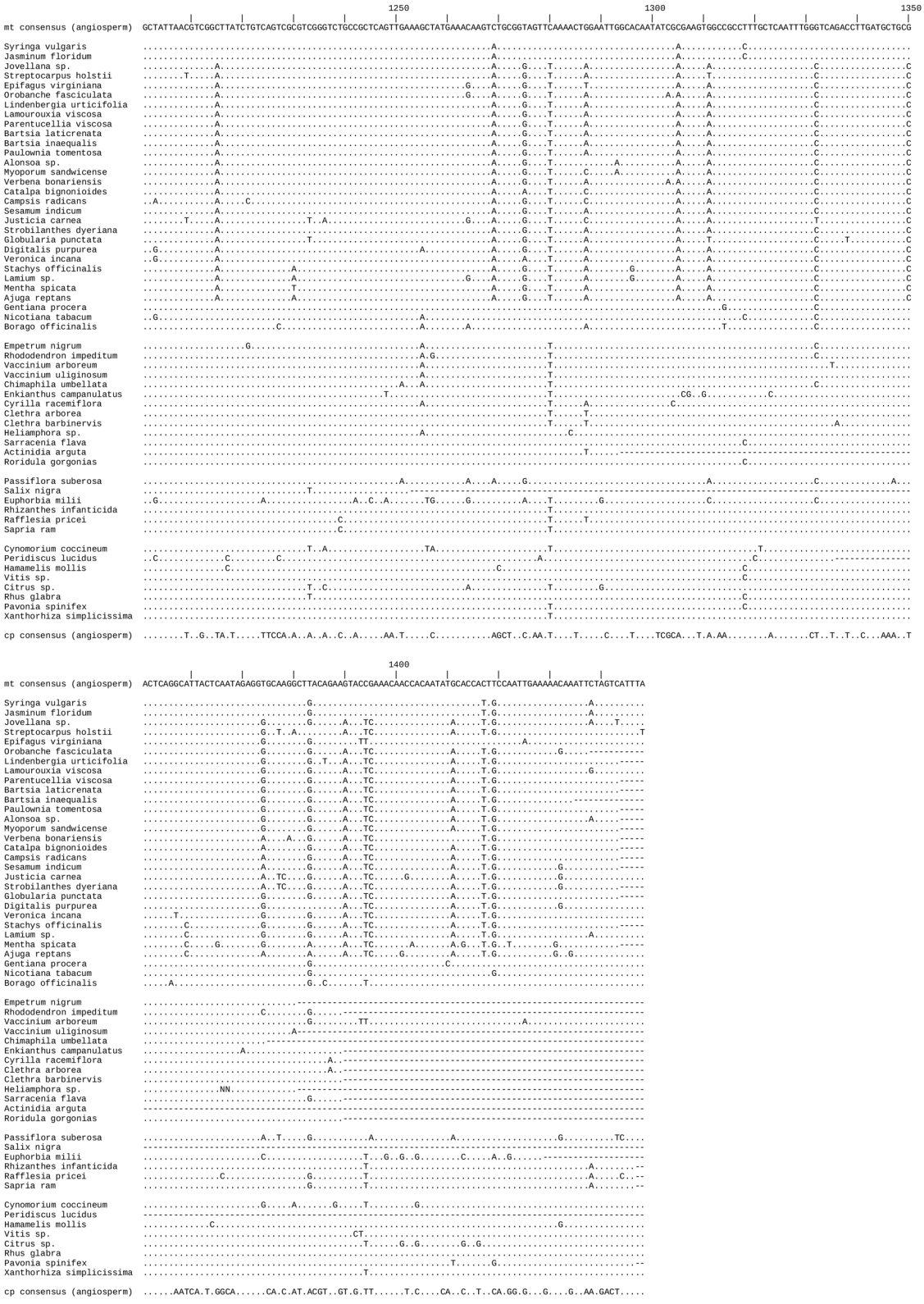

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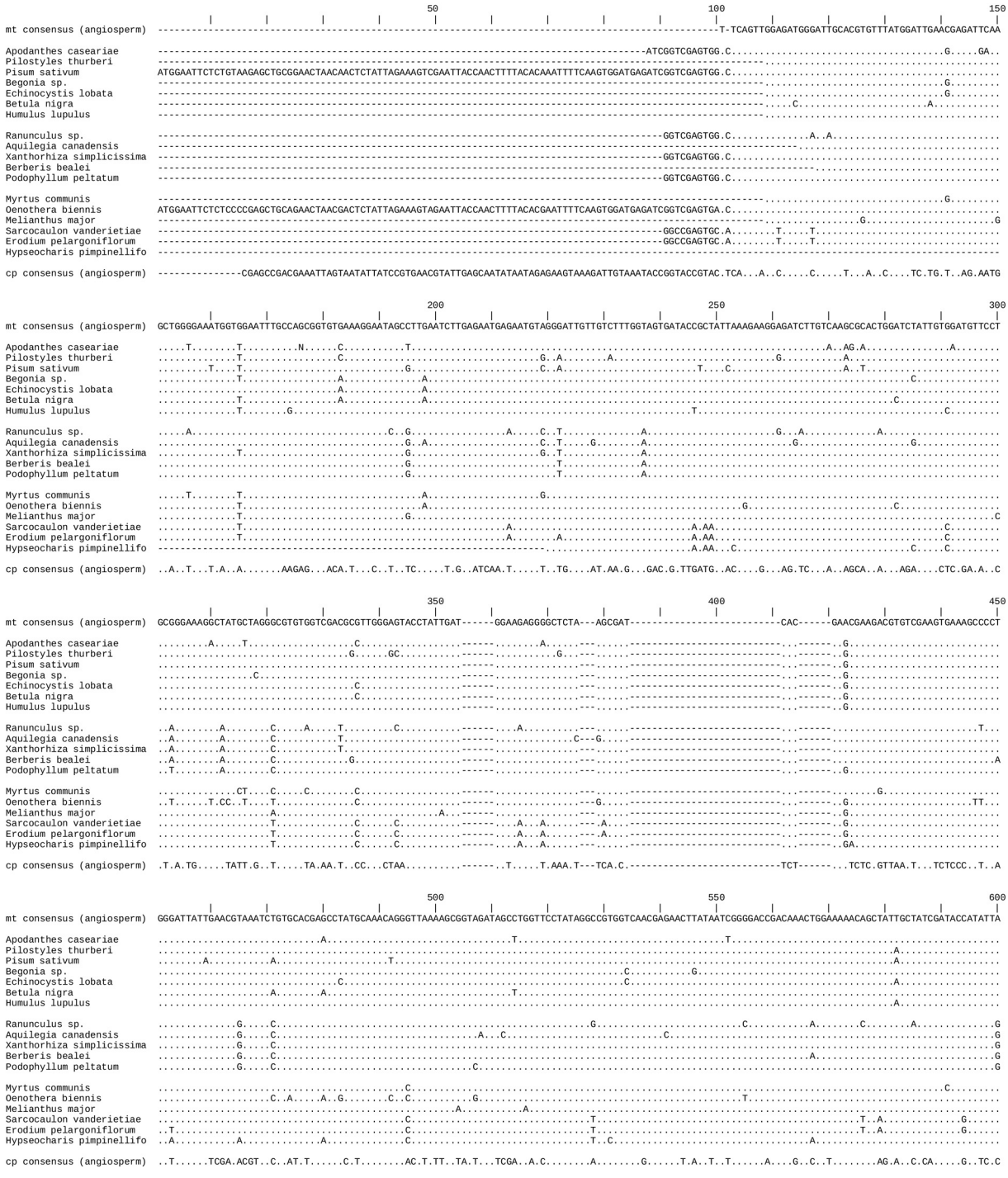
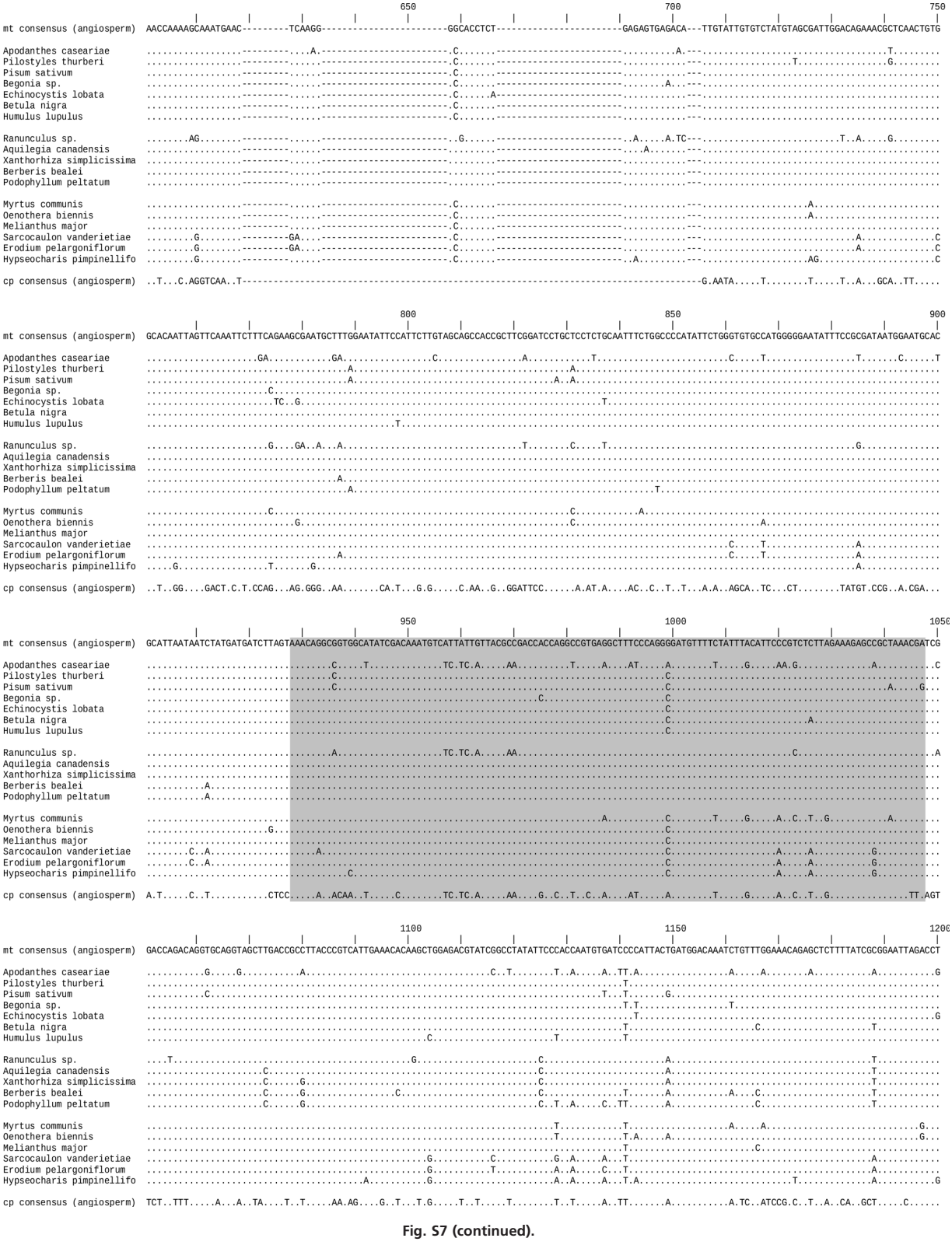


Fig. S7 (continued).



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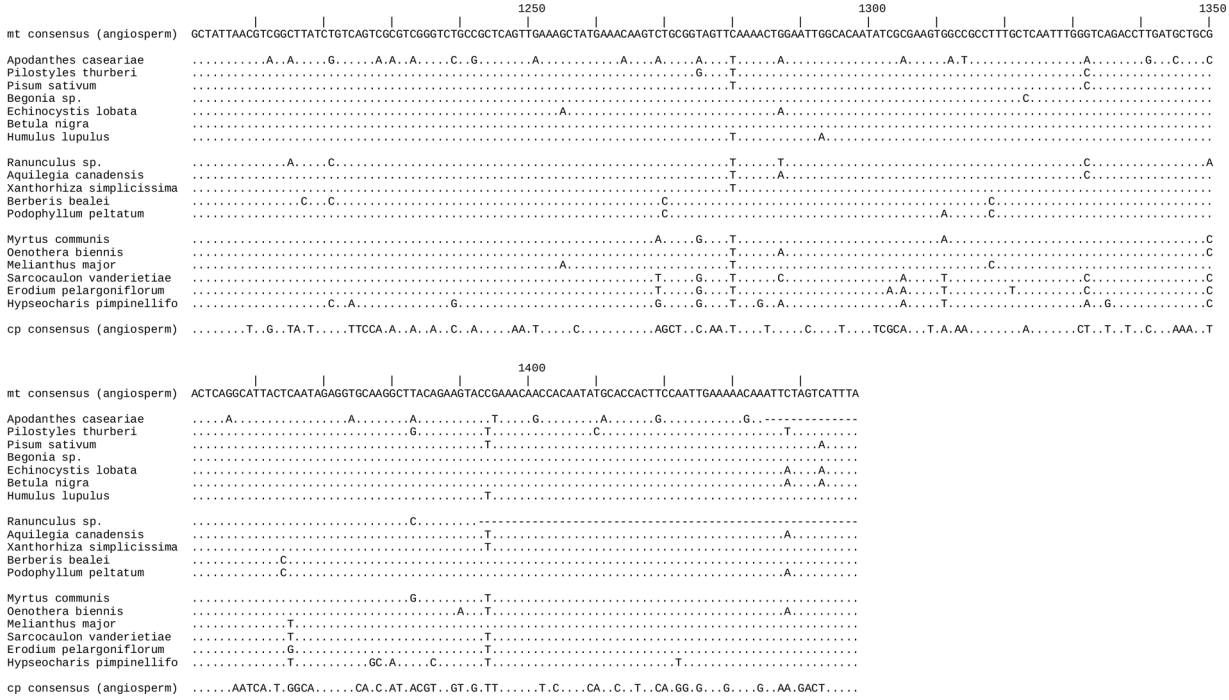

Fig. S7 (continued).

Table S1. All potentially chloroplast-derived regions in mitochondrial *atp1* genes with $P < 0.05$ before correction for multiple tests

Event	Species	Start	End	*P*-value
1	*Apodanthes casearіae*	942	1020	1.27×10^{-10}
2	*Catalpa bignonioides*	1110	1141	6.87×10^{-09}
	Paulownia tomentosa	1110	1141	6.87×10^{-09}
	Campsis radicans	1110	1141	9.73×10^{-09}
	Digitalis purpurea	1110	1141	9.73×10^{-09}
	Parentucellia viscosa	1110	1141	1.01×10^{-08}
	Alonsoa sp.	1110	1141	1.03×10^{-08}
	Globularia punctata	1110	1141	1.03×10^{-08}
	Sesamum indicum	1110	1141	1.03×10^{-08}
	Stachys officinalis	1110	1141	1.03×10^{-08}
	Lamourouxia viscosa	1110	1141	1.04×10^{-08}
	Orobanche fasciculata	1110	1141	1.08×10^{-08}
	Bartsia inaequalis	1110	1141	1.10×10^{-08}
	Lindenbergia urticifolia	1110	1141	1.48×10^{-08}
	Mentha spicata	1110	1141	1.50×10^{-08}
	Veronica incana	1110	1141	1.58×10^{-08}
	Verbena bonariensis	1110	1161	4.59×10^{-08}
	Strobilanthes dyeriana	1110	1141	5.48×10^{-08}
	Justicia carnea	1110	1141	1.33×10^{-07}
	Ajuga reptans	1110	1141	1.35×10^{-07}
	Bartsia laticrenata	1110	1141	2.13×10^{-07}
	Lamium sp.	1110	1141	3.00×10^{-07}
	Epifagus virginiana	1110	1141	3.04×10^{-07}
	Myoporum sandwicense	1110	1141	3.11×10^{-07}
	Streptocarpus holstii	1110	1141	5.35×10^{-07}
3	*Clethra barbinervis*	1119	1141	3.15×10^{-07}
	Clethra arborea	1119	1141	3.30×10^{-07}
4	*Ranunculus sp.*	957	970	3.58×10^{-06}
5	*Myrtus communis*	1008	1029	1.24×10^{-05}
6	*Cynomorium coccineum*	1119	1149	1.66×10^{-05}
7	*Passiflora suberosa*	1128	1141	1.01×10^{-04}
8	*Citrus sp.*	1110	1141	3.98×10^{-04}
9	*Empetrum nigrum*	1128	1149	9.49×10^{-05}
	Rhododendron impeditum	1104	1141	2.50×10^{-04}
	Chimaphila umbellata	1128	1141	9.81×10^{-04}
	Vaccinium arboreum	1128	1141	6.60×10^{-03}
	Vaccinium uliginosum	1128	1141	8.86×10^{-03}
10	*Podophyllum peltatum*	1128	1149	1.16×10^{-03}
11	*Fouquieria sp.*	138	145	1.23×10^{-03}
12	*Scaevola plumieri*	1110	1215	2.26×10^{-03}
13	*Ternstroemia stahlii*	1128	1141	2.32×10^{-03}
14	*Plantago crassifolia*	933	1020	3.46×10^{-03}
	Plantago coronopus	903	970	1.03×10^{-02}
15	*Plantago crassifolia*	1104	1164	4.91×10^{-03}
	Plantago coronopus	1104	1164	4.75×10^{-02}
16	*Euphorbia milii*	1119	1149	5.29×10^{-03}
17	*Carex interior*	519	735	4.30×10^{-03}
	Cyperus alternifolius	519	735	6.80×10^{-03}
	Aponogeton crispus	453	618	9.46×10^{-03}
	Juncus bufonius	519	559	9.72×10^{-03}
	Juncus turkestanicus	519	559	1.14×10^{-02}
	Tonina fluviatilis	450	787	1.33×10^{-02}
	Egeria najas	544	708	1.45×10^{-02}
	Elodea sp.	544	708	1.66×10^{-02}
	Blyxa aubertii	544	618	1.75×10^{-02}
	Najas guadalupensis	544	717	2.04×10^{-02}
18	*Apodanthes casearіae*	1119	1167	8.56×10^{-03}
19	*Tetramerista sp.*	1137	1338	1.35×10^{-02}
	Pentamerista neotropica	1137	1338	2.11×10^{-02}
	Pelliciera rhizophorae	1137	1338	2.18×10^{-02}
20	*Dendrophthoe pentandra*	1230	1311	1.84×10^{-02}
21	*Plantago crassifolia*	1230	1242	2.01×10^{-02}

Event	Species	Start	End	*P*-value
22	*Baldellia ranunculoides*	1104	1161	2.55×10^{-02}
	Limnobium laevigatum	1140	1164	2.94×10^{-02}
	Hydrocharis morsus-ranae	1140	1164	2.96×10^{-02}
	Alisma plantago-aquatica	1140	1161	3.46×10^{-02}
23	*Cercis canadensis*	970	1438	4.95×10^{-02}
24	*Leucocrinum montanum*	1141	1350	4.97×10^{-02}

To see how putative conversion events were inferred, please see Fig. 2. Events are grouped from lowest to highest *P*-values, with the lowest *P*-value within an event group determining its position.

Table S2. P-values for chloroplast/mitochondrial recombinant segments measured by GENECONV[a]

Species	P-value		Position	
	GENECONV	Bonferroni[b]	Start	End
Lamiales[c]			1105	1162
Mentha spicata	<0.0001	0.00042		
Campsis radicans	0.0001	0.00062		
Empetrum nigrum	—	—	—	—
Rhododendron impeditum	—	—	—	—
Ternstroemia stahlii	—	—	—	—
Vaccinium arboreum	—	—	—	—
Chimaphila umbellata	—	—	—	—
Clethra arborea	<0.0001	0.00039	1114	1162
Clethra barbinervis	<0.0001	0.00050	1114	1162
Passiflora suberosa	—	—	—	—
Cynomorium coccineum	—	—	—	—
Citrus sp.	—	—	—	—
Apodanthes caseariae	0.0076	0.04019	949	974
" "	0.0375	0.15679	982	1020
Ranunculus sp.	0.0087	0.03626	943	974
Myrtus communis	—	—	—	—

[a]Analyses were performed using mitochondrial *atp1* sequences from each phylogeny in Figure 2 and chloroplast *atpA* sequences from the following six representatives: *Jasminum nudiflorum* (asterids), *Oenothera biennis* (rosids), *Beta vulgaris* (Caryophyllales), *Ranunculus macranthus* (stem eudicots), *Triticum aestivum* (monocots), *Amborella trichopoda* (stem angiosperms). Dashes are shown if no significant region was detected at $P < 0.05$.

[b]P-values after Bonferroni correction to the GENECONV data.

[c]Of the 27 species of Lamiales examined, only the two with the largest and smallest P-values are shown.