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The complete mitochondrial genome of carnivorous *Genlisea tuberosa* (Lentibulariaceae): Structure and evolutionary aspects

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ABSTRACT

Sequenced genomic data for carnivorous plants are scarce, especially regarding the mitogenomes (MTs) and further studies are crucial to obtain a better understanding of the topic. In this study, we sequenced and characterized the mitochondrial genome of the tuberous carnivorous plant *Genlisea tuberosa,* being the first of its genus to be sequenced. The genome comprises 729,765 bp, encoding 80 identified genes of which 36 are protein-coding, 40 tRNA, four rRNA genes, and three pseudogenes. An intronic region from the *cox1* gene was identified that encodes an endonuclease enzyme that is present in the other sequenced species of Lentibulariaceae. Chloroplast genes (pseudogene and complete) inserted in the MT genome were identified, showing possible horizontal transfer between organelles. In addition, 50 pairs of long repeats from 94 to 274 bp are present, possibly playing an important role in the maintenance of the MT genome. Phylogenetic analysis carried out with 34 coding mitochondrial genes corroborated the positioning of the species listed here within the family. The molecular dynamism in the mitogenome (e.g. the loss or pseudogenization of genes, insertion of foreign genes, the long repeats as well as accumulated mutations) may be reflections of the carnivorous lifestyle where a significant part of cellular energy was shifted for the adaptation of leaves into traps molding the mitochondrial DNA. The sequence and annotation of *G. tuberosa*'s MT will be useful for further studies and serve as a model for evolutionary and taxonomic clarifications of the group as well as improving our comprehension of MT evolution.

1. Introduction

The genomes of Lentibulariaceae species have particular structural traits and evolutionary dynamics, and for this reason, they have received special attention (Albert et al., 2010; Vu et al., 2015; Silva et al., 2020a). Recently, several species of this family had their complete plastid and nuclear genomes sequenced (e.g. Leushkin et al., 2013; Silva et al., 2016, 2019; Lan et al., 2017). However, only a pair of mitogenomes has been sequenced for *Utricularia gibba* L. (Ibarra-Laclette et al., 2013) and *U. reniformis* A.St.-Hil. (Silva et al., 2017) so far. Concerning other families of carnivorous plants, there has been, so far, only one sequenced mitogenome made in a natural hybrid *Nepenthes* × *ventrata* Hort. ex Fleming, a pitcher plant member of the Nepenthaceae family (Gruzdev et al., 2018). For a long time, the classification within the genera of Lentibulariaceae was based on only morphological characteristics (e.g. Taylor, 1989). Recently, with the increased sequencing of several coding and noncoding DNA and a few complete genomes, several studies have concentrated efforts to resolve interspecific relationships in the family (e.g. Silva et al., 2018, 2020a; Fleischmann et al., 2010, 2014), yet only one leveraged the mitochondrial genes (Silva et al., 2017).

In *Utricularia* and *Genlisea* plastid genomes studied, some sites revealed evidence of RNA edits and a progressive loss and

Abbreviations: CDS, coding DNA sequence; HGT, horizontal gene transfer; mtDNA, mitochondrial DNA; MT, mitogenome; MTs, mitogenomes.

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pseudogenization of the NDH complex which could be involved in environmental stress (Silva et al., 2016; 2017; 2018). In Droseraceae and Nepenthaceae, other carnivorous plant families, specifically in the genera *Drosera* and *Nepenthes*, it was noted that their plastidial genomes have many repetitive regions and high rearrangement levels, including the loss of NDH genes, in addition to *ycf*1 and *ycf*2, which are possibly involved in photosynthetic processes (Gruzdev et al., 2019; Nevill et al., 2019). These organellar gene losses could have an impact on the investment of the carnivorous lifestyle at the expense of autotrophy, and it may also be linked to other organelles such as mitochondria.

Mitochondria are essential components of plants and are responsible for the energy production associated with the fundamental metabolic mechanisms necessary throughout plant cells and organs (Roger et al., 2017). Plant mitochondrial genome organization can have multiple arrangements due to sets of variable encoding genes, including many repetitive and recombination regions which can lead to instability in its structure and configuration (Mower et al., 2012; Gualberto et al., 2014). Despite its considerable molecular plasticity, the evolution of genes encoding proteins in the mitochondrial respiratory chain, whether the loss or gain of their functions, is directly linked to morphophysiological adaptations in Lentibulariaceae species, largely as a result of their living in extreme environments (Albert et al., 2010). Jobson et al. (2004) revealed that mutations in the *cytochrome c oxidase* gene, especially in the *Genlisea* and *Utricularia* genera, are associated with the specialization process of traps, but that such events do not affect genome reduction, according to Veleba et al. (2020). In adaptive terms, energy consumption is proportionally higher in traps, given the high investment in the effectiveness of capturing prey as a source of nutrients than in the other organs of the plant with a high photosynthetic rate (Adamec, 2006; 2007; Laakkonen et al., 2006).

The *Genlisea* genus comprises 31 species split into two subgenera occurring throughout central and southern America as well as in Africa (Fleischmann et al., 2010; Silva et al., 2020b; Adamec et al., 2021). The species are rootless and recognized for having their modified body plan with underground leaves evolved as a vesicular bulb bifurcating in two helical arms responsible for attracting and capturing soil organisms, including microalgae, protozoa, microcrustaceans, and nematodes (Płachno et al., 2005a, Płachno et al., 2005b, 2008; Fleischmann et al., 2010; Fleischmann 2012). The genus stands out for having ultra-small nuclear genomes and the smallest among angiosperms is *G. tuberosa* Rivadavia, Gonella & A.Fleischm. (Fleischmann et al., 2014). However, especially for *Genlisea*, few mitochondrial genes have been employed in phylogenetic analyses, and no complete sequenced genome has been reported for any species of this genus so far.

The *Genlisea* species have been studied on plastidial and nuclear DNA (e.g. Leushkin et al., 2013; Vu et al., 2015; Silva et al., 2018). However, exploring mitogenomes can be beneficial for understanding evolutionary events at various taxonomic levels, within species, genera, and families, as well as serving as a model within angiosperms. Here, we present the assembled mitochondrial genome of *G. tuberosa*, which can be a fruitful model for the field of genetics and adaptations to nutrient-poor soil conditions in which the plant grows. Such information may provide better insights into the importance of mitochondrial DNA for the evolutionary process of carnivory in different lineages within angiosperms.

2. Material and methods

2.1. Plant sampling, DNA extraction, and sequencing

Total genomic DNA was extracted from silica-dried flower tissue using DNeasy Plant Mini Kit extraction kit (Qiagen) according to Silva et al. (2018) protocol. The specimens were collected in Delfinópolis municipality in the Minas Gerais State, Brazil (Collecting permits - Sisbio #26938; Sisgen #A47D0CF). Voucher specimens were deposited at Herbarium JABU (collector number V.F.O. Miranda et al., 2001). The DNA quality and concentration were measured with a NanoDrop-2000 spectrometer (Thermo Scientific, U.S.A.) and by Qubit fluorometer (Thermo Fisher Scientific), respectively. The libraries were constructed using manufacturers' protocols and sequenced using Illumina MiSeq (paired-ends of 2 × 300 bp).

2.2. Mitochondrial genome assembly and annotation

The assembly of mitochondria was performed using high-quality filtered reads (>Q30 and reads with less than 50 bp were discarded) resulting from the software Seqyclean (Zhbannikov et al., 2017). The assembly was done using the pipeline GetOrganelles v. 1.6.4 (Jin et al., 2020) using parameters suggested by the authors (-R 50 -k 75,95,105,115,127 -P 1000000 -F embplant_mt). In total, 2 × 2,758,854 paired-end reads were generated from the sequencing. The results of the *de novo* assembled contigs were visually inspected with Bandage (Wick et al., 2015) and those were further joined with reads mapping, using bowtie2 (parameters: -D 20 -R 3 -N 1 -L 20 -i S,1,0.50), for accuracy check. Mitochondria annotations were done with GESeq (Tillich et al., 2017) implemented in Chlorobox Web Service (Tillich et al., 2017) using previously published Lentibulariaceae and other well-annotated species (NC_034982, NC_037304, and NC_021152). The final adjustments were manually edited in comparison with previously published Lentibulariaceae mitochondrial genome (Ibarra-Laclette et al., 2013; Silva et al., 2017) and published contigs using Blastn and tBlastx (Camacho et al., 2009). Chloroplast regions, which could be transferred horizontally, were annotated according to tblastn and blastn searches with *G. tuberosa* plastid as reference (NC_037082) and *ndh* genes according to *U. gibba* plastidial genomes (NC_021449). The pseudogenes were characterized according to the absence of start and/or stop codon, frameshift, and genes with more than 50% of coverage and 50% of coding region identity. The tRNAs annotations were performed with the software tRNAscan-SE (Chan and Lowe, 2019), implemented in the GESeq platform, whereas the rRNAs were annotated using the RNAmmer v.1.2 (Lagesen et al., 2007). Genome maps were drawn using Organellar GenomeDraw software (OGDRAW, Lohse et al., 2013).

2.3. Phylogenetic reconstruction of mitochondrial genes

The phylogenetic tree was estimated using the maximum likelihood (ML) approach with a concatenated matrix composed of 36 genes encoding mitochondrial genomes of Lentibulariaceae and all Lamiales species with sequenced data available to date in the public GenBank database. (Supplementary data 1). The ML tree was calculated using IQ-Tree 2 (Minh et al., 2020) with the best-of-fit model GTR + F + I + G4, according to AIC criteria (Akaike, 1974), with the software ModelFinder (Kalyaanamoorthy et al., 2017). The clade support was estimated with the ultrafast bootstrap (UFBoot) and SH-aLRT algorithms (Hoang et al., 2018) with 1,000 replicates. Tree rooting was based on the *Arabidopsis thaliana* (Genbank access: NC_037304), *Asclepias syriaca* (NC_022796) and *Liriodendron tulipifera* (NC_021152) species as the outgroup. The tree drawing was performed using FigTree v. 1.4.4 (Rambaut, 2010).

2.4. Repeats analyses

To determine forward and palindromic repeats, the REPuter tool (Kurtz et al., 2001) was used whose parameters were ≥ 30 bp, sequence identity ≥ 90%, and hamming distance of 3.

2.5. Identity and synteny analyses

The identity of mitochondrial genes was assessed using online mVista software (Frazer et al., 2004), with Shuffle-LAGAN model, using the concatenated genes of mtDNA CDS with reference to previously published MT genome of *Utricularia reniformis* (NC_034982). The Lentibulariaceae MTs previously available in Genbank (*Utricularia*

reniformis: NC_034982 and *U. gibba*: KC997786) were employed in order to compare closely related species.

3. Results and discussion

3.1. Genome structure

Assembling the mitochondrial genome in angiosperms is a major challenge. Most assemblies are unsuccessful even with long reads due to the many variants integrated into the genome, such as repeated regions, the presence of multiple linear and circular multipartite structures, which requires improvement in sequencing technologies to have better genome-target coverage (Claros et al., 2012; Mower, 2020). Nevertheless, the genome of *Genlisea tuberosa* was assembled into four contigs and these contigs were joined with mapped paired-end reads (R1 and R2) across the contigs, which supported our assembly and contigs organization (Supplementary data 2). Although the data suggest a circular structure, other conformations should not be discarded, given that one of the junctions has few reads as support and the assembly graph (Supplementary data 3), which is usual for considering plant mitochondrial genomes (Lonsdale, 1984; Gualberto et al., 2014; Zardoya, 2020). The physical analyses of the mtDNA molecules includes not only identified circular structures but also linear, branched and branched circular structures (Kozik et al., 2019), indicating that the circular representation may not be the only description of the natural molecular conformation of the MT genome.

The mitochondrial genome of *Genlisea tuberosa* is 729,765 bp (Fig. 1), with 36 coding genes (two putative as they are almost entire: rps10 and rpl16), 40 tRNAs and four rRNAs with GC content equal to 43.4% (Table 1). The MT is smaller than that of *U. reniformis*, which is 857,234 bp and has 42 functional genes. Among the absent genes when compared to *U. reniformis* are *rps2* and *rps19* (Silva et al., 2017). *Genlisea tuberosa* and *U. reniformis*, in addition to *U. gibba* (Ibarra-Laclette et al., 2013), have highly repetitive genomes (Silva et al., 2017).

Interestingly, there was a mutation in the 116-Leucine/117-Serine motif (ancestral/preserved state in *Pinguicula* and angiosperms) in the subunit I from *cytochrome c oxidase* gene (*cox*1) of *G. tuberosa* MT, while *U. reniformis* and *U. gibba* share 116-Cysteine/117-Cysteine. According to Jobson et al. (2004), these two codons are important in the evolution of Lentibulariaceae, because in the *Genlisea-Utricularia* lineage there

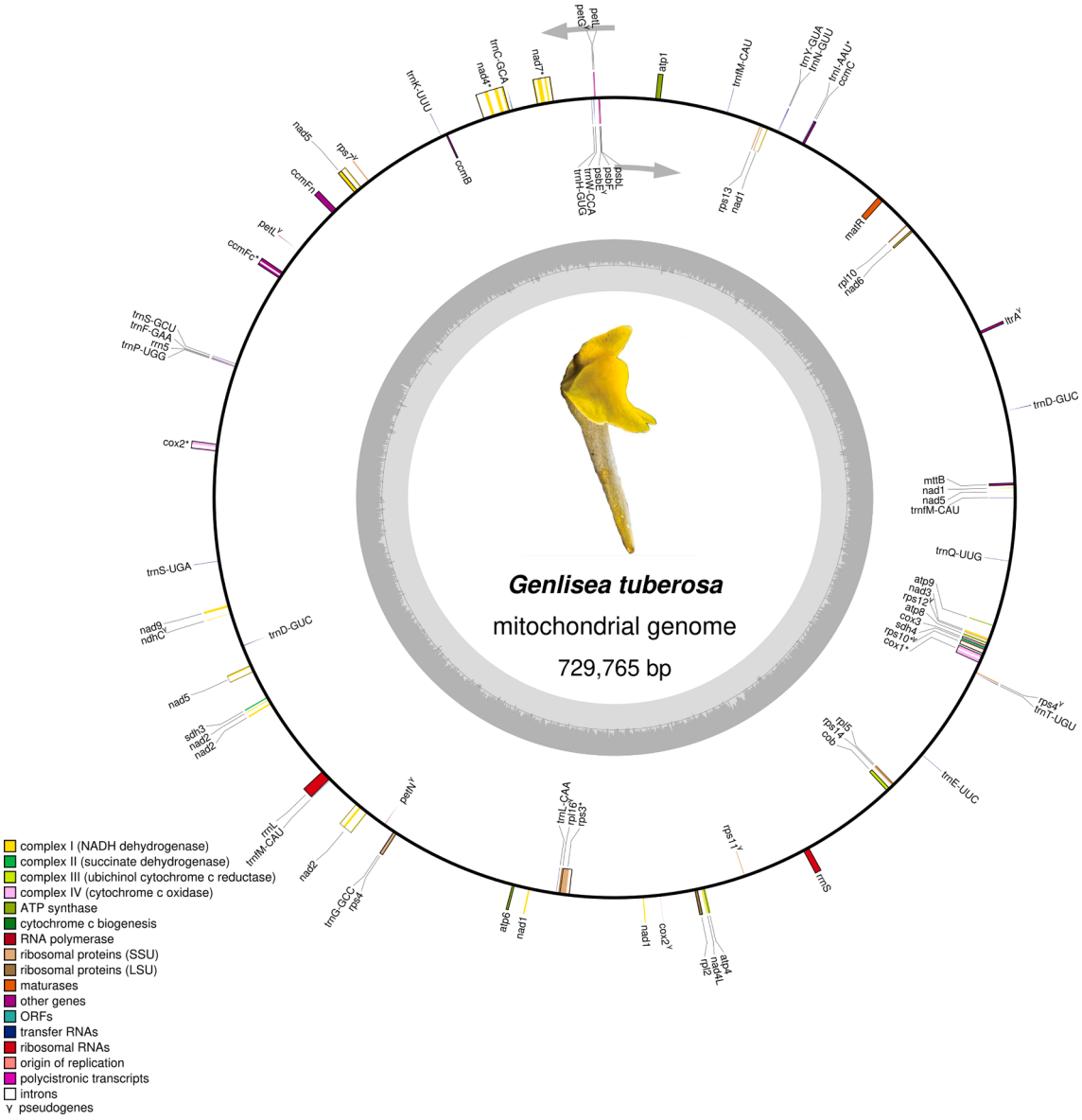

Fig. 1. Genomic map of the *Genlisea tuberosa* MT genome. Genes shown on the outside of the map are transcribed clockwise, whereas genes on the inside are transcribed counter-clockwise. Genes are color coded by their function in the legend. The gray arrows represent the direction of gene transcription in the genome.

Table 1
Genes encoded by the mtDNA genome of *Genlisea tuberosa*.

Category	Group of identified genes
Complex I (NADH dehydrogenase)	*nad1*, *nad2*, *nad3*, *nad4*, *nad4L*, *nad5*, *nad6*, *nad7*, *nad9*
Complex II (succinate dehydrogenase)	*sdh3*, *sdh4*
Complex III (ubiquinol cytochrome *c* reductase)	*cob*
Complex IV (cytochrome *c* oxidase)	*cox1*, *cox2*, *cox3*
Complex V (ATP synthase)	*atp1*, *atp4*, *atp6*, *atp8*, *atp9*
Cytochrome *c* biogenesis	*ccmB*, *ccmC*, *ccmFc*, *ccmFn*
Ribosomal proteins (SSU)	*rps3*, *rps4*, *rps7*$^{\psi}$, *rps10**, *rps11*$^{\psi}$ *rps12*, *rps13*, *rps14*
Ribosomal proteins (LSU)	*rpl2*, *rpl5*, *rpl10*, *rpl16**
Maturases	*matR*
Transport membrane proteins	*mttB*
Others	*LAGLIDAD* endonuclease (intron region of *cox1* gene), *ltrA*$^{\psi}$ (promotes group II intron splicing and mobility)

Pseudogene (ψ). Putative coding gene (*). Total GC content (43.4%).

were functional changes in these codons from Leu/Ser to Cys/Cys. This same mutation also occurred in *G. hispidula* A.St.-Hil., but differently in *G. aurea* Stapf (Cys/Ser) which are members of the same subgenus (*G.* subg. *Genlisea*), besides *G. tuberosa*. In addition, *G. violacea* A.St.-Hil. (*G.* subg. *Tayloria*) remained with the conserved motif (Leu/Ser). For *G. tuberosa*, there was probably a reversion in the second codon to an ancestral state (Cys/Ser), also present in the other lineages of angiosperms. According to Jobson et al. (2004), this residual motif must have gone through a purifying selection and is involved in the formation of an adjacent vicinal disulfide bridge in helix-3 of the protein subunit I encoded by *cox1*. Such events may be related to the requirement of a high respiratory rate in the process of active carnivory in *Utricularia* traps, which exhibit high rates of water pumping out of the traps. However, in *Genlisea*, there was a progressive loss of this water pumping resulting in a passive biodynamic process in traps (Jobson et al., 2004; Albert et al., 2010). Furthermore, *G. tuberosa* accumulated other three amino acid substitutions (Iso/Met-479; Val/Leu-496; Leu/Pro-502) and eight non-synonymous nucleotides when compared to *U. gibba* and *U. reniformis*.

Genlisea tuberosa contains an intron region in *cox1* that encodes the *LAGLIDAD* endonuclease which is a group of enzymes with functions of catalytic mechanisms within introns (Edgell, 2009). The sequence of this enzyme has evolutionarily replaced 30 amino acid residues when compared to *U. reniformis* and *U. gibba*, resulting in a similarity of 94% and 92%, respectively. The acquisition of this coding intron by these species comes from a common ancestor (Silva et al., 2017) and is present in more than eight species of Lamiales and possibly in the main lineages of Lentibulariaceae. The beginning of the *ltrA* coding region has not been identified and most likely has evolved to a pseudogenic state, just like in *U. gibba*. In contrast, in *U. reniformis*, the sequence of this gene is complete and points to a likely functional state in the species. However, despite having functions, like mobility and putative splicing, *ltrA* is characterized as one of the least expressed genes but still needs to be investigated for the reasons of its permanence in the species (Silva et al., 2017). Here, *ltrA* and the ribosomal genes *rps7* and *rps11* are given as possible pseudogenes or non-functional as the sequences are incomplete and with in-frame stop codons along with them, but there was no analytical confirmation of its sequencing in the genome of *G. tuberosa* in this study. Most of the ribosomal genes have been identified, but the beginning of the sequence of *rps10* and *rpl16* was not found and both contain two stop codons in the coding frame. It is known that the mitochondrial DNA undergoes RNA editing causing, at a post-transcriptional level, whose process can cope with the lack of start and/or presence of stop codons (Allen et al., 2003; Small et al., 2019).

Corroborating the structural and functional dynamics of the mitochondrial DNA of *G. tuberosa*, the results of the annotations identified intact genes of chloroplast origin, *psbF*, *psbL* and *petL*, belonging to a protein complex of Photosystem II. These genes function to generate O_2 and a proton gradient from the light energy later used to form ATP (Shen, 2021). The insertion of these genes may have been due to a horizontal transfer (HGT) between chloroplast and mitochondria, which also happened in *Vitis vinifera* (Goremykin et al., 2009). But, in *G. tuberosa* they are intact, whereas in grapes they are pseudogenes.

The *psbE* and *psbF* genes originated from the ancestral angiosperms and were transferred from the chloroplast to the mitochondria approximately 150 million years ago, but they are degenerated with their transfer losing their primary function yet getting other structural activities in the MT genome (Wang et al., 2007). This event occurred in the genome of *G. tuberosa* and may be derived from the increasing loss of dispensable genes from the chloroplast genome in Lentibulariaceae, mainly in the *Genlisea-Utricularia* lineage (Silva et al., 2016; 2018).

3.2. Repeat analysis

A total of 50 pairs of forward and palindromic repeats from 94 to 274 bp long were identified in the genome (Supplementary data 4). Most repeats are in intergenic spaces associated with RNA transporters and ribosomal genes (*trnC(GCA)*, *trnE(UUC)*, *trnF(GAA)*, *trnI(AAU)*, *trnK (UUU)*, *trnM(CAU)*, *trnN(GUU)*, *trnQ(UUG)*, *trnT(UGU)*, *trnY(GUA)*, *rpl10*, *rps4*, *rps7ψ*, *rps10*, *rps11*, *rrn5S*, *rrn16S*), chloroplast origin genes (*psbL*), and other mitochondrial respiratory chain genes (*atp1*, *atp6*, *atp9*, *ccmB*, *cob* and *sdh3*). It is noteworthy that the repeats inserted along the sequences of the genes *nad1*, *nad2*, *nad4*, *nad5*, *nad6* and *nad7* are situated before and after the coding region, which may be involved in the flanking process or that regulate gene transcription (Binder and Brennicke, 2003).

3.3. Identity analysis of MT genome content

In comparison with previously available genomic data for Lentibulariaceae, the MT gene content is highly conservative across species as they are relatively close phylogenetically (Fig. 2). The nucleotide sequence identity of *G. tuberosa* with *U. gibba* and *U. reniformis* is over 50% in almost all coding genes. It is interesting to note that the genes of the mitochondrial respiratory chain *cox1* (protein complex IV) and the genes *nad1*, *nad2*, *nad4*, *nad5*, *nad7* and *nad9* (complex I) have identities between 90 and 100%. These subunits are fundamental in the electron transfer process to create an electrochemical gradient resulting in the formation of ATP and consequently the production of energy to supply cellular metabolic needs (Braun, 2020).

The species of Lentibulariaceae, in general, live in stressful aquatic or wetland environments, oligotrophic or dystrophic (Adamec, 2012; Ellison and Adamec, 2018) and needed to develop, through the evolution, highly specialized and modified leaves adapted to capture prey and assimilate their subproducts resulted from digestion as a source of nutrients (Ellison and Adamec, 2018; Adamec et al., 2021). The *cox* and *nad* genes are key components to increase energy capacity in these species which demand a high respiratory rate from the mitochondria (Braun, 2020). It is important to emphasize that the *G. tuberosa'* MT molecular plasticity, such as the loss or pseudogenization of genes, insertion of foreign genes, the long repeats as well as accumulated mutations in the mitogenome, may reflect the carnivorous lifestyle. During its evolution, a significant part of cellular energy was relocated for adaptation from leaves into traps, molding mitochondrial DNA. Special attention deserves to be given to the impacts that reactive oxygen species (ROS) present in oxidative phosphorylation, which may alter the mitogenome when there is an excess of these reactions in the cells caused by these environmental factors, they can damage the DNA and thus result in important genetic and phenotypic changes throughout the evolution of these plants under such conditions (Albert et al., 2010; Ibarra-Laclette et al., 2011; Cejudo et al., 2021).

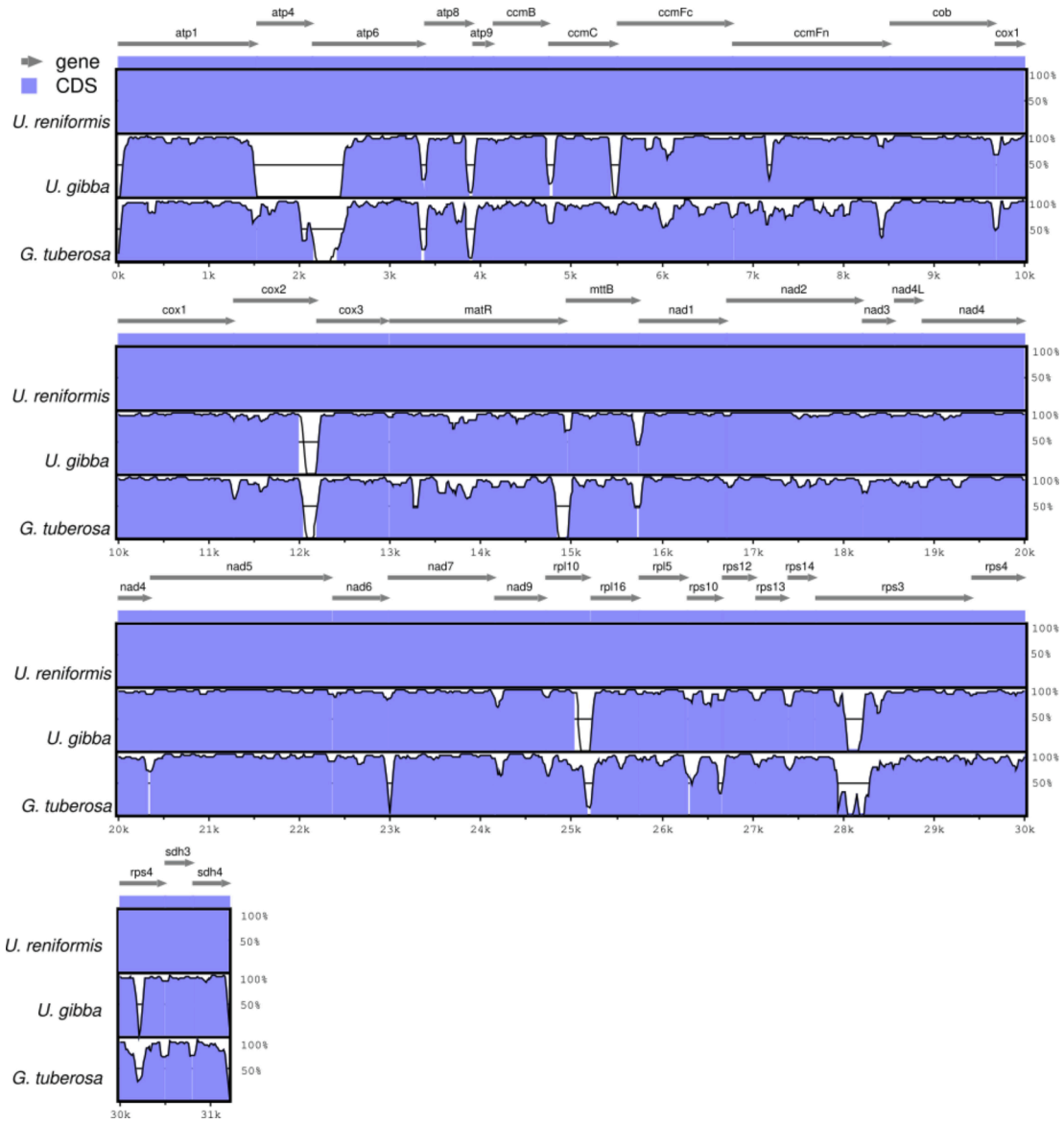

Fig. 2. Identity comparison between mitochondrial genes of *G. tuberosa* and published Lentibulariaceae species (*Utricularia gibba* and *U. reniformis*).

3.4. Phylogenetic hypothesis

Despite the scarce data on mitochondrial DNA sequences in Lentibulariaceae, *G. tuberosa* and the *Utricularia* species are supported as a monophyletic group, as shown in previous studies (e.g. Müller et al., 2006, Silva et al., 2018), based on 36 MT coding genes (Fig. 3). The available sequences of Lamiales in complete mitochondrial genomes in the GenBank database with our data were analyzed. The results showed that the Lentibulariaceae clade is sister to Lamiaceae (*Salvia miltiorrhiza*, *Scutellaria tsinyunensis*, *Pogostemon heyneanus*, *Rotheca serrata* and *Ajuga reptans*), which confirms its monophyly. The tree also support the monophyly of other families of Lamiales (represented in the tree with greater than 2 taxa), such as Orobanchaceae (*Castilleja paramensis* and *Aeginetia indica*), Gesneriaceae (*Haberlea rhodopensis* and *Boea hygrometrica*), Plantaginaceae (*Aragoa cleefii* and *A. abietina*) and Oleaceae (*Osmanthus fragrans*, *Hesperelaea palmeri* and *Fraxinus angustifolia*).

4. Conclusion

The mitochondrial genome of *G. tuberosa* was sequenced and analyzed which is 729,765 bp resulting in useful new datasets for Lentibulariaceae. This is the first MT genome described for the *Genlisea* genus. The genome content indicates a contraction with a gene loss when compared to its phylogenetically related species herein. Nonetheless, the MT genomes of *G. tuberosa* and *Utricularia* species share a high identity regarding the mitochondrial respiratory chain dehydrogenase complex and *cytochrome c oxidase* genes, which are fundamental for energetic demand from the traps. *Cox*1 mutations in *G. tuberosa* indicate that this gene could be related to carnivory specialization, especially in the *Genlisea-Utricularia* lineage. The identification of chloroplast coding sequences in the mitogenome reinforces the importance of gene transfer between the chloroplast and the mitochondria, but further clarification is needed on these foreign genes' functionality. These findings provide new insights into Lentibulariaceae and suggest the importance of mitochondria for the evolutionary history of carnivorous plants, particularly the *Genlisea–Utricularia* lineage.

CRediT authorship contribution statement

Ramon Guedes Matos: Conceptualization, Methodology, Formal analysis, Resources, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Saura Rodrigues da Silva:**

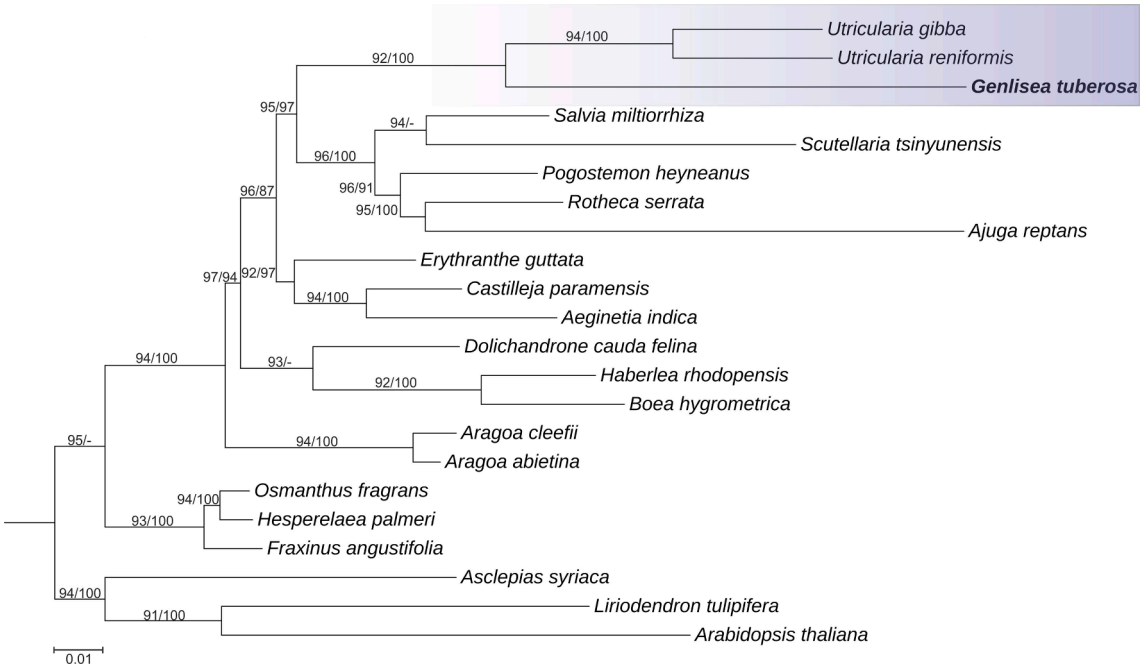

Fig. 3. Maximum likelihood tree based on 36 mitochondrial genes. The values on clades denote the SH-aLRT and ultrafast bootstrap (UFBoot) supports, respectively.

Conceptualization, Methodology, Formal analysis, Resources, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Bartosz Jan Płachno:** Writing – review & editing. **Lubomír Adamec:** Writing – review & editing. **Todd P. Michael:** Conceptualization, Funding acquisition, Resources, Writing – review & editing. **Alessandro de Mello Varani:** Methodology, Writing – review & editing. **Vitor F.O. Miranda:** Conceptualization, Methodology, Resources, Formal analysis, Investigation, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Data availability

The complete mitochondrial genome sequence can be found in GenBank with accession no. (OK274069) after acceptance of the manuscript. The alignment and phylogeny inferred in this study are available from Zenodo (doi: 10.5281/zenodo.6110103).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gene.2022.146391.

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Internet Resources

MPI-MP Chlorobox, https://chlorobox.mpimp-golm.mpg.de/ (May 12, 2021).

RNAmmer v.1.2, http://www.cbs.dtu.dk/services/RNAmmer/ (May 13, 2021).