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Genome size and carnivory in plants

Ph.D. Dissertation

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Abstrakt

Masožravé rostliny fascinovaly vědce od doby, kdy byla u nich masožravost rozpoznána. Nejprve především morfologie, anatomie a fyziologie jejich pastí, v posledních desetiletích jsou však terčem intenzivního výzkumu i jejich genomy. Ačkoli se masožravé rostliny vyvinuly nezávisle v různých kládech krytosemenných rostlin, je evoluce masožravosti obecně podmíněná především nedostatkem živin za současného dostatku vody a světla. Několik nezávislých kládů tak sdílí obecně definované podmínky, které mohou ovlivňovat i vlastnosti jejich genomů, což z masožravých rostlin dělá zajímavou skupinu pro různé srovnávací analýzy.

V čeledi Lentibulariaceae (Lamiales) byly nalezeny nejmenší genomy mezi krytosemennými rostlinami. Detailní analýza velikosti genomu v této čeledi ukázala, že k extrémní miniaturizaci genomů dochází pouze v některých fylogenetických kládech, ačkoli všechny druhy této čeledi mají genomy menší než blízce příbuzné nemasožravé rostliny (**článek I**). Obsah GC bází v genomech těchto rostlin je navíc neobvykle variabilní (**článek I**).

Druhově nejbohatší masožravý klád se nachází v řádu Caryophyllales a genomicky nejzajímavější je zde čeleď Droseraceae, u jejíchž zástupců byla zjištěna přítomnost holokinetických chromozomů. Zatímco velikost genomů masožravých rostlin v této skupině se nelišila od jejich nemasožravých příbuzných, ukázalo se, že nezanedbatelná variabilita obsahu GC bází v genomu souvisí s vnějšími podmínkami, neboť druhy přímo vystavené klimatickým extrémům (sucho, mráz) měly významně vyšší obsah GC bází, což pravděpodobně zvyšuje stabilitu DNA v těchto potenciálně klastogenních podmínkách (**článek II**). Za jeden z možných důsledků chromozomálního holokinetismu je považována negativní korelace mezi počtem chromosomů a velikostí genomu napříč liniemi s touto chromosomální strukturou, což bylo potvrzeno u části čeledi Droseraceae (**článek II**). Nicméně, až výsledky **článku III** ukázaly, že holokinetismus je zřejmě apomorfií celé čeledi Droseraceae.

Opakovaně testovaná souvislost mezi dostupností živin v prostředí a velikostí genomu organismu v tomto prostředí žijícím nebyla u masožravých rostlin potvrzena. Rozsáhlá analýza velikosti genomu zástupců sedmi masožravých kládů nepotvrdila miniaturizaci genomu spojenou s evolucí masožravosti, uvažovanou právě v souvislosti s výskytem masožravých rostlin na živinami chudých půdách (**článek IV**). Je možné, že masožravost vyvažuje nedostatek živin do té míry, že výrazná miniaturizace genomu není nezbytná a extrémně malé genomy některých masožravých rostlin jsou výsledkem procesů nezávislých na okolním prostředí. Menší velikost genomu nebyla spojena ani s jednoletými masožravými rostlinami, u nichž by mohla být limitace živinami zesílena nutností rychlého růstu. Vliv vytrvalosti a jednoletosti na velikost genomu se však potvrdil u nemasožravých rostlin, což je sice obecně akceptovaný trend, avšak dosud nebyl otestován na takto rozsáhlém datovém souboru fylogeneticky korigovanou analýzou.

Abstract

Carnivorous plants have fascinated scientists since their carnivory was recognized. At first especially the morphology, anatomy and physiology of their traps, but their genomes have also been the subject of intensive research in recent decades. Although carnivorous plants evolved independently in several clades of flowering plants, the evolution of carnivory is generally conditioned especially by a lack of nutrients with sufficient water and light. Several independent clades thus share generally defined conditions that may affect the properties of their genomes, making carnivorous plants an interesting group for various comparative analyses.

The smallest genomes among flowering plants have been found in the family Lentibulariaceae (Lamiales). Comprehensive genome size analysis of this family showed that extreme miniaturization of genomes occurs only in some phylogenetic clades, although all species of this family have genomes smaller than closely related non-carnivorous plants (**Paper I**). Notably, the content of GC bases in the genomes of these plants is unusually variable (**Paper I**).

The most species-rich carnivorous clade is found in the order Caryophyllales and its most genomically interesting clade is the family Droseraceae, as holokinetic chromosomes have been reported in some of its representatives. While the genome size of carnivorous plants in this group did not differ from their non-carnivorous relatives, it was shown that the remarkable variability of the GC content in their genome was related to external conditions, as species directly exposed to climatic extremes (drought, frost) had significantly higher content of GC bases, which probably increases DNA stability in these potentially clastogenic conditions (**Paper II**). One of the possible consequences of the chromosomal holokinetism is the negative correlation between the chromosome number and the genome size across lineages with such chromosomal structure, as confirmed in part of the Droseraceae family (**Paper II**). However, only the results of **Paper III** have shown that holokinetism appears to be an apomorphy of the entire Droseraceae family.

The repeatedly hypothesized connection between nutrient availability in the environment, and the genome size of the organism living in this environment has not been confirmed in carnivorous plants. An extensive genome size analysis of the representatives of the seven carnivorous clades did not confirm the miniaturization of the genome associated with the evolution of carnivory, considered in particular in relation to their general occurrence on nutrient-poor soils (**Paper IV**). It is possible that carnivory counterbalance the nutrient limitation to the degree that no prominent genome miniaturization is necessary and extremely small genomes of some carnivorous plants resulted from processes independent of the outer environment. The smaller genomes were not connected even with the annual carnivorous plants, in which the nutrient limitation could be increased by the necessity of the fast growth. However, the influence of life histories on the genome size have confirmed in non-carnivorous plants, which is generally accepted trend, but it has not been tested on such large dataset with phylogenetically corrected analysis so far.

Poděkování - Acknowledgements

Author contributions to the papers in the thesis

Paper I

Veleba A, Bureš P, Adamec L, Šmarda P, Lipnerová I, Horová L. 2014. Genome size and genomic GC content evolution in the miniature genome sized family Lentibulariaceae. *New Phytologist* **203**: 22–28.

AV sampled the plant material, AV, LH and IL analysed the samples. IL, PŠ and AV analysed the data, PŠ, PB, AV, LA, and IL cooperated on the manuscript, commented the results and their interpretations.

Paper II

Veleba A, Šmarda P, Zedek F, Horová L, Šmerda J, Bureš P. 2017. Evolution of genome size and genomic GC content in carnivorous holokinetics (Droseraceae). *Annals of Botany* **119**: 409–416.

AV sampled and LH analysed the plant material. AV, PŠ and FZ analysed the data, AV, PB, FZ, JŠ and PŠ prepared the manuscript, commented the results and their interpretations.

Paper III

Kolodin P, Cempírková H, Bureš P, Horová L, Veleba A, Francová J, Adamec L, Zedek F. 2018. Holocentric chromosomes may be an apomorphy of Droseraceae. *Plant Systematics and Evolution* **304**: 1289–1296.

PB and FZ designed the experiment, AV, LA and HC secured the samples and their cultivation, HC, JF, and PK prepared and cultivated in vitro cultures. LH, FZ, and PK analysed the plant material in laboratory. FZ analysed the data, interpreted the results and led the writing, PB, LA, HC, PK, and AV commented and co-worked on the manuscript.

Paper IV

Veleba A, Zedek F, Horová L, Veselý P, Srba M, Šmarda P, Bureš P. (unpubl.) Is the evolution of carnivory connected with a genome miniaturization? Large-scale test of the nutrient limitation hypothesis. [*submitted* to the American Journal of Botany]

AV and MS collected the samples, LH analysed them. PB, FZ, PŠ, and PV excerpted the data from literature. AV and FZ performed statistical analyses, AV led writing, FZ and PB co-worked on the manuscript and results interpretations.

Content

Preface

Everyone should have a hobby. It has been repeatedly proven that it is helpful for human mental health. But sometimes it is more than that. Sometimes it helps to decide the important life questions, sets directions, and goals one wants to achieve. Carnivorous plants fascinated me from the childhood to the degree that they directed me to study botany. My passion for them is so strong that it overcome even my deep hatred to statistics.

However, this fascination, either scientific or inexpert, has its rightful basement. Carnivorous plants are not only showy and popular for their unique properties, they represent rare examples of the plant evolution in very specific conditions. And despite this uniqueness, they have evolved repeatedly in completely different clades of flowering plants, showing extremely interesting adaptations to catch, kill, digest and use the prey. All of this is inevitably based in their genome and makes them interesting for studies at molecular scale.

The specificity of conditions where carnivorous plants can evolve influence many things in the plants, supposedly also the genome as a whole. That makes carnivorous plants interesting also for studies of genomes interacting with the surrounding environment. As a botanist, I have always considered this direction more interesting than deep "molecular diving". This work therefore aims more to search for various connections between genome as a whole and the outer environment.

Carnivorous plants

The model group of this dissertation are carnivorous plants – mixotrophic organisms that photosynthesize and can be fully autotrophic, but their adaptation allows them to acquire additional nutrients and even complex molecules (e.g. amino acids, Karagatzides & Ellison 2009) to enhance their growth. They have evolved in ten clades of flowering plants, and comprise species with various life strategies, life histories, and distribution (Fleischmann et al. 2018): Bromeliaceae, and Eriocaulaceae (Poales), Cephalotaceae (Oxalidales), Droseraceae, Drosophyllaceae, Nepenthaceae, and Dioncophyllaceae (Caryophyllales), Roridulaceae, and Sarraceniaceae (Ericales), Byblidaceae, Lentibulariaceae, and Plantaginaceae (Lamiales).

Carnivorous plants are characterized by a certain set of features that are different or completely unique when compared to the non-carnivorous ones (Ellison & Adamec 2018a):

1. capturing or trapping prey in specialized, usually attractive, traps;
2. killing the captured prey;
3. digesting the prey;
4. absorption of metabolites (nutrients) from the killed and digested prey;
5. use of these metabolites for plant growth and development.

The most prominent organs of carnivorous plants are usually their specialized traps. There are basically two most widespread mechanisms of prey trapping: gravity and adhesive traps.

The adhesive traps evolved convergently in five independent clades (clade of carnivorous Caryophyllales, Lentibulariaceae, Byblidaceae, Roridulaceae and genus *Philcoxia*) and they are the most widespread in the sense of species number. The principle lies in a secretion of a sticky fluid by specialized glands on leaves, where relatively small prey gets trapped. Defensive glandular hairs have almost surely served as pre-adaptations for the evolution of these traps (Givnish et al. 2018). It is not uncommon that these traps are capable of slow movement, grasping the prey more tightly.

The adhesive traps have also served as a pre-adaptation for most of the more complex traps. In Lentibulariaceae it served as a pre-adaptation for eel traps of *Genlisea* or suction traps of *Utricularia* (Fleischmann 2012). The adhesive traps in carnivorous clade of Caryophyllales evolved into specialized forms with "snapping tentacles" in *Drosera glanduligera* (Poppinga et al. 2012), but they also gave rise to unique snap traps of *Dionaea muscipula* and *Aldrovanda vesiculosa*, as well as gravity traps of *Nepenthes* (Heubl et al. 2006).

The gravity traps evolved to accumulate the prey in pitcher-shaped leaves (Sarraceniaceae, Nepenthaceae, Cephalotaceae) or in a cistern formed in the center of the leaf rosette (carnivorous bromeliads and *Paepalanthus bromelioides*). They convergently evolved six times, either from previously carnivorous plants with adhesive traps or from structures accumulating water. These traps include various

adaptations to raise the probability of successful capture, and they can accumulate relatively large amounts of prey or capture a relatively large one (even small vertebrates).

However, it would be a mistake to understand carnivory and non-carnivory as a simple two sided coin. The carnivorous plants are still "only" green flowering plants, and their life depends on the availability of water, light and mineral nutrition. Individual clades, genera or even species also differ in their efficiency of carnivory – different trap types involve different investments, maintenance, but also benefits for their bearers.

The attempts to quantify the measure of carnivory via nutrient gain, efficiency of carnivory or growth benefit (reviewed in Adamec 2011, 2017, Adamec & Pavlovič 2018) do not provide us with a general solution. The consequences, which should be considered in such quantification are wider than one might expect. Carnivorous plants are known for a low relative growth rate and low photosynthetic rate (Ellison & Adamec 2011), but the reutilization of N and P from senescing organs is exceptionally high (Adamec & Pavlovič 2018). Moreover, due to their reverted relationship with animals, the ecological interactions with other organisms include wider set of options than in standard non-carnivorous flowering plants. Carnivorous plants has to solve a trade-off between captured prey and successful pollination (Cross et al. 2018). Their traps can be specialized to capture a prey of a certain type (Darnowski et al. 2018), but they can also host a very broad scale of various inquilines (Bittleston 2018, Miller et al. 2018, Sirová et al. 2018). Even a nutritional mutualistic symbiosis has been documented in *Roridula* and some *Nepenthes* species (Moran et al. 2018).

The premises of the evolution of carnivory – is there anything common after all?

There are slightly more than 800 carnivorous species currently recognized (Ellison & Adamec 2018a), which is only about 0.2 % of the estimated species richness of flowering plants (Stevens 2001 onwards). The carnivory is clearly an adaptation to gain more nutrients in nutrient poor habitats and it might be considered as a competitive advantage. However, the first evaluation of costs and benefits of carnivory (Givnish et al. 1984) explained that despite the beneficial effect of supplementary nutrients released from the bodies of trapped prey, the traps are photosynthetically inefficient and costly compared to normal leaves, and the benefits of carnivory exceed the costs only in nutrient poor, but sunny and moist habitats.

This model has been recently revisited and further expanded (Givnish et al. 2018). The evolution of carnivory is truly most probable in nutrient poor, but sunny and moist habitats. However, there are other assumptions to be considered. The evolution of carnivory is more probable when certain pre-adaptations are present, such as defensive glandular hairs. It is also probable that not only soil infertility, but also soil anoxia and toxicity should favour carnivorous plants, as carnivory enables lower allocations to roots due to nutrient uptake from traps. On the other hand, the need of water availability limits the probability of evolution of carnivory in epiphytic species, because

they often undergo short, unpredictable periods of drought. Carnivorous plants can grow in seasonal climates, where the water availability is predictable, manifesting carnivorous syndrome only during the favourable season.

The spatial occurrence of many carnivorous plants is sparse and scattered, but the nature range of some carnivorous genera or even species can comprise a significant part of the globe. The cost-benefit model explains what habitats and conditions facilitate the evolution of carnivory in plants. Though the ten carnivorous clades do not share a common ancestor, age or place of origin, they often share the same habitats all around the world, which makes them interesting and potentially very promising model group.

Genome size

The amount of genetic information of the given Eukaryotic organism spatially defines the size of its cell nuclei. This has been described by the terms "genome size" or "C-value". Greilhuber et al. (2005) further suggested the delimitation of 1C and 2C, defined as genome size of cells in haploid (or holoploid) and diploid state, respectively, which is widely followed including this thesis. Finally, Cx refers to the "monoploid genome size", and is used preferably in recent polyploids to express the amount of DNA of the single set of chromosomes (Cx = 2C/ploidy level).[1]

The genome size varies greatly among different species (200,000-fold in Eukaryota; >2400-fold in Angiosperms [Fig. 1]; Olefeld et al. 2018; Bennett & Leitch 2012, respectively), but the intraspecific variability, though it may occur, remains only on finer scales (Šmarda & Bureš 2010). It is therefore a species-specific characteristic, entangled with the evolutionary history of the given species.
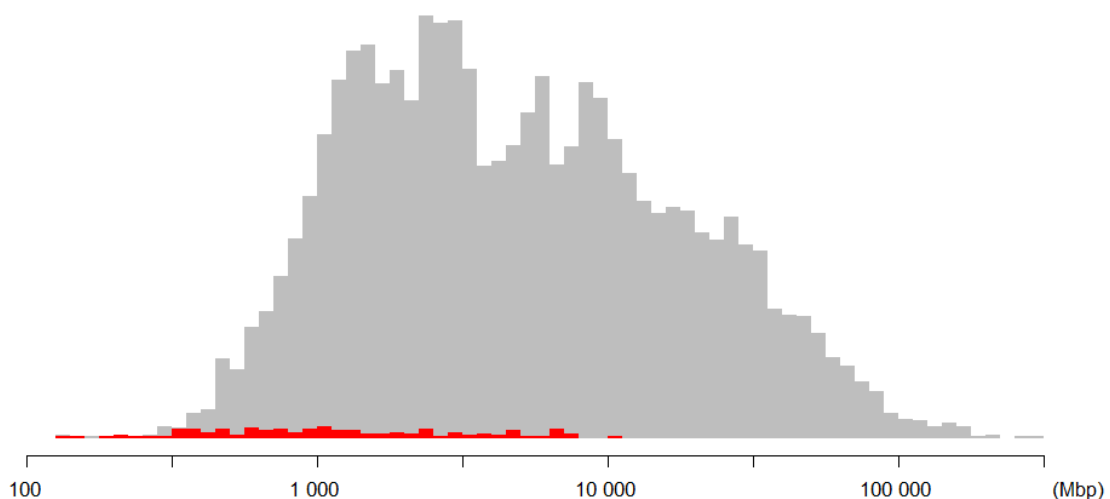
Figure 1: Distribution of 2C genome sizes in carnivorous plants (red) and other flowering plants (grey). Data from Plant DNA C-value Database (Bennett & Leitch 2012) and **Paper IV**, log10 transformed.

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[1] Please note, this thesis presents genome sizes as 2C, but they were presented as 1C in Paper I and Paper IV and both 2C and Cx was used in Paper II. The reader should keep this in mind, as it might cause confusion when comparing results of different papers.

The minimal amount of genetic information is surprisingly low, the theoretical minimum of diploid plant genome has been calculated to about 100 Mbp (Bennett & Leitch 2005) and some species truly possess such extremely small genomes: *Genlisea tuberosa* and *G. aurea* (2C = 122 Mbp and 127.2 Mbp, respectively; Fleischmann et al. 2014). However, some of the plant genomes can be more than 2400-times larger, as the largest genome size is currently known from *Paris japonica* (2C = 297 761.8 Mbp; Pellicer et al. 2010).

Such variation usually results from two main processes. In long term, genomes mostly expand or shrink by proliferation or removal of retrotransposons (Bennetzen et al. 2005), while fast, evolutionary recent genome expansions result from polyploidization events.

Genome miniaturization in the family Lentibulariaceae

The family Lentibulariaceae (order Lamiales) comprise three genera: *Pinguicula*, *Genlisea*, and *Utricularia*. The common ancestor of this family was probably close to the extant species of *Pinguicula* (Fleischmann 2012). The species of this genus trap small arthropods on the adhesive surface of their leaves. The genera *Genlisea* and *Utricularia*, which form a sister clade to *Pinguicula*, are highly specialized plants with significantly altered body plan (Rutishauser 2016). Traps of both genera are modified leaves, homological to the adhesive leaves of *Pinguicula*. In *Genlisea*, the leaves are changed into rhizophylls: two helically twisted arms are shaped like an eel trap, and capture small prey living in a wet soil or water. Photosynthetic above-ground leaves are of different ontogenetic origin (Rutishauser 2016). The same pays for genus *Utricularia*, whose traps are the small (usually a few millimetres) sucking bladders, working only in the presence of water. The cells actively transport water outside the bladder which forms negative pressure inside. Once the prey triggers the trap door, it is suctioned inside and the door closes again.

The genome miniaturization in this family was originally pointed out by Greilhuber et al. (2006), presenting the smallest Angiosperm genome found in *Genlisea aurea*. Though that study presented only a relatively small proportion of the total species richness, they found several other miniature genomes and inspired further genomic research in this family.

Our study (**Paper I**) substantially increased the number of the analysed species, which allowed us a reconstruction of the evolution of the genome size in this family. Though all genomes of Lentibulariaceae species are small in the context of flowering plants, which could support the nutrient limitation adaptive hypothesis proposed by Leitch & Leitch (2008), the prominent miniaturization has been actually detected only in some clades. These are the genus *Utricularia* and one clade of *Genlisea*. There are however two other clades in the genus *Genlisea*, whose species actually possess the largest genomes in the family Lentibulariaceae, and the genomes of *Pinguicula* also tend to increase their sizes in comparison with their ancestors. The genomic evolution in Lentibulariaceae is not uniform and the changes are the most dramatic in the *Genlisea-Utricularia* clade.

The genera *Genlisea* and *Utricularia* were already known for extremely high substitutional rates (Jobson & Albert 2002). Their cytochrome *c* oxidase was found altered in comparison to other plants in the database (Jobson et al. 2004), and it is probable that this alteration is capable of faster adenosine triphosphate production (Laakkonen et al. 2006). However, its drawback is the increased production of reactive forms of oxygen (= reactive oxygen species, ROS) which can damage the cell, including the DNA (Albert et al. 2010, Renner et al. 2018). The bladders of *Utricularia* has truly been shown to promote significantly higher respiration than vegetative tissues (Adamec 2006), which was later confirmed by significantly increased expression of genes involved in respiration (Ibarra-Laclette et al. 2011a). The ROS hypothesis might therefore explain not only increased substitutional rates, but also the extreme genome miniaturization, both resulting from numerous repairs of the DNA damaged by ROS (Renner et al. 2018).

Ibarra-Laclette et al. (2013) considers also the possibility of strong mechanisms of retrotransposon silencing coupled with preferential deletion over insertion. This selectively neutral mechanism would explain the genome size decrease simply by random genetic drift. The comparative analysis of genomes of *G. hispidula* and *G. nigrocaulis* by Vu et al. (2015) supports this hypothesis. The sequences of extremely miniaturized *G. nigrocaulis* showed not only very low proportion of retrotransposones (7.3%), but its whole genome seems to be influenced by the genome shrinkage process (e.g. lower number of genes, shorter introns etc.). Vu et al. (2015) further suggest a necessity of whole genome duplication at some point, or the genomes could shrink below the point of the species viability.

The driving process of the genome miniaturization in Lentibulariaceae, particularly in the *Utricularia-Genlisea* clade, has not been completely resolved yet. While none of the proposed processes or even their combination cannot be excluded, the fully sequenced genome of *U. gibba* (Ibarra-Laclette et al. 2013) and partially sequenced genomes of *G. aurea*, *G. hispidula*, and *G. nigrocaulis* (Leushkin et al. 2013, Vu et al. 2015) allow us to conclude the results of the miniaturization. The *Genlisea-Utricularia* clade seems to lack a substantial number of genes involved in root regulation. While this is apparently connected with their altered body plan (Rutishauser 2016), the total number of *U. gibba* genes is actually slightly higher than in *Arabidopsis thaliana* (Ibarra-Laclette et al. 2013). But most importantly, non-coding regions in the extremely small-genomed species of Lentibulariaceae are almost completely absent, leaving the genome purified nearly to the theoretical minimum of the plant genome size.

Genome size in the family Droseraceae

The family Droseraceae covers a substantial part of the most species-rich and oldest known carnivorous clade in the non-core group of Caryophyllales (Stevens 2001 onwards), which is sometimes delimited as a separate order Nepenthales (Fleischmann et al. 2018). In **Paper II**, we have calculated the minimal age of carnivory in this clade to about 74.48 Mya, but other studies found it even older (Fleischmann et al. 2018:

85.6 Mya). The first carnivorous ancestor almost surely trapped its prey by flypaper traps, which has possibly evolved from secretory glands, similar to the multicellular salt-secretory glands found in some extant members of Plumbaginaceae, Frankeniaceae, and Tamaricaceae. The flypaper traps with movement ability in *Drosera*, snap traps of *Dionaea muscipula* and *Aldrovanda vesiculosa*, as well as pitchers of *Nepenthes*, eventually evolved from this common ancestor (Heubl et al. 2006).

In **Paper II**, we have compared the genomes of carnivorous and non-carnivorous species of non-core Caryophyllales with special emphasis on family Droseraceae. Their genomes are small in relation to the genome size variation across whole Angiosperms, but far from extremely miniaturized like in some Lentibulariaceae (Droseraceae median 2C = 1252 Mbp [**Paper II**] vs. Lentibulariaceae median 2C = 560 Mbp [**Paper I**]). There have not been any difference found between the genome sizes of carnivorous and non-carnivorous species in this clade, which does not support the nutrient limitation hypothesis we aimed to test.

Physiological, anatomical, and ecological limitations in the evolution of genome size

The genome size is not only a descriptive characteristic, even the plain amount of DNA in the nuclei has been repeatedly presented as evolutionary important in various consequences. The genome size (~ nuclear volume) is correlated with the cell size (Cavalier-Smith 2005; Jorgensen et al. 2007), which has been shown important in tall woody flowering plants. In order to keep the mechanical properties (especially diameter) of their xylem cells suitable for the long water and nutrient transport, their diploid genomes does not exceed about 10 Gbp (Stebbins 1938; Beaulieu et al. 2008).

Similarly, short living species (annuals) are hypothesised to be limited by their life expectancy. As the greater amount of DNA takes longer time to replicate, the genomes of short living organisms should be selectively kept in the size which allows them to finish their life cycle in the time they have – shorter life means smaller genome (Bennett 1971, 1972, 1987). The replication time of the DNA is not the only limit, since the short living organisms need to grow fast and their demands for nutrients are quite high in the given time, which should again favour smaller genomes over large ones as well (Hessen et al. 2008).

The DNA-molecule is rich in phosphorus (P) and nitrogen (N), hence the larger the genome is, the higher are its needs for these two macroelements (Hessen et al. 2009, Elser et al. 2011). The soil nutrient P or N content has been hypothesised to promote selection for genome size, allowing the successful growth of plants with larger genomes on nutrient rich soils, while nutrient poor soils should promote selection for small-genomed species (Leitch & Leitch 2008, **Paper I**). This tendency has been experimentally supported in two similar long-term fertilization experiments, where both Šmarda et al. (2013) and Guignard et al. (2016) recorded more species with larger genomes in N and P enriched plots. Also, members of the genus *Primulina* with smaller genomes were favoured in N-poor environment of limestone karsts (Kang et al. 2015).

On the other hand, the global distribution of polyploids did not follow the soil P availability (Rice et al. 2019). Carnivorous plants, as a phylogenetically diverse group restricted to nutrient poor habitats, might serve as a suitable model for further development of this hypothesis.

The results are ambiguous. Indeed, carnivorous plants of the family Lentibulariaceae have strikingly miniature genomes, much smaller than those of their non-carnivorous relatives (**Paper I**), but the genome sizes of carnivorous and non-carnivorous species of the non-core Caryophyllales (**Paper II**) do not differ at all. We have therefore analysed genomes of species from seven independent carnivorous clades in a large scale analysis and compared them with genome sizes of their non-carnivorous relatives in **Paper IV**. However, no significant difference was observed, the genomes of carnivorous species are not significantly smaller than those of their non-carnivorous relatives.

We have to consider that despite growing on nutrient poor soils, carnivorous plants obtain additional nutrients from carnivory, which is actually an adaptation avoid this limitation. The degree, to which they are successful or not, is hard to quantify, but they can obtain up to 100% of the N and P they need from the prey (Adamec & Pavlovič 2018), which can play against the expected selection of nutrient poor habitats for small genomes. As it has been already mentioned, carnivory has evolved as one of the responses to nutrient scarcity (Givnish et al. 1984, 2018), but is barely the only ecological factor driving their evolution and the evolution of their genomes. There are many other plant species successfully growing in the same habitats and they often share other adaptations for these habitats, carnivorous or non-carnivorous plants side by side.

We have also considered the influence of life forms and life histories on genome size and our analysis revealed a tendency of short living plants to have smaller genomes than their perennial relatives. Though this tendency is widely accepted, it is based on the work of Bennett (1972), which has been published before the rise of the phylogeny based statistics. There are studies supporting this hypothesis (Albach & Greilhuber 2004, Zahradníček et al. 2018), but these have worked on a small phylogenetic scale. The **Paper IV** is the first one, which confirms smaller genome sizes in short living plants on a large dataset and broad phylogenetic scale.

GC content

It is well known that four bases form the DNA: adenine (A), thymine (T), guanine (G), and cytosine (C). Always two of them stack together, A and T are connected by a double bond, G and C by a triple bond. As they form stable pairs and these pairs have different properties, it is meaningful to recognize and analyse the so called "GC content", which express the proportion of the GC bases in the whole DNA of the given species.

The GC content in coding regions is clearly a result of selection for the optimal gene sequence, but the majority of the average plant genome is formed by noncoding DNA, particularly retrotransposons (Bennetzen et al. 2005, Grover & Wendel 2010). Their activity together with random mutations on the genome are responsible for the variability of this genomic parameter (Šmarda & Bureš 2012, Veselý et al. 2012). The GC content of genomes of flowering plants usually vary between 35 – 40 %, but it can be as much as 33 – 50 % (Šmarda & Bureš 2012). The relationship of the genome size and GC content across all flowering plants is a quadratic correlation with the peak around 18 400 Mbp (Veselý et al. 2012). However, the majority of plant genomes is smaller than this value and most of the studies found only positive correlation of the genome size with the GC content, which is true also for the **Paper I** and **II**.

The guanine and cytosine are more complex molecules, whose synthesis is more nutrient and energy demanding (Rocha & Danchin 2002). The selection for lower GC content might be therefore at play to save resources (Veselý et al. 2012). However, compared to the overall nutrient and energy consumption of the whole genome and its variation, the additional consumption of GC richer genome is only marginal and might play a significant role only in the largest of genomes.

The AT and GC base pairs also differ in their properties. The AT double bond might be preferred in the largest of genomes, because it allows higher degree of curvature, thus the DNA can be more condensed (Veselý et al. 2012). On the other hand, due to the triple bond and higher stacking interactions, the GC base pairs are more stable (Biro 2008, Šmarda & Bureš 2012). There has been repeatedly detected a positive correlation of GC content and thermal optimum of bacteria, which indicates that the stabilizing effect of the GC base pairs on the DNA could be the reason (Nishio et al. 2003; Foerstner et al. 2005; Musto et al. 2006; Mann & Phoebe-Chen 2010). Though the GC variation in plants is lower than in bacteria, Šmarda et al. (2014) found higher GC contents connected to higher cold and drought tolerance.

Our study of the family Lentibulariaceae (**Paper I**) showed an extremely high GC content variation for a single flowering plant family: 11.1% between the GC richest and poorest genome of Lentibulariaceae species. This variation is actually true only for the *Utricularia-Genlisea* clade, as the GC content variability in the genus *Pinguicula* is only 4.5%. While it could be accounted for the activity of retrotransposons with different GC content, this clade has already been shown to be unique in genome size and other genomic properties. The same mechanisms, which were hypothesised to shape the whole genome and increase the mutational rates, might be also responsible

for the extreme GC content variability. Thought the study of Ibarra-Laclette et al. (2011b) could not confirm the ROS influence on the GC content of *Utricularia gibba*, the sequences of *U. gibba* used in that study were incomplete, showing different GC content (49.2%) than was later estimated based on the whole genome sequence (40%; Ibarra-Laclette et al. 2013) and confirmed also by **Paper I** (39.9%).

In **Paper II**, we have analysed the genomes of Droseraceae. While their GC content variability was not that extreme as in Lentibulariaceae, it was still remarkably high (7.6%) and unlike Lentibulariaceae, Droseraceae does not exhibit any known peculiarity in its genomic properties. We have accounted it to the various ecological strategies to survive in different climatic conditions. The GC content was truly positively correlated with the annual temperature fluctuations, with the highest GC contents in species openly exposed to hot summer or freezing winter temperatures. Species growing in more stable climatic conditions were among the most GC poor in the dataset. Our results are therefore in general concordance with the predicted stabilizing effect of increased GC content in the genome under stressing factors.

Holokinetic chromosomes in Droseraceae

The "standard" monocentric chromosomes, forming from the cell nucleus during cell division, have a centromeric region, often visually prominent as a constriction on the chromosome, which ensures connection and polar bi-orientation of sister chromatids, and where the kinetochore is formed. Acentric fragments of such chromosomes are therefore lost during the cell division.

On the other hand, the kinetochores of the holokinetic chromosomes are formed along most of the poleward chromatide surfaces. As a result, chromosomal fusions and fissions are tolerated and chromosomal fragments are regularly inherited (Melters et al. 2012, Bureš et al. 2013). Such chromosomal arrangement can substantially affect the evolution of the karyotype and genome of holokinetic organisms.

In monocentrics, a model of centromeric drive has been proposed to explain the paradox situation, where centromeric function is essential and conserved in all eukaryotic organisms, but the size and complexity of centromeres varies significantly and evolves rapidly (Henikoff et al. 2001, Malik & Henikoff 2009). This phenomenon occurring only in organisms with asymmetric meiosis (typically female in which only one from four meiotic products survives), where the sister centromeres compete for the microtubules emanating from egg- or polar body-poles during cell division via their size to increase their probability to be transmitted to the egg (Talbert et al. 2008, Burrack et al. 2011, Bureš & Zedek 2014). The evolution of holokinetism could be understood as an adaptation to avoid the negative consequences of centromeric drive (e.g., against hitch-hiker mutations accumulated in pericentromeric areas of driving centromeres; Talbert et al. 2008, Zedek & Bureš 2016). However, the holokinetic lineages are often remarkable for their genome size and chromosome count variability, with a common negative correlation between these two parameters (reviewed in Bureš & Zedek 2014). This situation, where species with more chromosomes has smaller genome than its relatives with less chromosomes has been explained by a holokinetic drive (Bureš & Zedek 2014), which is analogous process to the centromeric drive, only concerning the whole chromosome size instead of the size of the centromeric region (because in holokinetics the centromere is actually whole chromosome; Bureš & Zedek 2014).

The chromosomal holokinetism is widely distributed across eukaryote phylogeny: it has evolved either in plants or in animals, e.g. Juncaceae, Cyperaceae, Droseraceae, several clades of nematodes, spiders, scorpions, millipeds or insects (Melters et al. 2012, Bureš et al. 2013). It remains unclear, what adaptive causes and enables the evolutionary switch from monocentric to holocentric chromosomes. Apart from already mentioned attempt to avoid the negative consequences of centromeric drive (Zedek & Bureš 2016), the holokinetic chromosomes lend their bearers other distinctive features. Since the chromosomal fragments are regularly inherited in holokinetic species, their resilience to clastogenic factors (e.g. high-energy electromagnetic radiation, desiccation, freezing, and chemicals) which can damage the chromosomes is higher than in monocentrics (Melters et al. 2012, Zedek & Bureš 2018). Through this increased resilience to the outer clastogens, holokinetism has been hypothesised to be a characteristic enabling the exploitation of new habitats, including

even the colonisation of the land (Zedek & Bureš 2018). The evolution of holokinetism (meaning the switch from monocentrism) might be therefore random, but holokinetism itself represents a potential advantage in exploiting stressing habitats. On the other hand, number of cross-overs in holokinetics is limited to one or two (Nokkala et al. 2004), which can be an evolutionary disadvantage, once the organism adapts to its new habitat.

Among carnivorous plants, only members of the family Droseraceae have been reported to possess holokinetic chromosomes (Rothfels & Heimburg 1968; Sheikh et al. 1995; Kondo & Nontachaiyapoom 2008; Shirakawa et al. 2011a, b; Zedek et al. 2016), but the literature reports were ambiguous. The chromosomal structure of *Aldrovanda vesiculosa* was suggested holokinetic (Shirakawa et al. 2011a), but its closest relative *Dionaea muscipula* was considered a monocentric (Hoshi and Kondo 1998; Shirakawa et al. 2011a). The genus *Drosera* was considered holokinetic, but some researches proposed five *Drosera* species being monocentric (Shirakawa et al. 2011b, Demidov et al. 2014). In **Paper II** we have considered all *Drosera* species except one being holokinetic, and Drosera regia, Dionaea muscipula and Aldrovanda vesiculosa as monocentrics. We aimed to test the difference between genome size and GC content of the holokinetic and monocentric species in the clade of non-core Caryophyllales. Bureš et al. (2013) suggested a genome size decrease connected with the evolution of holokinetism (the dataset included also several *Drosera* species) and the study of Šmarda et al. (2014) found significant decreases of both of these characteristics in holokinetics of the cyperid clade. However, the genome size and GC content between holokinetic and monocentric species did not differ.

Still, the outcome of the hypothesised holokinetic drive (Bureš & Zedek 2014), the negative correlation between genome size and chromosome number, was confirmed in genus *Drosera*. It was particularly obvious in the "Australian clade" (see the **Paper II** for details), where *D. micrantha* has about nine times larger genome size than *D. peltata*, while its chromosome count is only about one third of the chromosome count of *D. peltata* (*D. micrantha* 2n=10 and 2C=7489 Mbp, *D. peltata* 2n=32 and 2C=829 Mbp).

The **Paper III** shed new light on the chromosome structure in Droseraceae. We have used a method based on flow cytometric analysis of gama-irradiated samples (Zedek et al. 2016), which is completely independent of the microscopic methods analysing chromosomal kinetochore histochemically, chromosomal anaphase behaviour or heritability of induced chromosomal fragments/micronuclei formation in next cell generations (Shirakawa et al. 2011b, Bureš et al. 2013, Demidov et al. 2014). The results were quite surprising, but not lacking parsimony, as the holokinetism was detected in all tested members of Droseraceae, while the chromosomal structure of *Drosophyllum lusitanicum* (family Drosophyllaceae, a part of the sister clade to the family Droseraceae) was confirmed to be monocentric. The holokinetism could be therefore an apomorphy of the family Droseraceae[2].

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[2] Even with new data from **Paper III**, the results of **Paper II** are the same: there is no difference between the genome size or GC content of the holokinetic and monocentric species in this clade.

Summary of used methods

The experiments performed during the research in this thesis included methods shortly presented below. The detailed description of the experimental procedures and data processing is a part of each paper enclosed to this thesis.

Flow cytometry

This method enables genome size and base content estimation. The procedure has been described in Šmarda et al. (2008) in detail. Fresh tissue (typically leaves) of both the measured sample and the internal standard is cut in Otto I buffer (Otto 1990), so the nuclei are released from cells. The suspension is filtered, incubated and Otto II buffer (Otto 1990) with a particular fluorochrome is added. Two fluorochromes were used in our study, intercalating propidium iodide (PI) and AT-specific 4',6-diamidino-2-phenylindole (DAPI). The co-processing of the sample with internal standard ensures maximum precision. Internal standards (Tab. 1) are based on the fully sequenced *Oryza sativa* subsp. *japonica* 'Nipponbare' (2C = 777.6 Mbp, GC = 43.6 %; International Rice Genome Sequencing Project, 2005).

The measurement itself was performed on flow cytometers CyFlow (Partec GmbH, Germany) equipped either with green laser (for PI fluorochrome) or UV led excitation source (for DAPI fluorochrome). The ratio between resulting peaks of sample and internal standard allows direct calculation of the complete genome size. The AT and GC content is calculated from ratios between sample and standard on PI and DAPI using the *regula falsi* method (Šmarda et al. 2008).

Standard	2C (Mbp)	GC (%)
Utricularia sandersonii	408.2	41.4
Oryza sativa 'Nipponbare'	777.64	43.6
Carex acutiformis	799.93	36.5
Raphanus sativus 'Saxa'	975.55	40.3
Lycopersicum esculentum 'Stupické polní tyčkové rané'	1696.81	38.7
Glycine max 'Polanka'	2030.89	37.9
Bellis perennis	3089.89	39.5
Pisum sativum 'Ctirad'	7841.27	41.8

Table 1: List of internal standards used in flow cytometric analyses.

Detection of holokinetism using flow cytometry

Apart from genome size and base content estimation, flow cytometry allows also chromosome type detection. In contrast with monocentric organisms, even small fragments of chromosomes are inherited in holokinetics (Sheikh et al. 1995; Shirakawa et al. 2011a). Artificially induced chromosomal fragmentation (e.g. by ionizing radiation) followed by direct microscopic observation has been used as a proof of holokinetism since its discovery (Nordenskiöld 1963; Murakami & Imai 1974; Sheikh et al. 1995; Jankowska et al. 2015). However, this process is time consuming and increasingly difficult in species with many small chromosomes. Zedek et al. (2016) developed detection method for plants independent of direct observation of chromosomes. The experimental samples (living plants) are irradiated (recommended dose 150 Gy) to induce chromosome fragmentation. As soon as the plants resume growth, the tissues grown from this irradiated apical meristems are analysed using flow cytometer for the increased portion of cells in G2 phase of cell cycle (cells in G2 have replicated DNA to 4C as a part of preparations for the mitosis). While the monocentric species increase the proportion of G2 nuclei compared to G0 and G1 nuclei (G0, and G1 cells have 2C) more than 1.5-times (but recorded up to 27.8-times; Zedek et al. 2016), the holokinetics are affected only mildly or not at all (typical G2/G0, G1 change ratio is below 1.5; Zedek et al. 2016).

Sequencing and phylogeny tree construction

Statistical analysis of heritable characteristics should be performed with proper phylogenetic corrections. It is therefore necessary to know the phylogenetic relationships of the analysed species, for which phylogeny trees were constructed in **Papers I** and **II**. The majority of the sequences were excerpted from the literature, but several species were newly sequenced for the purposes of the **Paper II**. The DNA of these species was isolated using commercial NucleoSpin Plant II kit (Macherey-Nagel, Germany) and commercially purified and sequenced by Macrogen, Inc.

The resulting concatenated matrices of sequences of chloroplast and nuclear DNA were aligned manually (**Paper I**) or using MAFFT algorithm (Katoh & Standley 2013; **Paper II**). Ultrametric phylogeny trees were constructed by Bayesian approach in **Paper I** and maximum likelihood approach in **Paper II**. The methods of preparations of the phylogeny trees are described in full detail in particular papers.

Statistics

The statistical analyses of the data were performed in R program (R core team, 2013). They included standard statistical methods available in particular R packages: phylogenetic generalized least squares, phylogenetic ANOVA, phylogenetic linear model, Mann-Whitney U test, ancestral character estimation. See chapters "Materials and Methods" in particular papers for detailed description.

Conclusions

Genome size and GC content describe important qualities of the species' genome. They are shaped by intrinsic processes in the DNA, but they can also directly influence the species' fitness in a given environment. As such, these parameters have adaptive value and can be shaped by both inner and outer selective pressures, such as environmental variables, life histories or life forms.

The evolution of the genome size in Lentibulariaceae includes both extreme genome miniaturization as well as significant genome expansions in its clades. Still, in the context of their non-carnivorous relatives, all members of Lentibulariaceae possess very small genomes, which might support the hypothesis that the evolution of their genomes is affected by the nutrient scarcity at their habitats. However, our later results rather support hypotheses that their unusual genome reduction is caused by some intrinsic process. This is also congruent with their wide variability of the GC content, which has not been explained otherwise.

The GC content in the family Droseraceae is also notably variable, but in this case we could have accounted it to a stress tolerance. The species which cope with dry and/or freezing periods have significantly elevated GC content in their genomes.

Albeit not connected with carnivory in any way, we have detected chromosomal holokinetism to be an apomorphy of the family Droseraceae. The most apparent consequences of holokinetism have been observed in one clade of the genus *Drosera*, where negative correlation between genome sizes and chromosome numbers indicate the presence of the mechanism called holokinetic drive.

If we accept the intrinsic source of genome miniaturization in the family Lentibulariaceae, the effect of nutrient poor habitats on genome size will be absent.

However, the life histories were detected to be a strong predictor of the genome size across tested non-carnivorous clades: the genomes of annuals are smaller than genomes of their perennial relatives. This confirms a more general trend, which has not been tested across a broad phylogenetic scale so far.

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Paper I

Veleba A, Bureš P, Adamec L, Šmarda P, Lipnerová I, Horová L. 2014.
Genome size and genomic GC content evolution in the miniature genome sized family
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Letters

Genome size and genomic GC content evolution in the miniature genome-sized family Lentibulariaceae

Introduction

Since the first measurements of genome size in the early 1950s (Swift, 1950), researchers have tried to estimate the maximum capacity of plants for genome growth and the minimum DNA content essential for proper cell function. Plants with smaller genome size soon became important subjects of study as it was possible to completely sequence their genome without the need for processing a huge amount of uninformative, repetitive DNA (Flagel & Blackman, 2012) which covers the bulk of their genomes (Bennetzen et al., 2005; Ambrožová et al., 2011). Unsurprisingly, the first nearly-complete genome sequence published was *Arabidopsis thaliana* (Arabidopsis Genome Initiative, 2000) as it was then considered to be the plant with the smallest genome (Bennett & Leitch, 2005). Analysis of the *Arabidopsis* genome ($1C \approx 157$ Mbp; Bennett et al., 2003) and the virtual removal of repetitive DNA and duplicated genes lead to the theoretical estimate of the minimum size of gene complement needed for plant functioning as $1C \approx 50$ Mbp (Bennett & Leitch, 2005).

Such small genomes were soon discovered by Greilhuber et al. (2006) in the carnivorous family Lentibulariaceae (Lamiales). They documented the genome size of two samples of *Genlisea aurea* as low as $1C = 63.4$ Mbp (originally, one sample of *G. aurea* was misidentified as *G. margaretae*). In addition to this, relatively small genomes with $1C < 1000$ Mbp were found to prevail in all three monophyletic lineages of the family, that is, the genera *Genlisea*, *Pinguicula* and *Utricularia*. Until recently, however, genome size is known only for *c.* 8% of the Lentibulariaceae species, which contains 29 *Genlisea*, *c.* 233 *Utricularia* and *c.* 101 *Pinguicula* species. This provides the challenge to search for other species with miniature genomes and possible genomic models.

Detailed sequence analyses of *G. aurea* and *Utricularia gibba* which have been published in the last months (Ibarra-Laclette et al., 2013; Leushkin et al., 2013) clearly confirm the expected minimalistic genome composition of these species and show that this is reached with the removal of duplicated or otherwise redundant genes (e.g. genes relating to roots in rootless *U. gibba*) and virtually all noncoding repetitive DNA (transposable elements). This finding suggests a limited role of repetitive DNA in the regulation of complex eukaryotic genomes. However, this tells nothing about the reasons and driving forces behind this extreme DNA shrinkage, which is important for understanding why variations in plant genome size and genome architecture exist. Clearly, answering this question will require future, targeted comparisons between species selected with regard to the evolutionary history of miniaturization events and the specific hypotheses addressed.

In order to extend the contemporary pool of suitable model species and to improve current knowledge on the history of miniaturization events in Lentibulariaceae, an extensive survey and phylogeny-based analysis of genome size evolution in 119 (*c.* 35%) of Lentibulariaceae species is presented. Genomic DNA base composition (GC content) is also reported for all taxa to add further to the knowledge of the process of genome miniaturization.

Materials and Methods

Samples for the measurements were mainly from the authors' private and institutional collections with a few species provided by other Czech carnivorous plant collections (Supporting Information Tables S1, S2). In most samples, original species identification was verified based on their flower morphologies. The genome size (referred to as the 1C value in this paper) and GC content were measured with flow cytometry on two CyFlow flow cytometers (Partec GmbH, Münster, Germany) using the base unspecific, intercalating fluorochrome propidium iodide (PI) and the AT-selective DAPI (4',6-diamidino-2-phenylindole). The details of the procedure and the concentrations of reagents followed Šmarda et al. (2008). The fully-sequenced *Oryza sativa* subsp. *japonica* 'Nipponbare' ($1C = 388.8$ Mbp, $GC = 43.6\%$; International Rice Genome Sequencing Project, 2005) was the internal reference standard and four other internal standards, whose genome size and GC content were derived from comparison with this *Oryza* cultivar, were used (Methods S1). Every sample was measured at least three times (on different days) and replicated measurements were averaged (Table S3).

In addition to the measured genomic characters, information on chromosome number, life-form, altitudinal and latitudinal distribution, and distributions on particular continents was compiled from the literature or based on personal experience (Table S2, Methods S1).

For the purpose of phylogeny-based analyses, we constructed a Bayesian, ultrametric phylogenetic tree for the measured species (Figs 1, S1). The tree is based on the concatenated alignment of available sequence data from one nuclear (ITS) and three plastid regions (*rps*16, *mat*K, *trn*L-F) searched in the NCBI GenBank database (Benson et al., 2013; Table S1). The details on the tree construction are found in Methods S1.

The relationships between genome size, GC content and other trait variables were tested using the phylogenetic generalized least-squares (*pgls*) in the *caper* package (function *pgls*; Orme et al.,
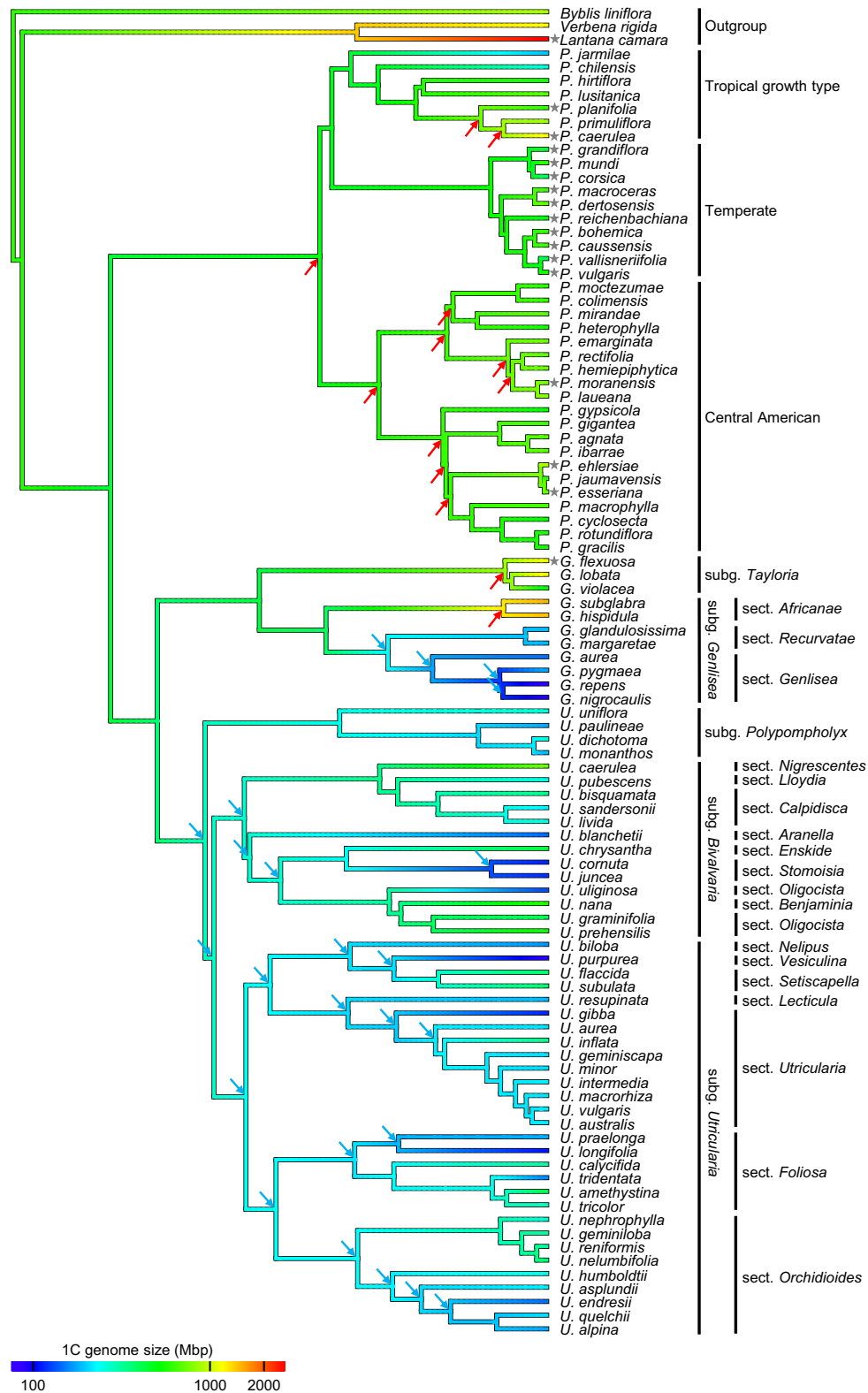
Fig. 1 Ancestral state reconstruction of genome size in Lentibulariaceae. Significant decreases and increases of genome size ($P < 0.05$) are marked, respectively, with blue and red arrows. Genome sizes referring to samples with probable recent polyploid origin are marked with grey asterisks.

2012) of R (R Core Team, 2013). Ancestral genome sizes were reconstructed using maximum likelihood (using function *ace* from R package *ape* v. 3.0-10; Paradis *et al.*, 2004) and visualized on the

tree with *contMap* function of R package *phytools* v. 0.2-80 (Revell, 2012). Significant increases or decreases in genome size (Fig. 1) or GC content (Fig. S2) were detected by comparing the actual

ancestral node values vs the random node values obtained with the same procedure, calculated with randomly reshuffled tip values. The randomization was repeated 999 times. All the statistics were done with $\log_{10}$ transformed data on genome sizes and logit transformed values (with natural logarithm) of the GC contents.

Results and Discussion

Summary and reliability of the data

The Lentibulariaceae species clearly have smaller genomes when compared with the related families of the Lamiales (Fig. 2). Approximately 95% of the 119 measured taxa have a 1C-value smaller than 1000 Mbp and 19 have a genome size smaller than that of *Arabidopsis* (Table 1). Our results mostly agree with those of Greilhuber *et al.* (2006), although some minor differences may appear due to the slightly different genome sizes assumed for the genome size standards (cf. Methods S1). The species with the smallest known genome size in the Lentibulariaceae (and all angiosperms) still remains *G. aurea* (63.4 Mbp; Greilhuber *et al.*, 2006). Our measurement of the genome size of this species (1C = 131 Mbp), however, is almost exactly double that reported by Greilhuber *et al.* (2006) and corresponds to a different ploidy level ('tetraploid') within this morphologically and karyologically variable species (Rivadavia, 2002; Albert *et al.*, 2010). Similarly, in *Pinguicula ehlersiae*, the two-fold difference in the measured genome size (1C = 978 Mbp in our study vs 1C = 487 Mbp by Greilhuber *et al.*, 2006) also corresponds with the existence of two
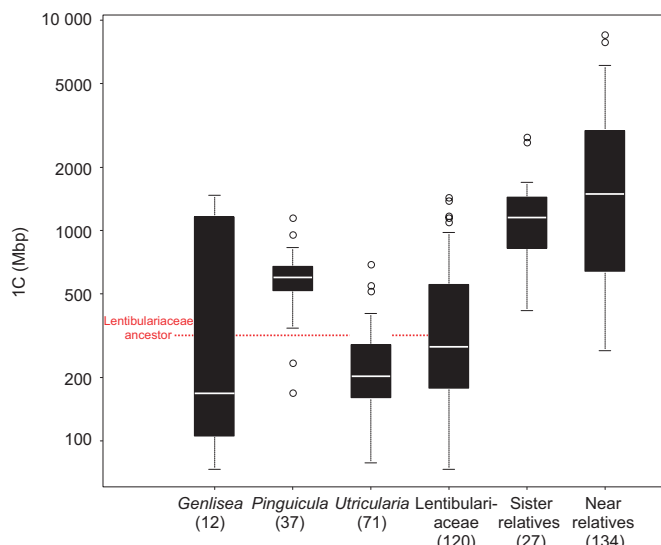
Fig. 2 Comparison of the measured genome sizes of Lentibulariaceae genera with genome size data from other Lamiales families in the Plant DNA C-value Database (Bennett & Leitch, 2005). Boxplots show the median (thick horizontal line), interquartile range (boxes), nonoutlier range (whiskers) and outliers (circles). The red horizontal line indicates the predicted genome size of the common Lentibulariaceae ancestor. Sister relatives: Acanthaceae, Bignoniaceae, Martyniaceae, Pedaliaceae, Verbenaceae; near relatives: Lamiaceae, Orobanchaceae, Paulowniaceae, Phrymaceae. Numbers of species displayed per group are given in brackets. The Lentibulariaceae family has a significantly smaller genome size than both its sister relatives and near relatives (two-sample Wilcoxon test; both comparisons $P < 0.05$).

Table 1 Results of genome size and genomic DNA base composition (GC content) measurements together with published data on chromosome number

Species	1C (Mbp)	GC (%)	2n
Genlisea			
aurea	131	38.9	(52[G])
flexuosa	1121	44.3	–
glandulossisima[A]	169	34.1	–
hispidula	1417	41.5	–
lobata	1200	44.0	16[G]
margaretae[A]	168	34.0	–
nigrocaulis clone1	80	38.9	–
nigrocaulis clone2	73	–	–
pygmaea	161	40.7	–
repens	77	38.8	–
subglabra	1471	41.7	–
violacea	460	43.7	–
Pinguicula			
agnata	651	41.1	22[H]
bohemica	590	39.8	64[H],(32[H])
caerulea	1178	40.8	32[H]
chilensis	241	39.4	16[H]
colimensis	600	42.5	22[H]
corsica	344	39.9	16[H]
hirtiflora	529	40.7	28[H]
cyclosecta	500	40.0	22[H]
dertosensis[A]	708	38.9	64[H]
ehlersiae	978	40.4	44[H],(22[H])
emarginata	717	40.9	22[H]
esseriana	760	40.5	32[H]
gigantea	598	40.8	22[H]
gracilis	518	40.9	22[H]
grandiflora	424	39.1	32[H]
gypsicola	501	40.3	22[H]
hemiepiphytica	702	41.8	22[H]
heterophylla	522	39.7	22[H]
ibarrae	676	41.2	22[H]
jarmilae	173	42.4	–
jaumavensis	495	40.4	22[H]
laueana	789	41.6	22[H]
longifolia ssp. *caussensis*[A]	623	39.2	32[H]
lusitanica	665	43.2	12[H]
macroceras[A]	591	39.9	64[H]
macrophylla	627	41.1	22[H]
mirandae	663	41.2	–
moctezumae	572	41.6	22[H]
moranensis	713	41.8	22[H],(44[H])
mundi	616	39.9	64[H]
planifolia	583	43.1	32[H]
primuliflora	830	39.8	22[H]
rectifolia	676	41.5	22[H]
reichenbachiana[A]	469	38.7	32[H]
rotundiflora	547	40.8	22[H]
vallisneriifolia	344	39.4	32[H]
vulgaris	583	38.8	64[H]
Utricularia			
alpina	159	39.9	18[E]
amethystina[A]	382	40.1	–
asplundii	202	41.1	–
aurea	193	38.3	42[E],80[D]
aureomaculata[A]	104	35.5	–
australis	200	40.0	36[E],38[E],40[E],44[E]
bifida	245	42.4	–

Table 1 (Continued)

Species	1C (Mbp)	GC (%)	2n
biloba	150	39.1	–
bisquamata	308	44.5	–
blanchetii	129	40.1	–
bremii	299	40.1	36[F]
caerulea	706	43.2	36[E],40[E]
calycifida	287	43.9	–
chrysantha	404	40.3	–
cornuta	102	39.8	18[E]
dichotoma	246	41.4	28[E]
dimorphanta	187	38.6	44[F]
endresii	133	38.4	–
flaccida	349	42.1	–
floridana	100	39.9	–
fulva	120	38.4	–
geminiloba	287	38.4	–
geminiscapa[A]	191	39.1	–
gibba	103	39.9	28[E]
graminifolia[A]	377	40.8	–
hirta	152	41.3	–
humboldtii	228	41.6	–
hydrocarpa	107	36.8	–
inflata	313	40.1	–
intermedia	203	39.2	44[E]
involvens[A]	287	41.2	–
juncea	106	39.4	18[E]
laxa	381	45.1	–
livida	239	42.0	36[E]
longeciliata	234	43.3	–
longifolia	97	41.1	–
macrorhiza	193	39.4	40[E],42[E],44[E]
menziesii	274	41.4	–
microcalyx	197	42.9	–
minor	190	38.8	36[E],40[E],44[E]
minutissima	203	42.1	–
monanthos	165	40.9	–
nana[A]	561	40.5	–
nelumbifolia	349	39.7	–
nephrophylla	247	37.0	–
ochroleuca	203	39.2	40[E],44[E],46[E],48[E]
paulineae	159	39.6	–
praelonga[A]	162	42.4	–
prehensilis	526	42.8	–
pubescens	232	42.8	–
purpurea	79	34.4	–
quelchii	191	40.7	–
radiata	163	38.4	–
reflexa	270	38.8	–
reniformis	292	38.0	–
resupinata	169	39.0	36[E],44[C]
rostrata	191	41.6	–
sandersonii	204	41.4	–
stellaris	192	39.5	40[B],42[E]
striata	117	41.1	–
stygia	315	40.6	–
subulata	340	41.2	30[E]
tenuicaulis	183	38.5	40[D]
tricolor	262	41.4	28[E]
tridentata[A]	142	39.3	–
uliginosa	116	39.6	–
uniflora	245	40.8	56[E]
volubilis	211	40.6	–
vulgaris	199	39.3	36[E],40[E],44[E]

Table 1 (Continued)

Species	1C (Mbp)	GC (%)	2n
warburgii	324	44.3	–
welwitschii	298	42.0	–

[A]Species where flowering individuals were not available for identification. Chromosome numbers were taken from [B]Sarkar *et al.* (1980), [C]Löve & Löve (1982), [D]Tanaka & Uchiyama (1988), [E]Taylor (1989), [F]Rahman *et al.* (2001), [G]Greilhuber *et al.* (2006), [H]Casper & Stimper (2009). Chromosome counts that probably do not refer to the measured plants are in brackets.

ploidy levels (2n = 22, 44; Casper & Stimper, 2009). Some other disagreements reported here, such as in *Genlisea violacea*, are perhaps due to the unrecognized taxonomic diversity, noting that the *G. violacea* complex has only recently been divided into five separate species (Fleischmann *et al.*, 2011). Unrecognized karyological variability (aneuploidy) known in several Lentibulariaceae species (cf. Table 1) may cause further differences.

Our GC content estimate of *U. gibba* (39.9%) agrees well with that reported for the complete genome sequence (GC = 40.0%; Ibarra-Laclette *et al.*, 2013). However, some difference is found between our GC content estimate of *G. aurea* (38.9%) and that reported from the partial genomic sequence (40.0%) by Leushkin *et al.* (2013). This difference might arise from gaps in the genomic data and/or may correspond to a different ploidy between races of *G. aurea*, with our sample possibly being tetraploid.

Genome size evolution

The genome size of the common ancestor of the family is estimated to be 414 Mbp (95% confidence interval: 284–603 Mbp), which is less than that of any of the close Lentibulariaceae relatives (Fig. 2). In spite of this relatively small ancestral genome size, further miniaturizations can be recognized in the evolution of the family. The exceptional tendency for genome miniaturization is most remarkable in *Utricularia* (Fig. 1), where ultra-small genomes
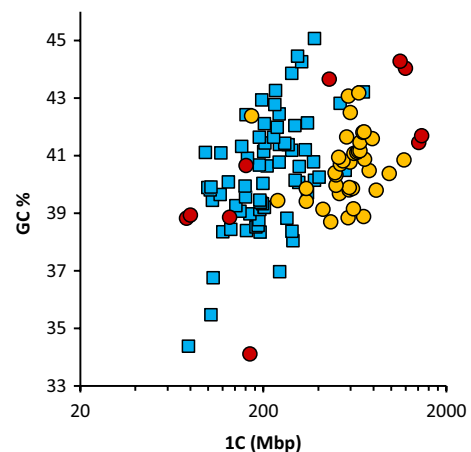

Fig. 3 Comparison of genome sizes with genomic DNA base composition (GC content) in particular Lentibulariaceae genomes. GC content is positively correlated with genome size in *Utricularia* (blue squares) and *Genlisea* (red circles) but not in *Pinguicula* (yellow circles) (*pgls* α = 0.05).

(1C < 100 Mbp) have evolved independently in three clades: *U.* sect. *Foliosa* – (*U. longifolia*), *U.* sect. *Vesiculina* – (*U. purpurea*) and *U.* sect. *Utricularia* (*U. floridana*; not shown in the phylogenetic tree because of absence of sequence data). Beyond *Utricularia*, other prominent miniaturization is found in *Genlisea*. Here, significant genome miniaturization accompanies the evolution of *G.* sect. *Genlisea* and *G.* sect. *Recurvatae* (Fig. 1). These sections typically contain species with very small genomes (all 1C < 170 Mbp; the smallest one in our dataset represented by *G. nigrocaulis* clone 2, 1C = 73 Mbp). This contrasts with other *Genlisea* clades possessing larger genomes, with *G. subglabra* (1C = 1471 Mbp) having the largest genome in the whole family (Fig. 1).

In contrast to *Utricularia* and *Genlisea*, genome size evolution in *Pinguicula* is less dramatic, showing a consistent tendency for genome expansion. The only miniaturizations appear in *P. jarmilae* and *P. chilensis* (Fig. 1). The quiet genome size evolution of *Pinguicula* allows some of the genome size differences to be ascribed to recent polyploidy, e.g. between the closely related *P. jaumavensis* (2n = 2x = 22, 1C = 495 Mbp) and *P. ehlersiae* (2n = 4x = 44, 1C = 978 Mbp). In *Utricularia* and *Genlisea* the chromosome counts do not correlate with the observed genome sizes in any predictable way. This suggests that recent polyploidy has only a limited effect on the extreme size dynamics of Lentibulariaceae genomes. Consequently, this variation is most likely to be caused by differences in the content of noncoding repetitive DNA, as was indeed documented by the recent detailed genomic data (Ibarra-Laclette *et al.*, 2013; Leushkin *et al.*, 2013). Variation in repetitive DNA is the general reason for large-scale variation in plant genome sizes (Bennetzen *et al.*, 2005; Grover & Wendel, 2010). In *Genlisea* and *Utricularia*, however, the turnover of noncoding DNA is unusually high, with large genome size differences generated relatively quickly, even among closely related species. This provides a unique opportunity for effective study of the principles and the reasons of genome size variation in plants.

While the outcome of genome miniaturization in Lentibulariaceae is recognized, the reasons for and driving forces behind this drastic genome miniaturization remain unclear. The obvious interest in Lentibulariaceae lies in carnivory, which is an adaptation to nutrient-poor environments. As expected by Leitch & Leitch (2008), the plants with larger genomes could be disadvantaged in such places, possibly because of phosphorus and/or nitrogen limitation. Members of the Lentibulariaceae usually grow under harsh conditions of nutrient-poor soils or waters. Here, the evolutionary pressure on genome size could be very strong, thus keeping the genome sizes of Lentibulariaceae species very low. However, species with miniaturized genomes did not show any common morphological and ecological features, and genome size showed no relationship with life-form or any ecological variables tested (*pgls*, $P > 0.05$). This indicates that nutrient availability or environmental selection play perhaps only a minor role in driving the extreme genome miniaturizations. Nevertheless, nutrient limitation and associated carnivory may have been the actual reason for the initial genome size reduction in the Lentibulariaceae ancestor as well as the factor preventing

excessive genome growth. This hypothesis needs further testing by comparing the genome sizes of carnivorous taxa with their noncarnivorous relatives.

Albert *et al.* (2010) and Ibarra-Laclette *et al.* (2011a,b) presented a unique mechanism of energy production which leads to the formation of reactive oxygen species. These can damage DNA molecules, possibly causing loss of the damaged DNA region. *Utricularia* and *Genlisea* might therefore be in an active process of genome downsizing without an external selection pressure. Both *Utricularia* and *Genlisea* (but not *Pinguicula*) are also known for extremely high substitution rates (Jobson & Albert, 2002; Müller *et al.*, 2004; Ibarra-Laclette *et al.*, 2011a,b), which could correspond with the influence of these reactive oxygen species. Such processes might indeed serve as a mechanistic explanation of the extremely high mutation rates and variable genome sizes observed in both genera. However, even with the data available on the complete sequence of *U. gibba*, the role of increased mutation rate in driving genome shrinkage in Lentibulariaceae genomes could not be verified (Ibarra-Laclette *et al.*, 2013).

GC content

This survey of the genomic GC contents in Lentibulariaceae has shown that both genome quantity and quality have a surprising pattern of variation within the group. The unusually wide variation of genomic GC contents appearing even within a genus (10.7% difference in *Utricularia* and 10.2% in *Genlisea*) is particularly interesting. This variation covers a substantial part of the entire known genomic GC content variation in vascular plants (ranging from 33% to 50%; Šmarda & Bureš, 2012) and represents the highest difference so far determined within a plant family or genus. The notably low GC contents are found in *G.* sect. *Recurvatae* (*G. margaretae*, *G. glandulossisima* with GC = 34.0% and 34.1%, respectively) and in *U. purpurea* (GC = 34.4%; Tables 1, S3, Fig. S2). The increased GC content is typical of *G.* sect. *Tayloria* (all GC > 43.7%) and occurs also in several clades of *Utricularia* with the most GC rich Lentibulariaceae genomes found in *U. laxa* (GC = 45.1%; Tables 1, S3).

GC content correlates well with genome size in both GC variable genera (Fig. 3), *Utricularia* (*pgls*, $\lambda = 1$, $P < 0.001$) and *Genlisea* (*pgls*, $\lambda = 1$, $P = 0.019$; excluding the outlying *G.* sect. *Recurvatae*). In *Pinguicula*, the phylogenetic trend between GC content and genome size is absent (*pgls*, $\lambda = 1$, $P = 0.497$; Fig. 3), perhaps due to the fact that *Pinguicula* genomes are mostly shaped by polyploidy (whole genome duplication) which has no direct effect on the overall genomic GC content. The correlation between GC content and genome size in *Genlisea* and *Utricularia* indicates that the extreme GC content variation of their genomes primarily relates to the high genome size dynamics and to the processes of genome miniaturization and genome growth. Assuming that coding DNA would form only a minor part of the removed or amplified DNA (because of the direct effect of gene loss or duplication on plant fitness), the most intuitive explanation for this trend would be the preferential removal or amplification of GC-rich, noncoding DNA (Šmarda & Bureš,

2012; Veselý *et al.*, 2012). However, the exact proof of this, with detailed sequence data, still poses a challenge.

Given that coding DNA is regularly the most GC-rich component of plant genomes and noncoding DNA is usually GC-poor when compared with genes (cf. Šmarda & Bureš, 2012), one would expect high GC-richness in the miniature Lentibulariaceae genomes. This work has, however, revealed several species whose very small genomes were surprisingly GC-poor (*Genlisea margaretae*, *G. glandulossisima* and *Utricularia purpurea* with 34.0%, 34.1% and 34.4%, respectively). These approach the minimum genomic GC content yet known in some Cyperaceae and Juncaceae species (Šmarda & Bureš, 2012; Šmarda *et al.*, 2012; Lipnerová *et al.*, 2013; P. Šmarda *et al.*, unpublished). These whole genome GC contents are even lower than the GC content of the noncoding genome fraction of *U. gibba* (GC = 35.9%; Ibarra-Laclette *et al.*, 2013), indicating a very different genome structure of the GC-poor species compared with the other miniature-sized genomes of Lentibulariaceae. Such a low GC content could be reached with the frequent presence of AT-rich, noncoding DNA, which is less probable due to the minimal genome size of all three species and the expected high content of coding DNA. Therefore, the depletion of GC bases must also include the coding DNA and perhaps affects the structure of genes. This suggests the existence of an additional mechanism shaping the miniature Lentibulariaceae genomes, together with the removal and amplification of noncoding DNA. Sequencing of any of the GC-poor miniature genomes of Lentibulariaceae and their comparison with the available genomic sequences for GC-rich *G. aurea* and *U. gibba* (Ibarra-Laclette *et al.*, 2013; Leushkin *et al.*, 2013) now seems to be a promising way of detecting this mechanism, which might substantially improve our understanding of the reasons behind the evolution of the GC-poor genome architectures also found in other small-genomed plants.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Detailed phylogenetic tree for the measured taxa.

Fig. S2 Ancestral state reconstruction of genomic GC content in Lentibulariaceae.

Table S1 List of species locations, details on subgeneric classification, and NCBI accesion numbers of used sequences

Table S2 Environmental data of species

Table S3 Detailed results of flow cytometry measurements

Methods S1 Details of the flow cytometry measurements, ecological traits and methods of phylogenetic tree construction.

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Key words: carnivorous plants, flow cytometry, GC content, genome miniaturization, genome size evolution, genomic DNA base composition, genomic models, Lentibulariaceae.

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Paper II

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Evolution of genome size and genomic GC content in carnivorous holokinetics
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Evolution of genome size and genomic GC content in carnivorous holokinetics (Droseraceae)

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● **Background and Aims** Studies in the carnivorous family Lentibulariaceae in the last years resulted in the discovery of the smallest plant genomes and an unusual pattern of genomic GC content evolution. However, scarcity of genomic data in other carnivorous clades still prevents a generalization of the observed patterns. Here the aim was to fill this gap by mapping genome evolution in the second largest carnivorous family, Droseraceae, where this evolution may be affected by chromosomal holokinetism in *Drosera*.
● **Methods** The genome size and genomic GC content of 71 Droseraceae species were measured by flow cytometry. A dated phylogeny was constructed, and the evolution of both genomic parameters and their relationship to species climatic niches were tested using phylogeny-based statistics.
● **Key Results** The 2C genome size of Droseraceae varied between 488 and 10 927 Mbp, and the GC content ranged between 37·1 and 44·7 %. The genome sizes and genomic GC content of carnivorous and holocentric species did not differ from those of their non-carnivorous and monocentric relatives. The genomic GC content positively correlated with genome size and annual temperature fluctuations. The genome size and chromosome numbers were inversely correlated in the Australian clade of *Drosera*.
● **Conclusions** Our results indicate that neither carnivory (nutrient scarcity) nor the holokinetism have a prominent effect on size and DNA base composition of Droseraceae genomes. However, the holokinetic drive seems to affect karyotype evolution in one of the major clades of *Drosera*. Our survey confirmed that the evolution of GC content is tightly connected with the evolution of genome size and also with environmental conditions.

Key words: DNA content, Droseraceae, carnivorous plants, flow cytometry, genome size evolution, GC content, DNA base composition, holocentric chromosomes, holokinetic chromosomes.

INTRODUCTION

Droseraceae consists of three carnivorous genera, two of which are monotypic and equipped with highly specialized snap-traps: *Dionaea muscipula* from the wetlands of North and South Carolina (USA); and *Aldrovanda vesiculosa*, an aquatic species with scattered distribution in Africa, Australia and Eurasia. The third genus, *Drosera* (sundews), includes approx. 250 sticky-leaved species distributed across all the continents except for Antarctica (McPherson, 2010; Gonella *et al.*, 2015). Sundews generally grow in wetlands, but some are adapted to seasonal droughts, especially the species from Australia (McPherson, 2008, 2010).

Flowering plants (Angiosperms) exhibit an extremely broad divergence in genome size compared with other Eukaryotes (Bennett, 1972). For instance, the difference between the largest and smallest angiosperm genome is > 2500-fold (Bennett and Leitch, 2012). This variation is considered to be the result of different selective pressures (ecological, physiological, morphological, etc.) on the outcomes of molecular processes (retrotransposon amplification, polyploidy), which vary in their degree across various angiosperm clades (Wendel *et al.*, 2013). The smallest angiosperm genomes are known from the carnivorous family Lentibulariaceae (Greilhuber *et al.*, 2006; Fleischmann *et al.*, 2014; Veleba *et al.*, 2014), making these miniature carnivorous species excellent candidates for whole-genome sequencing.

Indeed, complete genomic sequences have already been published for *Utricularia gibba* (Ibarra-Laclette *et al.*, 2013), *Genlisea aurea* (Leushkin *et al.*, 2013), *G. nigrocaulis* and *G. hispidula* (Vu *et al.*, 2015). Unlike Lentibulariaceae, the other prominent group of carnivorous plants, Droseraceae, has been analysed only sporadically, and the genome size is known for only nine of approx. 250 existing Droseraceae species (Rothfels and Heimburg, 1968; Veselý *et al.*, 2012; Jensen *et al.*, 2015). The reported genome sizes (2C = 587 Mbp in *Drosera capensis* to 2C = 5912 Mbp in *Dionaea muscipula*) seem to be generally larger than in Lentibulariaceae (2C = 126 Mbp in *Genlisea aurea* to 2C = 3020 Mbp in *Genlisea hispidula*; Greilhuber *et al.*, 2006) but still relatively small compared with genome sizes known in other angiosperms (Bennett and Leitch, 2012). Given the small number of analysed species and other characteristics noted below, it cannot be excluded that this family may still hide species with similarly miniaturized genomes as in the carnivorous family Lentibulariaceae.

It has been hypothesized that selection for small genome sizes may be promoted by nutrient limitation, namely by phosphorus and nitrogen (Leitch and Leitch, 2008), because both are abundant components of nucleic acids (Sterner and Elser, 2002). Carnivory is considered an adaptation to nutrient-poor habitats (Givnish *et al.*, 1984), and carnivorous plants could, therefore, act as suitable models to test this hypothesis by

comparing the genome sizes of carnivorous species and closely related non-carnivorous clades. Indeed, the predicted decrease in genome size has been observed together with the evolution/appearance of carnivory in Lentibulariaceae (Veleba *et al.*, 2014); however, studies on other carnivorous clades are necessary to generalize this trend.

Possibly, the major peculiarity of Droseraceae compared with other carnivorous lineages (including Lentibulariaceae) is its holokinetic chromosomes, which are typical for *Drosera* species (Rothfels and Heimburg, 1968; Sheikh *et al.*, 1995; Kondo and Nontachaiyapoom, 2008; Shirakawa *et al.*, 2011*a*, *b*; Zedek *et al.*, 2016) with a possible exception of *D. regia* (Shirakawa *et al.*, 2011*b*). In contrast to monocentric chromosomes, whose kinetochore formation is restricted to the small areas of the centromeres, holokinetic chromosomes lack primary constrictions and their kinetochores are formed along their poleward surfaces (Bureš *et al.*, 2013; Cuacos *et al.*, 2015). Holokinetic chromosomes, therefore, tolerate chromosomal fissions or fusions and do not allow more than two crossovers in meiosis (reviewed in Bureš *et al.*, 2013; Heckmann and Houben, 2013) which may substantially affect genome and karyotype evolution of their bearers (Escudero *et al.*, 2012; Bureš *et al.*, 2013; Bureš and Zedek, 2014; Lukhtanov *et al.*, 2015; Šíchová *et al.*, 2016). One such effect may be a negative correlation between genome size and chromosome number in holokinetic lineages (Nishikawa *et al.*, 1984; Roalson *et al.*, 2007; Záveská Drábková and Vlček, 2010; Bureš *et al.*, 2013; Lipnerová *et al.*, 2013; Bureš and Zedek, 2014). Based on the comparison of four holokinetic clades (cyperids, *Drosera*, *Chionographis* and *Myristica*) with their close monocentric relatives, Bureš *et al.* (2013) suggested that holokinetism might be associated with genome size decrease. This association was later confirmed for the cyperid clade with a larger data set and phylogeneticaly corrected analyses by Šmarda *et al.* (2014) who also found a decreased overall genomic percentage of guanine and cytosine (GC content) in this clade. However, the extent to which these trends are general outcomes of holokinetism remains unclear because relevant comparisons of these genomic parameters are lacking in other holokinetic clades.

Thus far, the GC content is known only in two Droseraceae species (*D. menziesii*, 41·3 %; and *D. peltata*, 44·2 %; Veselý *et al.*, 2012). In general, the GC content is extremely variable, particularly in bacteria, where it is known to relate to the ecology of particular taxa and lineages (correlated with the thermal optimum and thermal tolerance range; Nishio *et al.*, 2003; Foerstener *et al.*, 2005; Musto *et al.*, 2006; Mann and Phoebe-Chen, 2010). Although the variation in GC content is much narrower in flowering plants (Šmarda and Bureš, 2012), its ecological impact has also been found in monocots, in which a higher GC content was found to be correlated with cold and drought tolerance (Šmarda *et al.*, 2014). Droseraceae may serve as a good model for testing some of these predictions on a finer phylogenetic scale, particularly due to the contrasting ecology of Droseraceae species.

In this study, we aim (1) to analyse trends in the genome size and GC content evolution in the family Droseraceae and its close relatives and (2) to test whether the holokinetism in Droseraceae is associated with the predicted effects and patterns in the genome and karyotype evolution, namely (2a) genome downsizing, (2b) decreased GC content and (2c) the existence of a negative correlation between DNA content and

chromosome number. Finally, we aim (3) to test the relationship between climatic parameters and GC content on a narrower phylogenetic scale than in our previous analysis across whole monocots (Šmarda *et al.*, 2014).

MATERIALS AND METHODS

Most of the samples of Droseraceae were collected from the private collection of Adam Veleba; several samples originated from collections of other carnivorous plant enthusiasts. The related non-carnivorous plants were obtained from the Botanical Garden of the Faculty of Science, Masaryk University in Brno, or collected in the wild. The genomic data of 17 species were taken from the C-value database (Bennett and Leitch, 2012) and several other sources (for a detailed list, see Supplementary Data Table S1).

The samples for flow cytometry were prepared according to the protocol of Šmarda *et al.* (2008) and measured on two CyFlow flow cytometers (Partec GmbH, Münster, Germany; recently Sysmex) with internal standards whose genome size was derived from comparison with the completely sequenced *Oryza sativa* subsp. *japonica* 'Nipponbare' (International Rice Genome Sequencing Project, 2005; Supplementary Data Table S2). Each sample was processed with two fluorochromes: PI (propidium iodide) and DAPI (4',6-diamidino-2-phenylindole). The intercalating, base-unspecific PI was used to determine the absolute genome size, and the AT-selective DAPI, together with the results from measurements with PI, were used to calculate the genomic GC content. The procedure is detailed in Šmarda *et al.* (2008, 2014); for further details, see the Supplementary Data Methods.

The phylogenetic relationships of the analysed species (listed in Supplementary Data Table S1) were reconstructed based on a concatenated alignment of chloroplast (*rbc*L and *mat*K) and nuclear (ITS) markers (Supplementary Data Methods). The resulting maximum likelihood phylogenetic tree was calibrated using available fossil records and published age estimates (Supplementary Data Methods). Both non-dated and dated phylogenetic trees in Newick format are supplied in Supplementary Data Fig. S1).

The GIS layer of geographic distribution was prepared for each species based on the distribution data of Droseraceae species in the World Checklist of Selected Plant Families, Kew Databases (Govaerts and Cheek, 2014), using the digitized layers of 'TDWG areas of level 3' (*sensu* Brummitt *et al.*, 2001). The species concept was revised according to the current literature. For each species, the geographical distribution was transformed to the statistical distributions across each of the 19 bioclimatic variables (19 histograms) from the WorldClim database (Hijmans *et al.*, 2005), i e. for each species and a given bioclimatic parameter a histogram was constructed in which the height of each column was given by the area of intersection of the respective bioclimatic GIS (sub-)layer (= sub-range of a given bioclimatic variable) with the GIS layer of geographic distribution of the respective species. Subsequently, the minimum, median and maximum values of the calculated bioclimatic variables were calculated (Supplementary Data Table S3). The precipitation variables were log-transformed prior to all statistical analyses; the temperature variables were used as raw values.

Recent polyploidy events were identified based on a comparison of chromosome numbers taken from the published

literature and the measured genome sizes between closely related species (Supplementary Data Table S1). The analyses of genome size evolution were conducted with monoploid genome size (Cx; i.e. total 2C genome size divided by the ploidy level; Greilhuber *et al.*, 2005) instead of the raw measures of DNA content. The monoploid genome size was log10 transformed prior to all statistical analyses; the GC contents and the chromosome numbers were used as raw values.

The statistical tests of the relationships between monoploid genome size, GC content and chromosome numbers were performed using the phylogenetic generalized least-squares method (function 'pgls') using the 'caper' package (v. 0.5.2; Orme *et al.*, 2012) in R (v. 3·3; R Core Team, 2013) with λ (branch length transformation) determined by maximum likelihood.

The ancestral states of the monoploid genome size and GC content were reconstructed using the residual maximum likelihood method under the Brownian Motion model (function ace in the R package ape v. 3·5; Paradis *et al.*, 2004) and visualized on the phylogenetic tree using the function 'contMap' in the R package 'phytools' v. 0·5-20 (Revell, 2012). Significant changes of the monoploid genome size or GC content in particular nodes were detected by the random tip-value reshuffling algorithm in R (this procedure compares actual node values with values obtained from random reshuffling of the tip values; Šmarda *et al.*, 2014) based on 4999 randomizations.

The difference between the monoploid genome size of carnivorous and non-carnivorous species and between the monoploid genome size and the GC content of holokinetic and monocentric species was tested by phylogenetic analysis of variance (ANOVA; function 'aov.phylo', package 'geiger' v. 2.0.6; Harmon *et al.*, 2015).

The relationships between the genomic GC content and climatic variables were analysed with a multiple phylogenetic regression approach using the 'pgls' function (package 'caper' in R) and λ (branch length transformation) determined by maximum likelihood. In this analysis, the climatic variables were handled as explanatory variables and were manually forward selected into the final explanatory model of GC content based on the amount of explained variation (in each step, the significant variable with the highest explained variation was included in the model). The α-level for this analysis was 8·33E-4, as the Bonferroni correction was applied to avoid false-positive results.

With respect to particular analysed parameters, analyses were performed with the respective sub-sets of data (Datasets 1–6 in Supplementary Table S1).

RESULTS

Variation of genomic parameters in Droseraceae and related clades

The genomes of the 71 analysed Droseraceae species (Table 1; 66 newly reported here) were relatively small, with medians of 1252 Mbp for 2C and 509 Mbp for Cx. The smallest genome was found in *Drosera hamiltonii* (2C = 488 Mbp, Cx = 244 Mbp), while the absolute largest was detected in the tetraploid *D. ordensis* (2C = 10 927 Mbp, Cx = 2732 Mbp) and the largest monoploid genome size in *D. micrantha* (2C = 7489 Mbp, Cx = 3745 Mbp). The genomes of 42 species (Table 1; 17

newly reported here) of related families (Drosophyllaceae, Nepenthaceae, Ancistrocladaceae, Dioncophyllaceae, Plumbaginaceae, Polygonaceae and Tamaricaceae) varied from the smallest, 2C = 669 Mbp, Cx = 335 Mbp in *Plumbago auriculata* (Plumbaginaceae), to 2C = 20 833, Cx = 10 416 Mbp in carnivorous *Drosophyllum lusitanicum* (Drosophyllaceae).

The GC content variation in Droseraceae (Table 1) was 7·6 %, with the lowest value found in *Drosera prolifera* (37·1 %) and the highest in *D. oreopodion* (44·7 %). The values of species of related clades varied between 36·3 % (*Nepenthes pervillei*) and 45·1 % (*Rumex acetosa*).

Phylogeny of Droseraceae and related clades

The Caryophyllales diversified at the turn of the lower and upper Cretaceous (Supplementary Data Fig. S2). The carnivorous Caryophyllales (families Droseraceae, Nepenthaceae, Dioncophyllaceae, Ancistrocladaceae and Drosophyllaceae) form a monophyletic clade in which Ancistrocladaceae and Dioncophyllaceae were ancestrally carnivorous (Heubl *et al.*, 2006). They diverged from the Frankeniaceae + Tamaricaceae clade 93.31 Mya. The Polygonaceae + Plumbaginaceae clade diverged from the carnivorous Caryophyllales + (Frankeniaceae + Tamaricaceae) clade 98·69 Mya.

Within the carnivorous Caryophyllales, the crown node is 74·48 Ma old, marking the minimum age of carnivory in the Caryophyllales. The individual carnivorous genera evolved during the Palaeogene. The estimated crown age of the Droseraceae is 54·67 Ma (Fig. 1; Supplementary Data Fig. S2). Within Droseraceae, the two genera of snap-traps (*Aldrovanda* and *Dionaea*) split at least 45·09 Mya. There are two basal species of *Drosera*, i.e. *D. arcturi* and *D. regia*, which diverged from the rest of the genus 54·11 and 52·21 Mya, respectively. The remaining species of *Drosera* form two main clades that split 46·47 Mya. The first clade comprises the subgenera *Stelogyne*, *Theocalyx* and *Drosera* (*D. sessilifolia–D. trinervia* clade; hereafter referred to as the 'Cosmopolitan clade' because its members occur on all the continents except for Antarctica), and the second clade includes the subgenera *Bryastrum*, *Lasiocephala*, *Ergaleium* and *Phycopsis* (*D. binata–D. omissa* clade; hereafter referred to as the 'Australian clade' because most of its members are restricted to Australia and adjacent areas).

Genome size evolution in Droseraceae

The reconstructed evolution of the monoploid genome size shows opposite trends in the two main clades of the genus *Drosera* (Fig. 1). The genomes of the species from the Cosmopolitan clade show a reduction tendency, and multiple significant downsizing events have been detected in several nodes of this clade (Fig. 1). In contrast, the genomes of species from the Australian clade (particularly in the subgenera *Bryastrum* and *Lasiocephala*) exhibit a tendency for genome growth with multiple significant upsizing events detected (Fig. 1). The genome size in the rest of the Australian clade (i.e. the subgenera *Ergaleium* and *Phycopsis*) is relatively stable.

No difference was detected in a phylogeny-based comparison between monoploid genome sizes of carnivorous and non-

TABLE 1. *Results of genome size and genomic DNA base composition (GC content) measurements*

Species	2C (Mbp)	GC (%)	Ploidy level*	Cx (Mbp)
Droseraceae				
Aldrovanda vesiculosa	938	42·8	2	469
Dionaea muscipula	5705	43·9	2	2853
Drosera aberrans	987	41·9	2	494
D. adelae	594	37·6	2	297
D. admirabilis	792	39·7	–	–
D. afra	613	39·6	–	–
D. aliciae	1949	40·0	8	244
D. allantostigma	2858	43·5	2	1429
D. anglica	4715	44·2	4	1179
D. arcturi	1050	39·7	2	525
D. auriculata	846	42·3	2	423
D. barbigera	4215	43·2	2	2108
D. binata	1465	41·5	2	733
D. binata var. *multifida*	1519	41·4	–	–
D. burmannii	504	38·7	2	252
D. capensis	789	39·0	4	197
D. cistiflora	671	41·8	4	168
D. collinsiae	905	40·1	4	226
D. cuneifolia	702	40·3	4	176
D. dilatatopetiolaris	4868	42·8	2	2434
D. erythrorhiza	1687	42·7	–	–
D. falconeri	5253	43·0	2	2627
D. filiformis	4877	43·5	2	2439
D. filiformis var. *tracyi*	5930	42·8	–	–
D. gigantea	1060	40·2	2	530
D. grantsaui	1069	39·9	–	–
D. graomogolensis	1629	40·4	4	407
D. hamiltonii	488	40·1	2	244
D. helodes	3586	43·0	2	1793
D. hilaris	738	40·9	4	185
D. indica	1307	40·9	2	654
D. intermedia	2516	42·5	2	1258
D. kaieteurensis	2695	41·7	–	–
D. lanata	854	39·0	2	427
D. latifolia	1102	40·9	4	276
D. leucoblasta	4121	42·1	2	2061
D. menziesii	967	40·8	2	484
D. meristocaulis	2969	38·9	2	1485
D. micrantha	7489	44·4	2	3745
D. modesta	1158	40·7	–	–
D. monantha	776	40·3	–	–
D. natalensis	1040	40·8	4	260
D. neocaledonica	1136	38·1	4	284
D. nidiformis	1027	40·8	–	–
D. oblanceolata	1933	40·1	–	–
D. omissa	2170	42·2	2	1085
D. ordensis	10 927	44·2	4	2732
D. oreopodion	3292	44·7	–	–
D. peltata	829	43·0	2	415
D. petiolaris	4707	42·2	2	2354
D. prolifera	502	37·1	2	251
D. pulchella	1862	43·4	2	931
D. pygmaea	1252	41·6	2	626
D. ramentacea	1361	40·8	–	–
D. regia	835	40·2	2	418
D. roraimae	2683	41·9	–	–
D. roseana	3513	43·3	2	1757
D. rotundifolia	2331	44·5	2	1166
D. sessilifolia	497	38·4	2	249
D. sewelliae	3863	40·4	2	1932
D. schizandra	1186	40·1	2	593
D. spatulata	586	38·5	2	293
D. spiralis	1259	40·4	4	315
D. tomentosa	1105	40·0	4	276

(continued)

TABLE 1. *Continued*

Species	2C (Mbp)	GC (%)	Ploidy level*	Cx (Mbp)
D. trinervia	573	40·1	4	143
D. ultramafica	2325	40·6	–	–
D. venusta	1054	39·8	–	–
D. verrucata	4653	43·5	2	2327
D. viridis	2316	42·9	–	–
D. whittakeri	946	41·2	–	–
D. zonaria	889	41·5	–	–
Dioncophyllaceae				
Triphyophyllum peltatum	1167	40·2	2	584
Drosophyllaceae				
Drosophyllum lusitanicum	20 833	41·0	2	10 417
Plumbaginaceae				
Armeria alpina	7600	41·0	2	3800
A. vulgaris	8663	42·7	2	4332
Ceratostigma plumbaginoides	743	39·7	2	372
Plumbago auriculata	669	38·8	2	335
Polygonaceae				
Bistorta major	5354	42·2	4	1339
Fallopia dumetorum	1324	40·5	2	662
Muehlenbeckia complexa	1414	39·9	2	707
Oxyria digyna	1909	41·3	2	955
Persicaria amphibia	2732	39·7	4	683
P. hydropiper	1300	41·0	2	650
P. lapathifolia	1458	43·8	2	729
P. maculosa	3015	40·8	4	754
P. mitis	3071	40·3	4	768
Polygonum arenastrum	1445	44·9	4	361
Reynoutria japonica	8279	40·5	8	1035
Rumex acetosa	6104	45·1	2	3052
R. alpinus	868	44·0	2	434
R. arifolius	5912	44·1	2	2956
R. conglomeratus	1370	44·5	2	685
R. crispus	3948	40·8	4	987
R. maritimus	1962	40·3	4	491
R. patientia	4305	41·2	6	718
Tamaricaceae				
Myricaria germanica	2872	40·8	2	1436
Tamarix tetrandra	2823	37·0	2	1412

*For sources of chromosome number data, see Supplementary Data Table S1.

carnivorous species ($P = 0.680$; Supplementary Table S1: Dataset 1) or between holokinetic and monocentric species ($P = 0.600$; Supplementary Table S1: Dataset 1). Within the holokinetic species of *Drosera*, a weak negative correlation was observed between the Cx genome size and the monoploid chromosome number ('pgls' $\lambda = 1$, $P = 0.08$; Fig. 2; Supplementary Table S1: Dataset 4). This negative correlation was apparent in the Australian clade ('pgls' $\lambda = 0$, $P < 0.001$; Supplementary Table S1: Dataset 5), while it was absent in the Cosmopolitan clade ('pgls' $\lambda = 1$, $P = 0.813$; Supplementary Table S1: Dataset 6) when both clades were analysed separately (Fig. 2).

Genomic GC content evolution in Droseraceae

Several reductions in the GC content were observed in the Cosmopolitan clade, with the exception of four temperate species (*Drosera anglica*, *D. filiformis*, *D. intermedia* and *D. rotundifolia*), where the GC content increased (Fig. 1). A
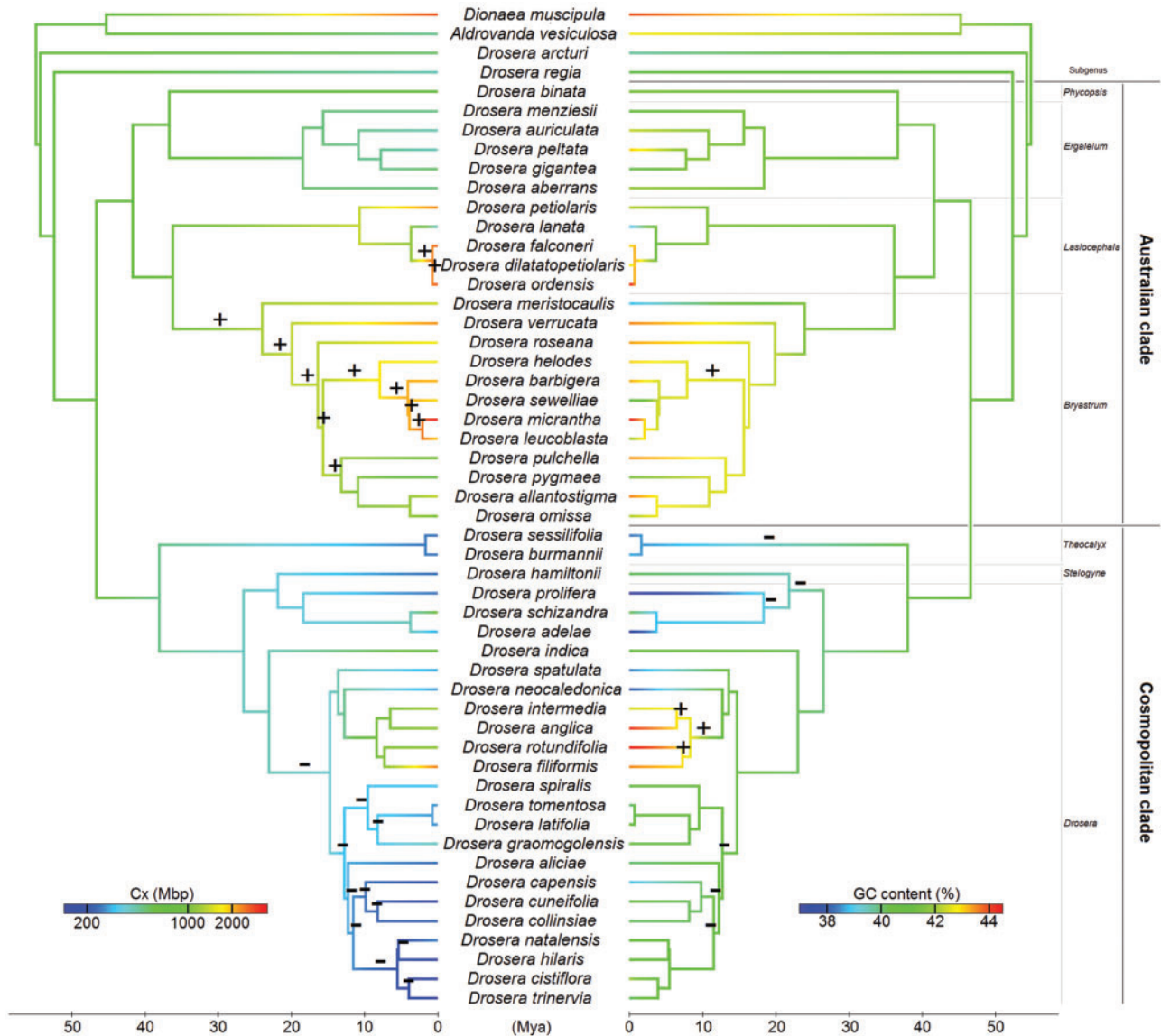
Fɪɢ. 1. Ancestral state reconstruction of monoploid genome size (left) and GC content (right) in Droseraceae. Significant increases and decreases ($P < 0.05$) of monoploid genome size or GC content are marked with '+' and '–' signs above the branches leading to particular nodes.

single GC increase was also detected in the Australian clade, subgenera *Bryastrum* (Fig. 1). No difference was found in the GC content between the holokinetic *Drosera* species and the closely related monocentric species ($P = 0.975$; Supplementary Table S1: Dataset 2).

The GC content variation of Droseraceae in the summary explanatory model is best explained by the genome size (log-transformed 2C), which is positively correlated with the GC content ($P = 4.06E-8$; explained residual variation = 45.57 %; Supplementary Table S1: Dataset 3). Removing the effect of genome size in the model, the GC content further increases with an increasing annual range of temperature (median temperature annual range Bioclim variable; $P = 4.41E-5$, explained residual variation = 21.5 %; Supplementary Table S1: Dataset 2). After removing the effect of genome size and median annual

temperature range, no other variable was able to explain the significant portion of the remaining residual variation in CG contents.

DISCUSSION

The genomes of the carnivorous species of the Caryophyllales have a 'standard' size which is comparable with its non-carnivorous relatives. Indeed, they are far from being truly miniature as in the carnivorous family Lentibulariaceae, whose genomes are strikingly smaller than the genomes of their non-carnivorous relatives (Veleba *et al.*, 2014). The family Lentibulariaceae represents a unique lineage with unusually structured genomes (Ibarra-Laclette *et al.*, 2013; Leushkin *et al.*, 2013) and overall morphology (absent roots and leaves in
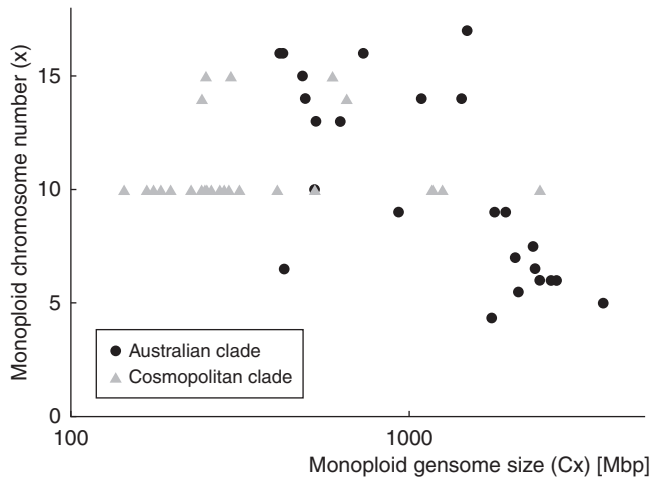
FIG. 2. Relationship between monoploid genome sizes (Cx) and basic (monoploid) chromosome numbers (x) in holokinetic species of *Drosera*. Note a negative correlation between both parameters in the Australian clade ($P < 0.001$), which probably resulted from the holokinetic drive.

Utricularia and *Genlisea*), while the morphological constitution of carnivorous Caryophyllales species is similar to a typical plant body. This questions whether genome downsizing in Lentibulariaceae is a direct consequence of carnivory and eventual nutrient starvation, or rather associated with some peculiar molecular properties of Lentibulariaceae (Jobson and Albert, 2002; Ibarra-Laclette *et al.*, 2011*a*, *b*), or connected with their extreme body reduction.

Holokinetism has been suggested to be associated with genome size and GC content decrease (Bureš *et al.*, 2013; Šmarda *et al.*, 2014). In the present study, we have not confirmed lower genome size previously reported in *Drosera* (Bureš *et al.*, 2013). This is most probably because we tested it phylogenetically this time. Similarly, we have not detected a decrease in the GC content associated with the evolution of holokinetism in *Drosera*. This suggests that genome downsizing and GC content decrease need not to be a direct consequence of holokinetism.

Aside from positive or no correlation between genome size and chromosome number (Zedek *et al.*, 2010; Chung *et al.*, 2012; Escudero *et al.*, 2015), a negative correlation is commonly detected in holokinetic lineages (Nishikawa *et al.*, 1984; Roalson *et al.*, 2007; Bureš *et al.*, 2013; Lipnerová *et al.*, 2013; Záveská Drábková and Vlček, 2010; Bureš and Zedek, 2014). It has been hypothesized that this negative correlation is promoted by the holokinetic drive, which is based on a size-dependent competition between homologous chromosomes in asymmetric meiosis (Bureš and Zedek, 2014). Indeed, we have observed such a negative correlation in the Australian clade of *Drosera*, where the holokinetic drive seems therefore to have shaped the karyotype evolution. There are species with a few large chromosomes (e.g. *Drosera micrantha*, 2C = 7489 Mbp, $2n = 10$, mean chromosome size, 2C/2n = 749 Mbp) as well as species with many small chromosomes (e.g. *Drosera peltata*, 2C = 829 Mbp, $2n = 32$, mean chromosome size, 2C/2n = 26 Mbp), which results in the above-mentioned negative correlation (Fig. 2). The presence of holokinetic chromosomes does

not automatically indicate the presence of the holokinetic drive (Bureš and Zedek, 2014). Likewise, the relatively stable chromosome counts and small differences in genome size among species in the Cosmopolitan clade indicate that the holokinetic drive plays no or only a negligible role there. Alternatively, it is possible that the holokinetic drive and the carnivory-driven selection for small genomes have opposite effects on genome size in Droseraceae. If the holokinetic drive prefers larger chromosomes, which may indeed be the case in the Australian clade of *Drosera* (Table 1; Fig. 1), the carnivory-driven selection for small genomes may be counteracted by genome size enlargement due to the holokinetic drive. Such opposition of the two evolutionary forces may have obscured any differences in genome size between carnivorous and non-carnivorous as well as holokinetic and monocentric species.

It should be noted that a recent study doubted the occurrence of holokinetic chromosomes in *Drosera aliciae*, *D. binata* and *D. rotundifolia* based on the chromosomal staining by a supposedly universal mitotic centromere marker H2AThr120ph (Demidov *et al.*, 2014). However, in *D. rotundifolia*, chromosomal fragments induced by gamma irradiation are regularly inherited by daughter cells during mitosis (Shirakawa *et al.*, 2011*a*) which is strong evidence for chromosomal holokinetism; *D. aliciae* and *D. binata* have not been studied this way. It is therefore possible that H2AThr120ph is not a universal mitotic centromere marker or at least not able definitely to distinguish between monocentric and holokinetic chromosomes. On the other hand, there is a hypothetical possibility that some species may be monocentric in mitosis but holokinetic in meiosis (Zedek and Bureš, 2016) which might be the case for *D. aliciae* and *D. binata*.

Both the genome size and GC content are perhaps often driven by the same process, such as the proliferation or removal of GC-rich or GC-poor transposable elements (Šmarda and Bureš, 2012), causing a commonly detected positive correlation of GC content with genome size in genera with relatively small genomes (Bureš *et al.*, 2007). However, the GC content also seems to have an adaptive role (Šmarda *et al.*, 2014), reflecting differences in the physical properties of GC and AT base pairs, such as the higher stacking interaction in GC base pairs and consequently a higher thermal stability of GC-rich DNA (Biro, 2008; Šmarda and Bureš, 2012). This trend has also been confirmed in monocots where higher GC contents are favoured in cold and dry climates (Šmarda *et al.*, 2014).

A similar pattern has also been found in Droseraceae, where species with higher GC content are mostly found in areas with stronger annual temperature fluctuations, typical of temperate and Mediterranean regions. As an example may serve northern temperate sundews (*Drosera anglica*, *D. rotundifolia*, *D. intermedia* and *D. filiformis*) or *Drosera* subgenera *Bryastrum* from the Mediterranean climate of West Australia (McPherson, 2008, 2010), all possessing relatively high GC contents (Table 1; Fig. 1). In contrast, low GC contents can be expected in areas with low temperature fluctuations, typically in the tropical regions. Examples include the species of the 'rainforest sundews' (*Drosera adelae*, *D. prolifera* and *D. schizandra*) from northern Queensland, in Australia (McPherson, 2008, 2010), or *Drosera meristocaulis* from the Neblina massif on the Brazilian–Venezuelan border (Rivadavia *et al.*, 2012).

SUPPLEMENTARY DATA

[Supplementary data](#) are available online at www.aob.oxfordjournals.com and consist of the following. [Supplementary Methods](#): detailed description of flow cytometry measurements, sequencing and phylogenetic tree construction. Figure S1: the phylogenetic tree with posterior values. Figure S2: the phylogenetic tree with node ages. Table S1: detailed information about accession numbers used for phylogenetic tree construction and genomic parameters of all analysed species. Table S2: results of flow cytometry measurements. Table S3: genomic and BioClim variables.

ACKNOWLEDGEMENTS

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Paper III

Kolodin P, Cempírková H, Bureš P, Horová L, Veleba A, Francová J, Adamec L, Zedek F. 2018. Holocentric chromosomes may be an apomorphy of Droseraceae. *Plant Systematics and Evolution* **304**: 1289–1296.

SHORT COMMUNICATION

Holocentric chromosomes may be an apomorphy of Droseraceae

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Abstract

Holocentric chromosomes have evolved in various plant and animal taxa, which suggests they may confer a selective advantage in certain conditions, yet their adaptive potential has scarcely been studied. One of the reasons may reside in our insufficient knowledge of the phylogenetic distribution of holocentric chromosomes across eukaryotic phylogeny. In the present study, we focused on Droseraceae, a carnivorous plant family with an unknown chromosomal structure in monotypic genera *Dionaea* and *Aldrovanda*, and a closely related monotypic family Drosophyllaceae. We used flow cytometry to detect holocentric chromosomes by measuring changes in the ratio of the number of G2 nuclei to the number of G1 nuclei in response to gamma irradiation and determined chromosomal structures in *Aldrovanda vesiculosa*, *Dionaea muscipula*, *Drosera tokaiensis*, and *Drosera ultramafica* from Droseraceae and *Drosophyllum lusitanicum* from Drosophyllaceae. We confirmed monocentric chromosomes in *D. lusitanicum* and detected holocentric chromosomes in all four Droseraceae. Our novel finding of holocentric chromosomes in monotypic genera *Aldrovanda* and *Dionaea* suggests that all Droseraceae may be holocentric, but to confirm that further research is needed due to previously reported conflicting results in *Drosera rotundifolia*.

Keywords *Aldrovanda* · *Dionaea* · *Drosera* · *Drosophyllum* · Flow cytometry · Gamma irradiation

Introduction

Holocentric chromosomes, which attach spindle microtubules to the kinetochore formed along most of their length (Cuacos et al. 2015), have evolved repeatedly in plants and animals (Melters et al. 2012; Bureš et al. 2013). Ever since holocentric chromosomes were recognized (Schrader 1935), many studies have focused on cytogenetics (e.g., Nordenskiöld 1963; Heckmann et al. 2011; Jankowska et al. 2015), cytogenomics (e.g., Marques et al. 2015; de Souza et al. 2018), cell biology (e.g., Wanner et al. 2015; Marques et al. 2016), genomics (e.g., d'Alençon et al. 2010), and other aspects of holocentric organisms, shedding light on structural and mechanistic differences between holocentric and monocentric chromosomes. But the question of why holocentric chromosomes appeared repeatedly over the course of evolution has been studied (Zedek and Bureš 2016; Márquez-Corro et al. 2018) or discussed (Wrensch et al. 1994; Talbert et al. 2008; Mandrioli and Manicardi 2012; Zedek and Bureš 2018) only rarely. Their repeated origin indicates that holocentric chromosomes confer some selective advantage, which may be a defense against centromere drive (Talbert et al. 2008; Zedek and Bureš 2016), an ability to rapidly change recombination rates via chromosomal rearrangements (Escudero et al. 2012), or tolerance to chromosome-breaking factors (Mandrioli and Manicardi 2012; Zedek and Bureš 2018).

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The adaptive role of holocentric chromosomes may be understudied because of their rarity in Eukaryotes (Mola and Papeschi 2006; Melters et al. 2012; Bureš et al. 2013). In animals, holocentric chromosomes have been documented in roundworms and in some groups of insects, mites, spiders, scorpions, and millipedes. In plants, holocentric chromosomes have been found in zygnematophycean algae; in the higher-plant families Cyperaceae and Juncaceae; and in the genera *Myristica* (Myristicaceae), *Chionographis* (Melanthiaceae), *Cuscuta* (Convolvulaceae), and *Drosera* (Droseraceae). Recent studies also found evidence for holocentric chromosomes in *Trithuria submersa* (Hydatellaceae; Kynast et al. 2014) and *Prionium serratum* (Thurniaceae; Zedek et al. 2016). It is possible that holocentric chromosomes are not rare at all and that their apparent rarity is an illusion caused by historical and methodical biases (discussed in detail in Zedek and Bureš 2018). Regardless, clear knowledge of the phylogenetic distribution of holocentric chromosomes is needed to understand their origin and adaptive potential.

Droseraceae is a dicot family of carnivorous plants containing approximately 200 species in three genera (Fig. 1): the genus *Drosera* (sundews) and two monotypic genera, *Aldrovanda* and *Dionaea*. The genus *Drosera* is distributed worldwide except Antarctica, *Dionaea muscipula* (Venus flytrap) occurs in the wetlands of North

and South Carolina (USA), and *Aldrovanda vesiculosa* (waterwheel plant) is an aquatic species with scattered distribution in Africa, Australia, and Eurasia (Veleba et al. 2017). Sundews (*Drosera*) are considered holocentric because their chromosomes lack primary constriction (Kondo and Lavarack 1984; Sheikh and Kondo 1995; Hoshi and Kondo 1998), segregate in parallel orientation in anaphase (Kondo and Nontachaiyapoom 2008; Shirakawa et al. 2011a), and attach microtubules along their length (Kondo and Nontachaiyapoom 2008), and also because their chromosomal fragments are regularly inherited (Sheikh et al. 1995; Shirakawa et al. 2011a; Jankowska et al. 2015). Two recent studies reported monocentric chromosomes in four *Drosera* species (Shirakawa et al. 2011b; Demidov et al. 2014) and in *Dionaea muscipula* (Shirakawa et al. 2011b), but they used markers that were not suitable for a reliable distinction between holocentric and monocentric chromosomes (see Discussion for details). Therefore, the chromosomal structure of *Dionaea muscipula* remains unknown. Because the chromosomal structure of *Aldrovanda vesiculosa* is also unknown, it is difficult to assess whether holocentric chromosomes occurred in the common ancestor of the family or appeared in sundews after they diverged from the common ancestor (Fig. 1). Such an uncertainty makes
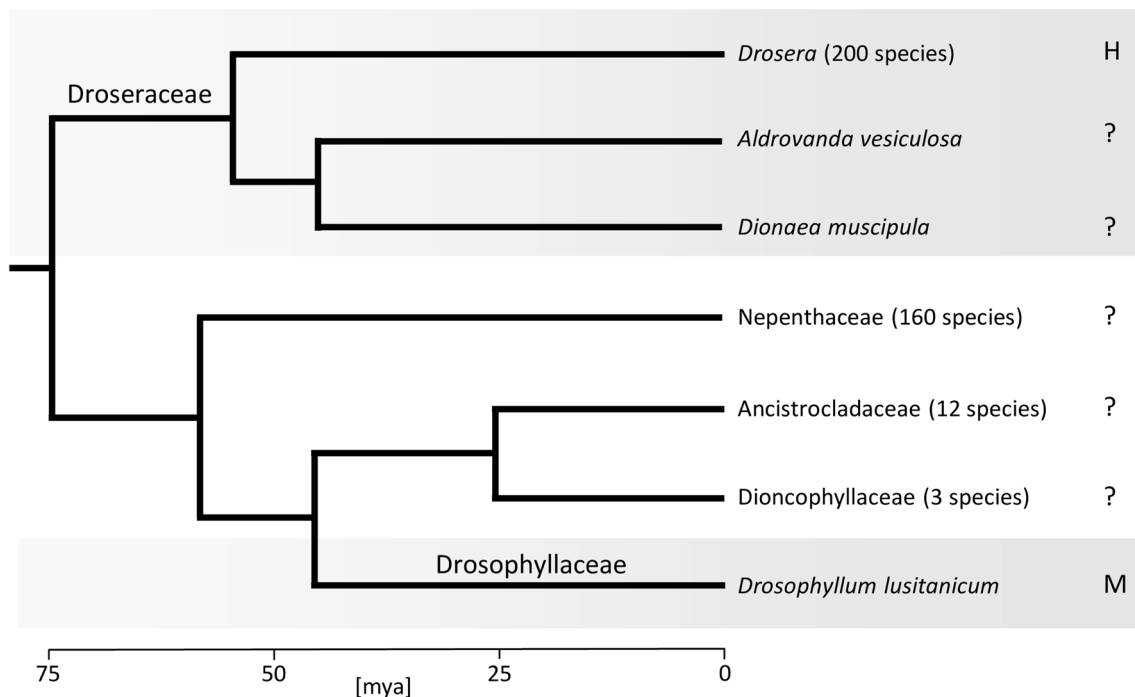
Fig. 1 Chromosomes in Droseraceae and closely related families. Current knowledge of chromosome types in Droseraceae and closely related families is shown next to the dated phylogenetic tree. *H* holocentric chromosomes, *M* monocentric chromosomes, *?* unknown chromosomes. Timescale indicates millions of years before present day. Species from shaded clades were analyzed in the present study. The phylogenetic tree was adopted and simplified from Veleba et al. (2017). Numbers of species were taken from Angiosperm Phylogeny Website (Stevens 2017)

it difficult to address questions of the adaptive potential of holocentric chromosomes in comparative studies.

In the present study, we aimed to determine chromosomal structure in four species (*Aldrovanda vesiculosa*, *Dionaea muscipula*, *Drosera tokaiensis*, and *Drosera ultramafica*) representing all genera of Droseraceae. We also included the presumably monocentric species *Drosophyllum lusitanicum* (Hoshi and Kondo 1998) from the closely related monotypic family Drosophyllaceae (Veleba et al. 2017). To determine chromosomal structure, we combined ionizing irradiation with flow cytometry. Ionizing radiation (e.g., gamma or x-rays) has commonly been used to detect holocentric chromosomes ever since they were discovered because it induces chromosome fragments that are regularly inherited in holocentrics but not in monocentrics. However, previous studies combined ionizing radiation with microscopic observations (e.g., Nordenskiöld 1963; Murakami and Imai 1974; Sheikh et al. 1995; Jankowska et al. 2015).

The flow-cytometric (FCM) method for detecting holocentric chromosomes has been developed for plants and is completely independent of microscopic observations (Zedek et al. 2016). The method relies on the tolerance of holocentric chromosomes to fragmentation and has two steps: (1) induction of chromosomal fragmentation, e.g., by ionizing radiation, in meristematic tissues and (2) flow-cytometric measurements of tissues grown from irradiated meristems. Specifically, flow cytometry is used to count nuclei in the G1 (2C nuclei) and G2 (4C nuclei) phases of the cell cycle. In monocentric plants, the cell cycle is stopped in the G2 phase to prevent cell division with broken chromosomes (Preuss and Britt 2003; Culligan et al. 2004; Carballo et al. 2006), because fragments would otherwise be lost. By contrast, this problem is much smaller or does not exist at all in holocentric organisms because their chromosomal fragments are regularly inherited during cell division (Sheikh et al. 1995; Shirakawa et al. 2011a). As a result, the G2/G1 ratio differs between irradiated plants and non-irradiated control plants in monocentrics, but does not differ in holocentrics (Zedek et al. 2016; see also Methods for details). Because the FCM method for holocentric chromosomes detection is based solely on counting nuclei in G1 and G2 phases of the cell cycle, it does not require an internal standardization. This is an important technical difference from FCM estimation of the nuclear DNA content (C-value), which is a more common FCM application in plant sciences and may be biased by instrumental or sample-preparation fluctuations.

Materials and methods

Species collection and cultivation

Specimens of analyzed species were obtained from the collection at the Institute of Botany of the Czech Academy of Sciences in Třeboň (*Aldrovanda vesiculosa*); from the in vitro collection at the Department of Experimental Biology, Masaryk University (*Drosera tokaiensis* and *Dionaea muscipula*); and from the private collections of Michal Kouba (in vitro culture of *Drosera ultramafica*) and David Švarc (seeds of *Drosophyllum lusitanicum*). *Aldrovanda vesiculosa* was cultivated outdoors in a 350 l container filled with CO_2 enriched water (Adamec 1997). *In vitro* cultures of *Drosera ultramafica*, *D. tokaiensis*, and *Dionaea muscipula* were cultivated in glass jars on agar with 1/3 strength Murashige and Skoog (MS) medium (Sigma Aldrich) with the addition of activated charcoal. Seeds of *Drosophyllum lusitanicum* were sterilized using a two-step procedure: First, seeds were submerged in 50% (v/v) ethanol with 3% H_2O_2 for 1 min; then seeds were immersed in 0.6% (v/v) sodium hypochlorite for 20 min. The seeds were washed 3 times with deionized sterilized water. The tips of the seeds were gently cut off with a razor to disrupt testa and induce germination. Then, the seeds were transferred to Petri dishes with agar containing the MS medium. After 2 weeks, seedlings were transferred and cultivated in vitro in glass jars with agar containing 1/3 MS medium and activated charcoal. Both seeds and in vitro cultures were placed in a growth chamber under the following conditions: 16 h light/8 h dark, 40 µmol m^{-2} s^{-1} at 23 °C.

Gamma irradiation and flow-cytometric (FCM) detection of holocentric chromosomes

Approximately half of the specimens (*A. vesiculosa*) or glass jars (remaining species) were randomly chosen for gamma irradiation with a 150 Gy dose (Cobalt-60, Bioster, Czech Republic) to induce chromosomal fragmentation, while the rest were kept as a control that was not exposed to gamma irradiation. As soon as the irradiated samples formed new tissues, typically after 2 weeks, we conducted FCM measurements.

Only the newly grown tissues from irradiated and non-irradiated control samples were subjected to FCM. We performed FCM analyses on a CyFlow ML flow cytometer (Partec, Germany) that was equipped with a UV-LED diode excitation source. We used a DAPI fluorochrome, applying a 2-step sample-preparation procedure (Otto 1990) and following the protocol developed for genome size measurements in Droseraceae (Veleba et al. 2017). We chose DAPI because it produces low background noise, but other fluorochromes, such as propidium iodide, may also be used. For each species, all of the irradiated and control samples were measured in a random order within a single day. For each sample, we measured 10,000 nuclei in total and we recorded the number of nuclei in the G1 and G2 peaks (FloMax software, Partec, Germany). The upper and lower boundaries of the G2 peak were always
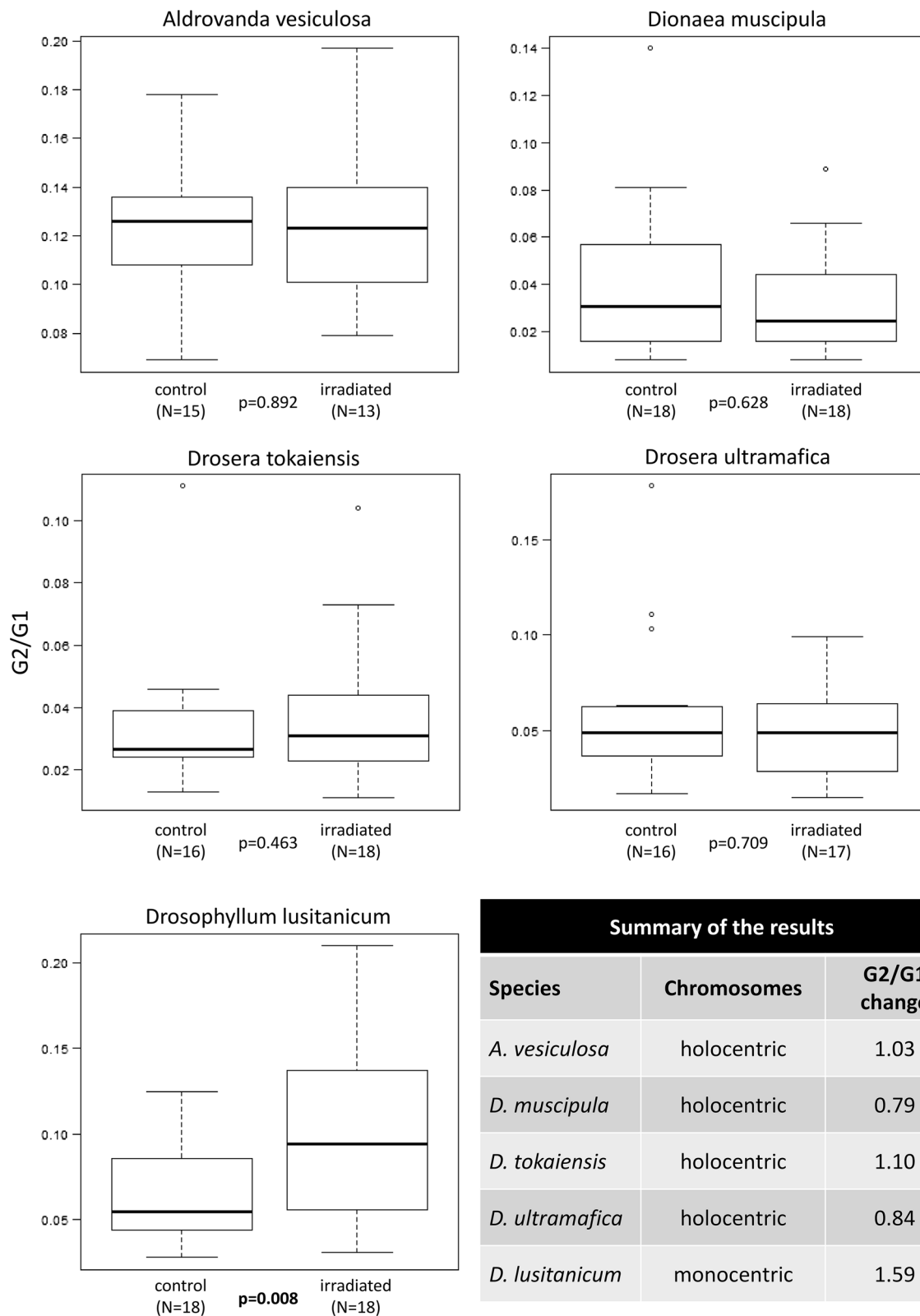
Fig. 2 Results of flow-cytometric determination of chromosomal structure. The comparison of G2/G1 ratio between control and irradiated plants is shown in box-plot graphs for each species. The significance of the Mann–Whitney U test is indicated by a p value below each graph. The value N refers to the number of measured samples. The table at the bottom right summarizes chromosomal structures that were determined for each species. The column "G2/G1 change" shows the average change in G2/G1 ratio in irradiated samples relative to non-irradiated controls and was calculated as the mean of G2/G1 in irradiated samples divided by the mean of G2/G1 in control samples

set manually and calculated as twice the upper and lower boundaries of the G1 peak to ensure comparability across samples. Finally, we calculated the G2/G1 ratio. Examples of flow histograms showing calculations of the G2/G1 ratios are supplied in Online Resource 1. Statistical differences between the G2/G1 ratios of the irradiated and control sample sets were tested using Mann–Whitney U tests.

Results

Using flow cytometry, we measured the G2/G1 ratio in 167 irradiated and control samples from *Aldrovanda vesiculosa* (13 irradiated and 15 control samples)*, Drosera tokaiensis* (18 irradiated and 16 control samples)*, Drosera ultramafica* (17 irradiated and 16 control samples)*, Dionaea muscipula* (18 irradiated and 18 control samples), and *Drosophyllum lusitanicum* (18 irradiated and 18 control samples). The G2/G1 ratio of each sample is supplied in Online Resource 2. The results are summarized in Fig. 2.

Aldrovanda vesiculosa, with a previously unknown chromosomal structure, has been determined to be holocentric because its G2/G1 ratio did not increase in irradiated plants. Also *Drosera ultramafica* and *Drosera tokaiensis* did not show an increase in the G2/G1 ratio in irradiated plants and, therefore, their chromosomes were determined to be holocentric. *Drosophyllum lusitanicum* showed a significantly increased G2/G1 ratio in irradiated plants ($p = 0.008$, Mann–Whitney U test), which agrees with the expectation of monocentric chromosomes in this species. Moreover, the average G2/G1 ratio was 1.59 times higher in irradiated samples of *D. lusitanicum* relative to the control samples, which is above the previously suggested threshold of 1.5 for monocentric chromosomes (Zedek et al. 2016). However, *Dionaea muscipula*, which was also expected to be monocentric, did not show any difference between irradiated and control samples (Fig. 2), suggesting that its chromosomes are, in fact, holocentric.

Discussion

We confirmed monocentric chromosomes in *Drosophyllum lusitanicum* (Drosophyllaceae) and identified all four Droseraceae species as having holocentric chromosomes (Fig. 2). In particular, we found evidence for holocentric chromosomes in *Aldrovanda vesiculosa*, which is consistent with a previous study suggesting that primary constriction is missing in this species (Shirakawa et al. 2011a). We expected holocentric chromosomes in *Drosera tokaiensis* and *Drosera ultramafica* because sundews were identified

as holocentric in previous studies (see Introduction). The finding of holocentric chromosomes in *Dionaea muscipula* (Fig. 2) contradicts previous reports that suggested monocentric chromosomes in this species (Hoshi and Kondo 1998; Shirakawa et al. 2011a).

However, the evidence for monocentric chromosomes in *D. muscipula* was based only on differential staining of mitotic metaphase chromosomes with chromomycin A3 (CMA) and 4′,6-diamidino-2-phenylindole (DAPI; Hoshi and Kondo 1998; Shirakawa et al. 2011a). In those papers, the authors observed weaker CMA and stronger DAPI signals in the central parts of chromosomes, which indicated localized centromeres. A similar observation also led to the suggestion of monocentric chromosomes in *Drosera regia* (Shirakawa et al. 2011b). However, these markers bind to GC (CMA)- and AT (DAPI)-rich regions in the minor groove of DNA and, therefore, are not inherently centromeric markers. Moreover, the same or very similar patterns of CMA and DAPI staining can also be seen in holocentric chromosomes of both plants (Guerra and García 2004) and animals (Kaur et al. 2012; Bardella et al. 2014). These observations strongly indicate that differential staining with DAPI and CMA is not a reliable marker to distinguish between holocentric and monocentric chromosomes.

Another marker that suggested monocentric chromosomes in *Drosera aliciae*, *D. binata*, and *D. rotundifolia* was the histone H2A phosphorylated at threonine 120 (Demidov et al. 2014). But the regular inheritance of induced chromosomal fragments in *D. rotundifolia* (Shirakawa et al. 2011a) is very strong evidence for holocentric chromosomes. Provided the specimens of *D. rotundifolia* analyzed by Demidov et al. (2014) and Shirakawa et al. (2011a) were not misidentified, these observations cast doubt on the reliability of H2AThr120ph as a marker for holo/monocentric distinction.

Although DAPI, CMA, and H2AThr120ph appear to be unreliable markers for distinguishing between holocentric and monocentric chromosomes, it is still possible that *D. muscipula* is monocentric and the flow-cytometric method has simply failed to detect it. In the two weeks that elapsed between irradiation and flow cytometry (see Methods), the chromosomal fragments may have repaired themselves enough so that the difference between irradiated and control plants would be lost. However, Shirakawa et al. (2011a) reported that *Drosera petiolaris* and *D. rotundifolia* that had been gamma-irradiated with 50 Gy showed chromosomal aberrations in more than 90% of cells 120 days after exposure. Similarly, doses of 5 and 30 Gy led to weeks-long persistence of chromosome abberations and fragments in *Chionographis japonica* (Tanaka and Tanaka 1977) and *Luzula elegans* (Jankowska et al. 2015), respectively. Because the dose of 150 Gy we

used for *D. muscipula* was much higher, it is reasonable to expect that a measurable difference between irradiated and control plants should not disappear.

Taking previous reports and our results together, we conclude that there is stronger evidence for holocentric than for monocentric chromosomes in Droseraceae. However, given the conflicting reports on mono/holocentrism in *Drosera rotundifolia* (see above) and possibility of switches between monocentrism and holocentrism even within a genus (see below), monocentric chromosomes in *Drosera* cannot be ruled out until more detailed analyses employing multiple methods are done. Because we identified holocentric chromosomes also in *Aldrovanda vesiculosa* and *Dionaea muscipula*, holocentrism may be an apomorphy of the entire family Droseraceae and we propose to consider this in future comparative studies addressing the evolutionary significance of holocentric chromosomes. However, it still remains unclear whether holocentric chromosomes are an ancestral or a derived state in the entire clade of Droseraceae and closely related families, because data on chromosome structure from Nepenthaceae, Ancistrocladaceae, and Dioncophyllaceae are lacking (Fig. 1).

Similar uncertainties about ancestral states are present also in other plant taxa in which holocentric chromosomes have been found, including algae (Charophyta; Godward 1966), basal angiosperms (family Hydatellaceae; Kynast et al. 2014), magnoliids (family Myristicaceae; Flach 1966), monocots (tribe Chionographidae from Melanthiaceae; Tanaka and Tanaka 1977), and eudicots (the genus *Cuscuta* from Convolvulaceae; Pazy and Plitmann 1994). Moreover, because back and forth transitions between holocentrism and monocentrism can happen (Melters et al. 2012; Escudero et al. 2016), it is possible that holocentric species are more common than currently thought but are intermingled with monocentric species at finer phylogenetic scales, e.g., within a genus as in *Cuscuta* (Pazy and Plitmann 1994) or within a family as in Melanthiaceae (Tanaka and Tanaka 1977). Although many studies conducted over past decades provided chromosome counts for approximately 70,000 plant species (ca 20–25% of plant species; Rice et al. 2015), only a minority of them inspected chromosome structure in order to determine whether chromosomes were monocentric or holocentric, and detailed sophisticated cytogenetic studies have been restricted to a few model taxa, among holocentrics mainly from Cyperaceae (e.g., Marques et al. 2015, 2016) and Juncaceae (e.g., Heckmann et al. 2011; Jankowska et al. 2015). We attempted to elucidate the ambiguity of chromosome types in Droseraceae, but further studies are needed to resolve the distribution of holocentric chromosomes in plants. Such studies should be based on the differential reaction of holocentric and monocentric organisms to chromosome-breaking factors (i.e., checking cell cycle responses or behavior of chromosomal fragments) as the tolerance to fragmentation is an undoubtable hallmark of holocentrism. Also, immunostaining of kinetochore proteins, such as CENH3, which should be distributed along the length of holocentric chromosomes, may shed more light into the chromosomal structure of Droseraceae and other families.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights statement No human participants or animals were involved in this research.

Information on Electronic Supplementary Material

Online Resource 1. Examples of flow histograms with the calculations of the G2/G1 ratios.
Online Resource 2. G2/G1 ratios of all analyzed samples.

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Paper IV

Veleba A, Zedek F, Horová L, Veselý P, Srba M, Šmarda P, Bureš P. (unpubl.) Is the evolution of carnivory connected with a genome miniaturization? Large-scale test of the nutrient limitation hypothesis. [*submitted* to the American Journal of Botany]

1   **Is the evolution of carnivory connected with a genome miniaturization?**

2   **Large-scale test of the nutrient limitation hypothesis.**

3

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11

13   **Running title:** Do the poor habitats limit genomes of carnivorous plants?

14

15   ABSTRACT

16   **Premise:** It has been repeatedly shown that the remarkable variation of the genome size of

17   angiosperms can be shaped by extrinsic selective pressures. The nutrient availability is hypothesised

18   to be one of them, as the DNA represents a significant N and especially P sink. Carnivory has evolved

19   independently in ten angiosperm clades, but all carnivorous plants share a common affinity to the

20   nutrient poor habitats. As such, the carnivory and genome miniaturization could be the response to

21   the same environmental pressure and evolved in parallel. Indeed, the smallest genomes among

22   flowering plants were found in carnivorous family Lentibulariaceae but a large scale test across

23   carnivorous clades was missing so far.

24   **Methods:** This paper presents a comparison of genome sizes of 126 carnivorous plants from 7 clades

25   and 1072 of their non-carnivorous relatives. Their diverse life histories and life forms were taken into

26   account.

27 **Results:** The genomes of carnivorous plants did not differ significantly from the genomes of their

28 non-carnivorous relatives. However, annuals had significantly smaller genomes than perennials.

29 **Conclusions:** The carnivory alone does not seem to significantly affect the genome size evolution. It is

30 plausible that carnivory actually does not synergically increase the effect of nutrient limitation on

31 genome size evolution, but rather counterbalance it. However, the annual species in our dataset

32 possessed smaller genomes than their perennial relatives which confirms the effect of life histories

33 on the genome size evolution on a large phylogenetic scale.

34 **Key words:** Carnivorous Plants; Genome Size; Genome Miniaturization; Nutrient Limitation; Life

35 Histories; Sarraceniaceae

36

37 INTRODUCTION

38 The genome size (GS) in Eukaryotes varies greatly (up to 200,000-fold; Olefeld et al., 2018). The

39 variation is attributed predominantly to the retrotransposon proliferation/removal and polyploidy,

40 driven to various degrees in different clades by selection (Wendel et al., 2013). The smallest genomes

41 among angiosperms were found in carnivorous family Lentibulariaceae (Greilhuber et al., 2006) and

42 the genome miniaturization in this family was later confirmed in other species, especially in the

43 genera *Genlisea* and *Utricularia* (Fleischmann et al., 2014; Veleba et al., 2014). As the smallest

44 Lentibulariaceae genomes are close to the theoretical size of the minimal plant genome (Bennet and

45 Leitch, 2005), the architecture of genomes in this family has become highly researched in an effort to

46 explain their extreme miniaturization.

47 Since the genomes of other carnivorous plants of the family Droseraceae are also relatively small

48 compared to other flowering plants (Veleba et al., 2017), we could consider that the evolution of

49 carnivory itself or the environmental traits shared by carnivorous lineages could adaptively promote

50 miniaturization of their genomes (hypothesised already in Veleba et al., 2014). The >800 currently

51 recognized species of carnivorous plants (Ellison and Adamec, 2018a) evolved independently in ten

52 clades among flowering plants (Fleischmann et al., 2018), and are widely but sparsely distributed

53   across the world. However, all their habitats share abundance of light and water and most

54   importantly low nutrient availability (Givnish, 1984; Givnish et al., 2018).

55   The nutrient availability has been hypothesised to be one of selective mechanisms of the genome

56   size evolution: the nitrogen (N) and phosphorus (P) are major components of DNA, RNA and proteins,

57   and their unavailability is supposed to promote selection for smaller eukaryotic genomes and N-poor

58   amino acids (Leitch and Leitch, 2008; Hessen et al., 2009; Elser et al., 2011; Veleba et al., 2014).

59   Šmarda et al. (2013) and Guignard et al. (2016) both presented similar results from the long-term

60   fertilization experiments: N and P enriched plots host species with larger genomes. However, in

61   natural conditions the trend has been illustrated only on a limited scale of a single genus *Primulina* in

62   relation to N-limitation (Kang et al., 2015), or found absent on global distribution of polyploids in

63   relation to P soil availability (Rice et al., 2019). Therefore, the worldwide distributed carnivorous

64   plants restricted in nutrient poor habitats might be an excellent model for testing this hypothesis on

65   the global scale.

66   The genomic gigantism of geophytic plants (Veselý et al., 2012) has been explained by the

67   combination of their larger supplies of nutrients with the lower demands for the fast growth (Veselý

68   et al., 2013). Hessen et al. (2008) documented a similar joint effect of nutrient availability with a fast

69   growth on genomes of Crustaceans. As suggested for therophyte species, the replication of larger

70   DNA alone (which means longer cell cycle duration) could sufficiently suppress genome expansion

71   when the fast growth is required by the environmental constraints (Bennett, 1971, 1987; Leitch and

72   Bennet, 2007; Francis et al., 2008). Truly, the genomes of annual species of *Andryala* (Zahradníček et

73   al., 2018) and also *Veronica* (Albach and Greilhuber, 2004) are smaller than the genomes of their

74   perennial sisters.

75   In this paper we attempt to compare carnivorous clades/species across angiosperm phylogeny

76   with their non-carnivorous relatives in a large-scale test of the hypothesis that carnivory, as an

77   adaptation to nutrient poor habitats, is associated with the decrease of the genome size. Since it has

78   been hypothesised that the selective effect of nutrient availability on genome size can be intertwined

3

79   with life forms or life histories, these factors have been included in the analysis to distinguish their

80   effect from the effect of carnivory/nutrient limitation.

81

82   MATERIALS AND METHODS

83   Species with known genomic data from the orders containing carnivorous clades (Caryophyllales,

84   Ericales, Lamiales, Oxalidales, and Poales; sensu Stevens, 2001 onwards; Smith and Brown, 2018)

85   were included in the dataset. In Poales where carnivory evolved relatively recently in two small

86   closely-related carnivorous clades in Bromeliaceae (*Brocchinia reducta* + *B. hechtioides*, *Catopsis*

87   *berteroniana*; Fleischmann et al., 2018) only species from the Bromeliaceae + Typhaceae clade were

88   included. For each sample (species) in the dataset (Appendix S1), the following categories were

89   determined: genome size (GS; explained variable, measured or excerpted from the literature),

90   carnivory (C: non-carnivorous or carnivorous; according to Ellison and Adamec, 2018a), life histories

91   (LH: annuals or perennials; Ellenberg and Mueller-Dombois, 1967), life forms (LF: cryptophyte,

92   epiphyte, helophyte, hemicryptophyte, hydrophyte, chamaephyte, phanerophyte, therophyte;

93   Ellenberg and Mueller-Dombois, 1967).

94   The samples of plant species newly analysed in this paper were collected from private collections

95   of Miloš Dobšík, Miroslav Srba, Adolf Tomandl, and Adam Veleba. The representatives of the three

96   carnivorous clades (*Paepalanthus bromelioides*, *Catopsis berteroniana* belonging to Poales, and

97   genus *Philcoxia,* Lamiales) were unavailable to the authors at the time of the study.

98   Young leaves of these plants were prepared according Šmarda et al. (2008, 2014) for the analysis

99   on flow cytometer. When necessary, the precision of measurements was improved by adjusting pH

100 (HCl added to achieve more acid pH), adding of concentrated detergents, and/or spinning the

101 samples and removing impurities from the solution. Internal standards based on completely

102 sequenced *Oryza sativa* subsp. *japonica* "Nipponbare" (International Rice Genome Sequencing

103 Project, 2005) followed Veleba et al. (2017). An intercalating base-unspecific propidium iodide (PI)

104 was used as a fluorochrome in cytometric genome size estimation. The measurement was performed

105   on a CyFlow flow cytometer (Partec GmbH, Germany) equipped with a green laser (100 mW Cobolt

106   Samba). Each sample was measured three times and averaged with target CV < 3 %.

107   The 1C genome sizes were log10 transformed prior to the analysis. All analyses were performed in

108   R (v. 3.5.2; R Core Team, 2018). The original angiosperm phylogeny tree ("GBMB tree", Smith and

109   Brown, 2018) was pruned to contain solely species from the prepared dataset. The phylogenetic

110   linear model (function 'phylolm', package 'phylolm' v. 2.6; Ho and Ane, 2014) with Pagel's λ

111   parameter determined by maximum likelihood (Pagel, 1999) was used to compare the data.

112   The genome sizes (GS) of carnivorous and non-carnivorous species (C) were compared in an

113   additive model, comprising life histories (LH) and life forms (LF) as covariates, i.e. the following four

114   models were considered: GS ~ C; GS ~ C + LH; GS ~ C + LF; GS ~ C + LH + LF. The lowest Akaike

115   information criterion (AIC; Akaike, 1974) was used to determine the most appropriate model.

116   To test the possibility of joint effect of nutrient availability and life histories on the genome size

117   evolution, an interactive model was performed to compare carnivorous annuals, non-carnivorous

118   annuals, carnivorous perennials and non-carnivorous perennials with a special interest in carnivorous

119   annuals: GC ~ C * LH.

120

121   RESULTS

122   Carnivorous species varied from the lowest value (1C = 63.5 Mbp, *Genlisea aurea*) to 1C = 10416.5

123   Mbp (*Drosophyllum lusitanicum*) while non-carnivorous varied from 1C = 166 Mbp (*Torrenia baillonii*)

124   to the largest value (1C = 29242.2 Mbp, *Monotropa uniflora*). Genome sizes for 18 angiosperm

125   species were cytometrically estimated for the first time in our study (Tab. 1).

126   It is notable that this paper presents the first published analysis of genome sizes in the family

127   Sarraceniaceae, covering a substantial proportion of its species diversity. Our data show that genome

128   sizes of the species within genera *Sarracenia* and *Heliamphora* varies only slightly: genus *Sarracenia*

129   varied from 1C = 3374 Mbp to 1C = 3597 Mbp (in *S. alata* and *S. oreophila*, respectively), genus

130   *Heliamphora* varied from 1C = 1110 Mbp to 1C = 1217 Mbp (in *H. nutans* and *H. chimantensis*,

5

131   respectively); monotypic *Darlingtonia californica* had 1C = 2411 Mbp. Thus, Sarraceniaceae are the

132   only one of the larger carnivorous clades where polyploidy has never been detected.

133   Of the tested additive models, the lowest AIC had the model: GS ~ C + LH (difference from the

134   second-best model Δ AIC = 5.1). This model did not show significant difference between carnivorous

135   and non-carnivorous species (P = 0.088).

136   In the test of the hypothesised joint effect of nutrient limitation and life histories on the genome

137   size (GS ~ C * LH) only the non-carnivorous annuals had significantly smaller genomes than the non-

138   carnivorous perennials (P = 0.003). The carnivorous annuals did not differ significantly from the

139   carnivorous perennials, non-carnivorous perennials or non-carnivorous annuals, and carnivorous

140   perennials did not differ significantly from carnivorous annuals, non-carnivorous perennials and non-

141   carnivorous annuals.

142

143   DISCUSSION

144   While some of the carnivorous groups possess miniature genomes, others have equal or even larger

145   genomes than the median genome size of their non-carnivorous relatives (Fig. 1). The evolution of

146   carnivory therefore does not seem to hold any significant connection to the genome miniaturization,

147   despite the well described affinity of carnivorous plants to nutrient poor habitats (Givnish, 1984;

148   Givnish et al., 2018).

149   To understand the carnivory and non-carnivory as a switch driving the genome size evolution in

150   one or another direction might be overly reductionistic. Carnivorous species and clades differ in their

151   investment in carnivory (the formation of specialized structures – traps – and their maintenance),

152   and in their benefits obtained from the prey, realized in the context of the nutrient availability in

153   their habitats. The degree of carnivory then results from all of these parameters, and the carnivory

154   and non-carnivory should be better understood as a continuum not alternatives. Unfortunately, even

155   the data reviewed in Adamec (2011, 2017) or Adamec and Pavlovič (2018) present seasonal gains of

156   nutrients obtained from the trapped prey or growth benefit the efficiency only for a handful of

6

157   species, sometimes also with great differences (e. g. Dixon et al., 1980 reported seasonal N gain from

158   carnivory in *Drosera erythrorhiza* in the field 11 – 17 %, while Watson et al., 1982 reported 100 %).

159   The quantification of carnivory in the scale needed for our analysis is therefore currently not

160   possible.

161   Since carnivory is hypothesised to evolve on nutrient poor sites, because only there the benefits

162   from additional nutrients from prey are higher than the costs of the trap construction and

163   maintenance (Givnish et al., 2018). The nutrient limitation pressed the hardest on the non-

164   carnivorous ancestors of the extant carnivorous taxa, therefore the genomes of recent carnivorous

165   clades shouldn't be necessarily smaller than those of their sister relatives.

166   The striking genome miniaturization in some Lentibulariaceae (Greilhuber et al., 2006;

167   Fleischmann et al., 2014; Veleba et al., 2014), incomparable to the observed genome downsizing in

168   other plants, is not necessarily adaptive (a consequence of carnivory). The complete or large-

169   coverage sequences of some *Genlisea* and *Utricularia* showed the genomes purified from non-coding

170   DNA, with lower numbers of copies of several genes, and even lacking some genes related to roots

171   (Ibarra-Laclette et al., 2013; Leushkin et al., 2013; Vu et al., 2015), as these two genera with highly

172   altered body plan lack the roots (Rutishauser, 2016). The mutation in cytochrome *c* oxidase in these

173   genera should release higher amounts of reactive oxygen types (Jobson et al., 2004; Albert et al.,

174   2010). This has been considered as a possible explanation of the genome miniaturization, as the

175   reactive oxygen can easily damage the DNA, which if deleted by the repairing mechanisms, would

176   result in a genome downsizing (Renner et al., 2018). Another explanation considered a strong

177   mechanism of retrotransposon silencing, which would prefer deletion over insertion (Ibarra-Laclette

178   et al., 2013). The genetic drift itself would be then enough to cause the genome miniaturization in

179   Lentibulariaceae and the comparative analysis of two *Genlisea* species with divergent genome

180   evolution supports this hypothesis (Vu et al., 2015).

181   The effect of life histories on the genome size, i.e. the fact that annuals have smaller genomes

182   than perennials, has been hypothesised already by Bennet (1972). However, the analyses in the

7

183   study have been published before the wider awareness of the necessity of the corrections for

184   phylogeny (Felsenstein, 1985) has spread. The later studies comparing plants with different life

185   histories are scarce and present analyses only among closely related species of the genera *Andryala*

186   (Zahradníček et al., 2018) and *Veronica* (Albach and Greilhuber, 2004). This study shows that among

187   non-carnivorous plants, genomes of annuals are smaller than those of perennials, even when they

188   are tested with the phyllogenetically corrected test on a large evolutionary scale. It is therefore

189   justified to consider that the genomes of annuals are limited by the duration of the cell cycle, which

190   depends also on the amount of DNA (Bennet, 1987), or by the limited nutrient uptake in organisms

191   with short life and fast growth (Hessen et al., 2008).

192

198

199   AUTHOR CONTRIBUTIONS

200   AV and MS collected the samples, LH analysed them. PB, FZ, PŠ, and PV analysed the literature data.

201   AV and FZ performed statistical analyses, AV led writing, FZ and PB co-worked on the manuscript and

202   results interpretations.

203

204   DATA AVAILABILITY

205   Data file 1 (Appendix S1) is available as online supporting material.

206

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337

338   **Table 1**: List of species and their cytometrically estimated genome sizes.

	1C (Mbp)
Oxalidales	
Cephalotaceae	
Cephalotus follicularis	1983.6
Lamiales	
Byblidaceae	
Byblis gigantea	494.9
B. liniflora	884.3
Scrophulariaceae	
Dermatobotrys saundersii	1096
Ericales	
Sarraceniaceae	
Sarracenia purpurea	3412.9
S. rubra	3443.7
S. leucophylla	3424.3
S. alata	3374.8
S. psittacina	3494.4
S. oreophila	3597.1
S. minor	3585.4
S. flava	3531.9
Heliamphora nutans	1110.3
H. heterodoxa	1166.9
H. pulchella	1197.7
H. minor	1169.7
Darlingtonia californica	2411.3
Poales	
Bromeliaceae	
Brocchinia reducta	371.9

339

340   **Appendix 1**: List of species used in the analysis, their genome sizes, life histories, life forms, carnivory

341   and references for the genome size.

342

343   **Figure 1**: Analysed carnivorous clades (red boxplots with names) in the context of the analysed tree

344   and their non-carnivorous relatives (grey boxplots). Boxplots show minimum, median, maximum, and

345   extreme values of log-transformed genome sizes.

Figure 1

Figure 1
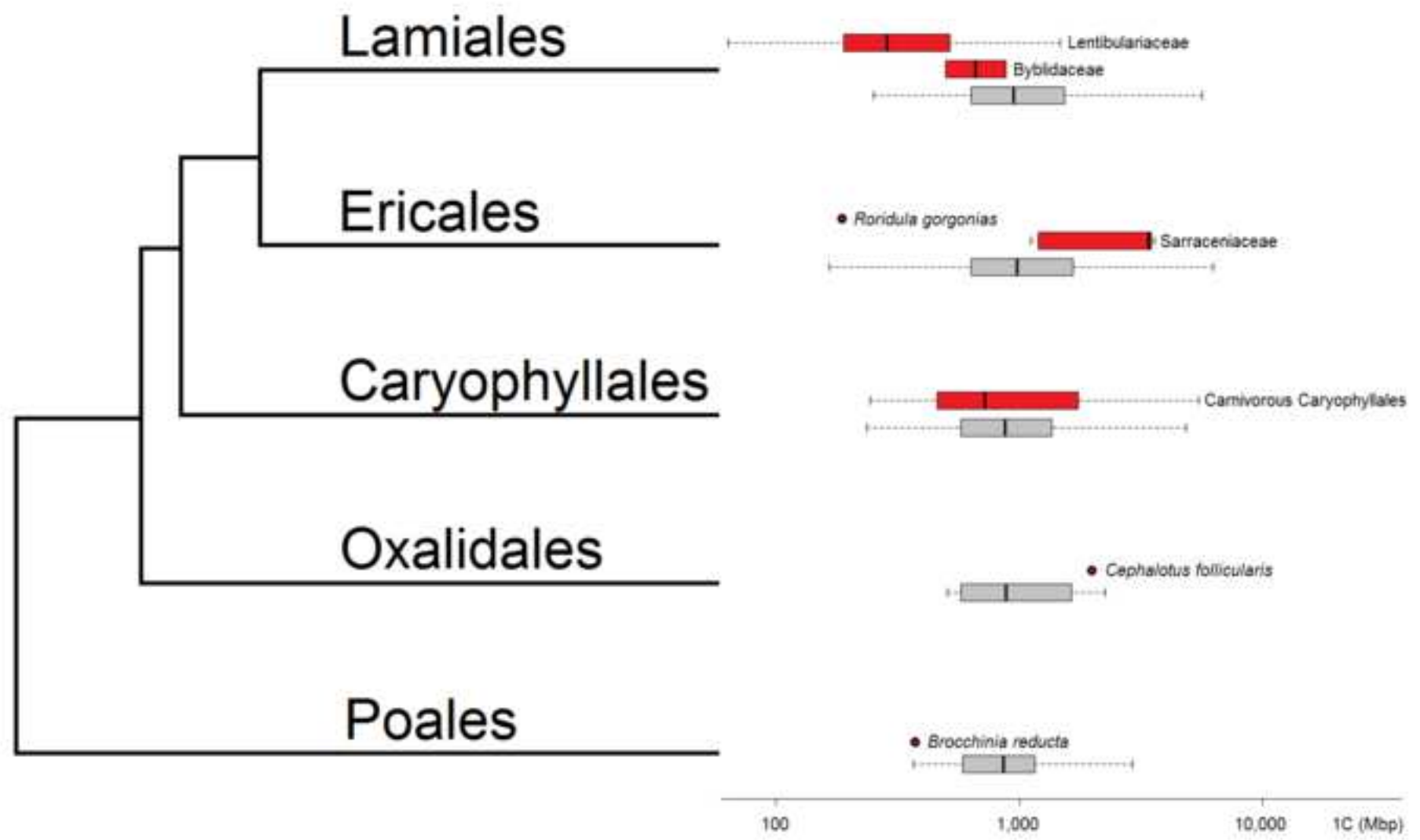
Order	Family	Species	1C (Mbp)	Life forms	Life histories	Carnivory	Reference
Caryophyllales	Aizoaceae	*Delosperma cooperi*	577	Hemicryptophyte	Perennial	Noncarnivorous	47
Caryophyllales	Aizoaceae	*Lampranthus bicolor*	949	Hemicryptophyte	Perennial	Noncarnivorous	47
Caryophyllales	Aizoaceae	*Lampranthus roseus*	1154	Hemicryptophyte	Perennial	Noncarnivorous	47
Caryophyllales	Aizoaceae	*Mesembryanthemum crystallinum*	416	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Aizoaceae	*Sesuvium portulacastrum*	4463	Hemicryptophyte	Perennial	Noncarnivorous	25
Caryophyllales	Amaranthaceae	*Alternanthera philoxeroides*	2093	Helophyte	Perennial	Noncarnivorous	18
Caryophyllales	Amaranthaceae	*Amaranthus acutilobus*	533	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus albus*	538	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Amaranthus arenicola*	439	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus asplundii*	535	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus australis*	824	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus blitoides*	459	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Amaranthus blitum*	749	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus californicus*	548	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus caudatus*	611	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Amaranthus crassipes*	513	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus crispus*	576	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus deflexus*	640	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus dubius*	712	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus fimbriatus*	527	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus floridanus*	658	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus hybridus*	504	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus hypochondriacus*	506	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus muricatus*	730	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus palmeri*	422	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus powellii*	469	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Amaranthus quitensis*	501	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus retroflexus*	446	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Amaranthus spinosus*	472	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus standleyanus*	503	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus tamaulipensis*	525	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus tricolor*	783	Therophyte	Annual	Noncarnivorous	57

Caryophyllales	Amaranthaceae	*Amaranthus tuberculatus*	676	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus viridis*	543	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Amaranthus wrightii*	534	Therophyte	Annual	Noncarnivorous	57
Caryophyllales	Amaranthaceae	*Atriplex canescens*	1601	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex halimus*	1193	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex hortensis*	1149	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex nummularia*	2924	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex patula*	1854	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Atriplex phyllostegia*	465	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex prostrata*	738	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex rosea*	929	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex sagittata*	962	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Atriplex semibaccata*	831	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex serenana*	416	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Atriplex truncata*	562	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Bassia prostrata*	1001	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Bassia scoparia*	1095	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Beta vulgaris*	1223	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Bosea yervamora*	1609	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Celosia argentea*	2748	Therophyte	Annual	Noncarnivorous	18
Caryophyllales	Amaranthaceae	*Celosia cristata*	1516	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Celosia trigyna*	1589	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Dysphania glomulifera*	428	Therophyte	Annual	Noncarnivorous	29
Caryophyllales	Amaranthaceae	*Dysphania pumilio*	362	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Dysphania schraderiana*	359	Therophyte	Annual	Noncarnivorous	29
Caryophyllales	Amaranthaceae	*Chenopodiastrum murale*	498	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Chenopodiastrum simplex*	1223	Therophyte	Annual	Noncarnivorous	4
Caryophyllales	Amaranthaceae	*Chenopodium album*	1594	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Chenopodium berlandieri*	1452	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Chenopodium desertorum*	1076	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Chenopodium ficifolium*	756	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Chenopodium fremontii*	573	Therophyte	Annual	Noncarnivorous	29
Caryophyllales	Amaranthaceae	*Chenopodium giganteum*	2147	Therophyte	Annual	Noncarnivorous	1

Caryophyllales	Amaranthaceae	*Chenopodium hians*	502	Therophyte	Annual	Noncarnivorous	29
Caryophyllales	Amaranthaceae	*Chenopodium neomexicanum*	585	Therophyte	Annual	Noncarnivorous	29
Caryophyllales	Amaranthaceae	*Chenopodium nutans*	983	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Chenopodium opulifolium*	1822	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Chenopodium pallidicaule*	465	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Chenopodium pratericola*	1027	Therophyte	Annual	Noncarnivorous	4
Caryophyllales	Amaranthaceae	*Chenopodium quinoa*	1447	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Chenopodium standleyanum*	586	Therophyte	Annual	Noncarnivorous	29
Caryophyllales	Amaranthaceae	*Chenopodium vulvaria*	392	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Lipandra polysperma*	696	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Oxybasis rubra*	819	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Polycnemum majus*	1584	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Amaranthaceae	*Salicornia europaea*	1345	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Salsola soda*	1281	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Sarcocornia fruticosa*	2890	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Sclerolaena diacantha*	1208	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Spinacia oleracea*	1002	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Suaeda maritima*	1032	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Amaranthaceae	*Teloxys aristata*	440	Therophyte	Annual	Noncarnivorous	29
Caryophyllales	Ancistrocladaceae	*Ancistrocladus abbreviatus*	603	Phanerophyte	Perennial	Noncarnivorous	64
Caryophyllales	Basellaceae	*Anredera cordifolia*	1423	Cryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Basellaceae	*Basella alba*	1753	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Astrophytum ornatum*	1790	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Carnegiea gigantea*	1403	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Cleistocactus icosagonus*	1638	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Cleistocactus smaragdiflorus*	1638	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Consolea corallicola*	2523	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Consolea falcata*	3756	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Consolea moniliformis*	2479	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Consolea nashii*	2489	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Consolea rubescens*	3765	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Consolea spinosissima*	2465	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Cylindropuntia imbricata*	3384	Chamaephyte	Perennial	Noncarnivorous	55

Caryophyllales	Cactaceae	*Disocactus flagelliformis*	1858	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Echinocactus grusonii*	1394	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Ferocactus wislizeni*	1369	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Gymnocalycium amerhauseri*	2032	Hemicryptophyte	Perennial	Noncarnivorous	**52**
Caryophyllales	Cactaceae	*Gymnocalycium erinaceum*	2054	Hemicryptophyte	Perennial	Noncarnivorous	**52**
Caryophyllales	Cactaceae	*Gymnocalycium robustum*	4076	Hemicryptophyte	Perennial	Noncarnivorous	**52**
Caryophyllales	Cactaceae	*Leptocereus quadricostatus*	778	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Maihuenia patagonica*	1311	Hemicryptophyte	Perennial	Noncarnivorous	**32**
Caryophyllales	Cactaceae	*Maihuenia poeppigii*	1178	Hemicryptophyte	Perennial	Noncarnivorous	**32**
Caryophyllales	Cactaceae	*Mammillaria albilanata*	1538	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria bocasana*	4768	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria boolii*	4499	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria crucigera*	1567	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria dixanthocentron*	1557	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria flavicentra*	1487	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria haageana*	1524	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria hahniana*	4792	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria huitzilopochtli*	1526	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria mazatlanensis*	5966	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria plumosa*	6479	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria supertexta*	1522	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Mammillaria zeilmanniana*	5648	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Neobuxbaumia polylopha*	1565	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Neolloydia conoidea*	4988	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Opuntia acaulis*	3716	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Opuntia dillenii*	2225	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Opuntia ficus-indica*	2396	Chamaephyte	Perennial	Noncarnivorous	**55**
Caryophyllales	Cactaceae	*Opuntia fuliginosa*	2269	Chamaephyte	Perennial	Noncarnivorous	**55**
Caryophyllales	Cactaceae	*Opuntia lasiacantha*	2333	Chamaephyte	Perennial	Noncarnivorous	**55**
Caryophyllales	Cactaceae	*Opuntia leucotricha*	2792	Phanerophyte	Perennial	Noncarnivorous	**55**
Caryophyllales	Cactaceae	*Opuntia macrocentra*	1990	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Opuntia microdasys*	2186	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Opuntia robusta*	2435	Chamaephyte	Perennial	Noncarnivorous	**55**

Caryophyllales	Cactaceae	*Opuntia tomentosa*	3633	Phanerophyte	Perennial	Noncarnivorous	56
Caryophyllales	Cactaceae	*Pereskia aculeata*	905	Chamaephyte	Perennial	Noncarnivorous	32
Caryophyllales	Cactaceae	*Pereskia bahiensis*	1149	Phanerophyte	Perennial	Noncarnivorous	32
Caryophyllales	Cactaceae	*Pereskia grandifolia*	1105	Chamaephyte	Perennial	Noncarnivorous	32
Caryophyllales	Cactaceae	*Pereskia nemorosa*	1330	Phanerophyte	Perennial	Noncarnivorous	32
Caryophyllales	Cactaceae	*Pereskia sacharosa*	1232	Phanerophyte	Perennial	Noncarnivorous	32
Caryophyllales	Cactaceae	*Pilosocereus royenii*	3183	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Stenocereus thurberi*	1682	Chamaephyte	Perennial	Noncarnivorous	1
Caryophyllales	Cactaceae	*Stetsonia coryne*	1491	Phanerophyte	Perennial	Noncarnivorous	5
Caryophyllales	Caryophyllaceae	*Agrostemma githago*	1751	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Arenaria gracilis*	582	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Arenaria grandiflora*	2076	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Arenaria serpyllifolia*	688	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Atocion rupestre*	1663	Hemicryptophyte	Perennial	Noncarnivorous	35
Caryophyllales	Caryophyllaceae	*Cerastium alpinum*	1809	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Cerastium arcticum*	3120	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Cerastium arvense*	665	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Cerastium brachypetalum*	1397	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Cerastium dinaricum*	1188	Hemicryptophyte	Perennial	Noncarnivorous	44
Caryophyllales	Caryophyllaceae	*Cerastium fontanum*	3103	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Cerastium latifolium*	1418	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Cerastium pumilum*	1469	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Cerastium semidecandrum*	538	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Cerastium tomentosum*	1141	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Corrigiola litoralis*	568	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus anticarius*	854	Hemicryptophyte	Perennial	Noncarnivorous	3
Caryophyllales	Caryophyllaceae	*Dianthus armeria*	450	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus broteri*	2305	Hemicryptophyte	Perennial	Noncarnivorous	3
Caryophyllales	Caryophyllaceae	*Dianthus carthusianorum*	498	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus caryophyllus*	611	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Dianthus deltoides*	495	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus gratianopolitanus*	1548	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus chinensis*	1208	Hemicryptophyte	Perennial	Noncarnivorous	20

Caryophyllales	Caryophyllaceae	*Dianthus integer*	1115	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Dianthus lumnitzeri*	1585	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus moravicus*	1584	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus petraeus*	1061	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Dianthus pontederae*	479	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus seguieri*	1165	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus superbus*	667	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Dianthus sylvestris*	592	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Dicheranthus plocamoides*	729	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Drypis spinosa*	421	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Gypsophila repens*	685	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Heliosperma alpestre*	2161	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Heliosperma pusillum*	1295	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Herniaria glabra*	583	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Holosteum umbellatum*	825	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Honckenya peploides*	4235	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Illecebrum verticillatum*	379	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Moehringia lateriflora*	1809	Hemicryptophyte	Perennial	Noncarnivorous	4
Caryophyllales	Caryophyllaceae	*Moehringia trinervia*	1217	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Myosoton aquaticum*	1867	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Paronychia canariensis*	1311	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Paronychia kapela*	626	Hemicryptophyte	Perennial	Noncarnivorous	62
Caryophyllales	Caryophyllaceae	*Polycarpaea latifolia*	435	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Sagina apetala*	426	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Sagina procumbens*	360	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Sagina saginoides*	425	Hemicryptophyte	Perennial	Noncarnivorous	21
Caryophyllales	Caryophyllaceae	*Saponaria officinalis*	2076	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Scleranthus annuus*	1678	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Scleranthus perennis*	820	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Schiedea adamantis*	1042	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea apokremnos*	826	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea globosa*	778	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea haleakalensis*	973	Hemicryptophyte	Perennial	Noncarnivorous	1

Caryophyllales	Caryophyllaceae	*Schiedea helleri*	885	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea hookeri*	939	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea jacobii*	1555	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea kaalae*	1399	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea kauaiensis*	934	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea kealiae*	1022	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea laui*	1531	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea ligustrina*	900	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea lydgatei*	1037	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea mannii*	1315	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea membranacea*	807	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea nuttallii*	1237	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea obovata*	905	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea pentandra*	1829	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea perlmanii*	966	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea salicaria*	929	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea sarmentosa*	872	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea spergulina*	914	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea stellarioides*	1159	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea verticillata*	1213	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Schiedea viscosa*	689	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Silene aegyptiaca*	1633	Therophyte	Annual	Noncarnivorous	37
Caryophyllales	Caryophyllaceae	*Silene baccifera*	6260	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Silene berthelotiana*	2499	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Silene ciliata*	924	Hemicryptophyte	Perennial	Noncarnivorous	35
Caryophyllales	Caryophyllaceae	*Silene dichotoma*	1303	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Silene dioica*	2458	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Silene flos-cuculi*	2602	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Silene lagunensis*	2538	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Silene latifolia*	2487	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Silene nocteolens*	2523	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Silene noctiflora*	2475	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Silene nutans*	2333	Hemicryptophyte	Perennial	Noncarnivorous	1

Caryophyllales	Caryophyllaceae	*Silene otites*	2520	Hemicryptophyte	Perennial	Noncarnivorous	62
Caryophyllales	Caryophyllaceae	*Silene pendula*	1149	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Silene pogonocalyx*	2557	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Caryophyllaceae	*Silene stellata*	5770	Hemicryptophyte	Perennial	Noncarnivorous	4
Caryophyllales	Caryophyllaceae	*Silene succulenta*	2137	Hemicryptophyte	Perennial	Noncarnivorous	37
Caryophyllales	Caryophyllaceae	*Silene viscosa*	1964	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Silene vulgaris*	968	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Spergula arvensis*	344	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Spergularia marina*	525	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Spergularia media*	277	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Spergularia rubra*	550	Therophyte	Annual	Noncarnivorous	30
Caryophyllales	Caryophyllaceae	*Stellaria alsine*	685	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Stellaria graminea*	869	Hemicryptophyte	Perennial	Noncarnivorous	60
Caryophyllales	Caryophyllaceae	*Stellaria holostea*	1033	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Stellaria longifolia*	1045	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Stellaria media*	933	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Stellaria nemorum*	822	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Stellaria pallida*	425	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Caryophyllaceae	*Uebelinia kiwuensis*	2069	Therophyte	Annual	Noncarnivorous	49
Caryophyllales	Caryophyllaceae	*Uebelinia scottii*	851	Therophyte	Annual	Noncarnivorous	49
Caryophyllales	Caryophyllaceae	*Viscaria vulgaris*	1962	Hemicryptophyte	Perennial	Noncarnivorous	59
Caryophyllales	Dioncophyllaceae	*Triphyophyllum peltatum*	584	Phanerophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Aldrovanda vesiculosa*	469	Hydrophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Dionaea muscipula*	2853	Hemicryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera aberrans*	494	Cryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera adelae*	297	Hemicryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera aliciae*	975	Hemicryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera allantostigma*	1429	Hemicryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera anglica*	2358	Hemicryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera arcturi*	525	Hemicryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera auriculata*	423	Cryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera barbigera*	2108	Hemicryptophyte	Perennial	Carnivorous	64
Caryophyllales	Droseraceae	*Drosera binata*	733	Hemicryptophyte	Perennial	Carnivorous	64

Caryophyllales	Droseraceae	*Drosera capensis*	395	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera cistiflora*	336	Cryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera collinsiae*	453	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera cuneifolia*	351	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera dilatatopetiolaris*	2434	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera falconeri*	2627	Cryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera filiformis*	2439	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera gigantea*	530	Cryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera graomogolensis*	815	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera hamiltonii*	244	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera helodes*	1793	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera hilaris*	369	Cryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera indica*	654	Therophyte	Annual	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera lanata*	427	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera leucoblasta*	2061	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera menziesii*	467	Cryptophyte	Perennial	Carnivorous	1
Caryophyllales	Droseraceae	*Drosera meristocaulis*	1485	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera natalensis*	520	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera neocaledonica*	568	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera omissa*	1085	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera ordensis*	5464	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera paleacea*	3745	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera peltata*	393	Cryptophyte	Perennial	Carnivorous	1
Caryophyllales	Droseraceae	*Drosera petiolaris*	2354	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera prolifera*	251	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera pulchella*	931	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera pygmaea*	626	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera roseana*	1757	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera rotundifolia*	1166	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera sessilifolia*	249	Therophyte	Annual	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera sewelliae*	1932	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera schizandra*	593	Hemicryptophyte	Perennial	Carnivorous	**64**
Caryophyllales	Droseraceae	*Drosera tokaiensis*	1746	Hemicryptophyte	Perennial	Carnivorous	**22**

Caryophyllales	Droseraceae	*Drosera trinervia*	287	Cryptophyte	Perennial	Carnivorous	64
Caryophyllales	Molluginaceae	*Mollugo verticillata*	782	Therophyte	Annual	Noncarnivorous	4
Caryophyllales	Montiaceae	*Claytonia perfoliata*	1438	Therophyte	Annual	Noncarnivorous	38
Caryophyllales	Montiaceae	*Claytonia sibirica*	3374	Therophyte	Annual	Noncarnivorous	1
Caryophyllales	Montiaceae	*Montia fontana*	286	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Nepenthaceae	*Nepenthes albomarginata*	1361	Phanerophyte	Perennial	Carnivorous	64
Caryophyllales	Nepenthaceae	*Nepenthes gracilis*	844	Phanerophyte	Perennial	Carnivorous	64
Caryophyllales	Nepenthaceae	*Nepenthes madagascariensis*	674	Phanerophyte	Perennial	Carnivorous	64
Caryophyllales	Nepenthaceae	*Nepenthes pervillei*	722	Phanerophyte	Perennial	Carnivorous	64
Caryophyllales	Nepenthaceae	*Nepenthes stenophylla*	1079	Phanerophyte	Perennial	Carnivorous	64
Caryophyllales	Nyctaginaceae	*Bougainvillea glabra*	3985	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Nyctaginaceae	*Bougainvillea spectabilis*	4303	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Nyctaginaceae	*Mirabilis jalapa*	1162	Cryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Nyctaginaceae	*Mirabilis nyctaginea*	929	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Phytolaccaceae	*Microtea scabrida*	2029	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Phytolaccaceae	*Phytolacca americana*	1443	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Phytolaccaceae	*Phytolacca dioica*	1271	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Plumbaginaceae	*Afrolimon purpuratum*	8407	Hemicryptophyte	Perennial	Noncarnivorous	64
Caryophyllales	Plumbaginaceae	*Armeria maritima*	4332	Hemicryptophyte	Perennial	Noncarnivorous	64
Caryophyllales	Plumbaginaceae	*Armeria splendens*	4592	Hemicryptophyte	Perennial	Noncarnivorous	35
Caryophyllales	Plumbaginaceae	*Limonium narbonense*	2474	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Plumbaginaceae	*Limonium sinuatum*	2781	Hemicryptophyte	Perennial	Noncarnivorous	64
Caryophyllales	Plumbaginaceae	*Limonium vulgare*	2302	Hemicryptophyte	Perennial	Noncarnivorous	64
Caryophyllales	Plumbaginaceae	*Plumbago auriculata*	335	Phanerophyte	Perennial	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Bistorta officinalis*	2677	Hemicryptophyte	Perennial	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Calligonum arborescens*	450	Chamaephyte	Perennial	Noncarnivorous	53
Caryophyllales	Polygonaceae	*Calligonum caput-medusae*	1462	Chamaephyte	Perennial	Noncarnivorous	53
Caryophyllales	Polygonaceae	*Calligonum densum*	685	Chamaephyte	Perennial	Noncarnivorous	53
Caryophyllales	Polygonaceae	*Calligonum junceum*	1477	Chamaephyte	Perennial	Noncarnivorous	53
Caryophyllales	Polygonaceae	*Calligonum leucocladum*	1467	Chamaephyte	Perennial	Noncarnivorous	53
Caryophyllales	Polygonaceae	*Calligonum mongolicum*	1418	Chamaephyte	Perennial	Noncarnivorous	53
Caryophyllales	Polygonaceae	*Calligonum roborowskii*	1345	Chamaephyte	Perennial	Noncarnivorous	53
Caryophyllales	Polygonaceae	*Calligonum rubicundum*	1374	Chamaephyte	Perennial	Noncarnivorous	53

Caryophyllales	Polygonaceae	*Coccoloba diversifolia*	999	Phanerophyte	Perennial	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Coccoloba uvifera*	1890	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Polygonaceae	*Fagopyrum esculentum*	1247	Therophyte	Annual	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Fallopia aubertii*	1360	Phanerophyte	Perennial	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Fallopia baldschuanica*	1360	Phanerophyte	Perennial	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Fallopia cilinodis*	1076	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Polygonaceae	*Fallopia convolvulus*	1282	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Fallopia dumetorum*	662	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Fallopia multiflora*	685	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Polygonaceae	*Fallopia sachalinensis*	4342	Hemicryptophyte	Perennial	Noncarnivorous	1
Caryophyllales	Polygonaceae	*Muehlenbeckia complexa*	707	Hemicryptophyte	Perennial	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Oxyria digyna*	955	Hemicryptophyte	Perennial	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Persicaria amphibia*	1366	Helophyte	Perennial	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Persicaria arifolia*	3521	Therophyte	Annual	Noncarnivorous	4
Caryophyllales	Polygonaceae	*Persicaria hydropiper*	650	Therophyte	Annual	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Persicaria japonica*	629	Hemicryptophyte	Perennial	Noncarnivorous	20
Caryophyllales	Polygonaceae	*Persicaria jucunda*	1116	Therophyte	Annual	Noncarnivorous	20
Caryophyllales	Polygonaceae	*Persicaria lapathifolia*	729	Therophyte	Annual	Noncarnivorous	64
Caryophyllales	Polygonaceae	*Persicaria longiseta*	1956	Therophyte	Annual	Noncarnivorous	4
Caryophyllales	Polygonaceae	*Persicaria maculosa*	1508	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Persicaria minor*	1370	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Persicaria mitis*	1535	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Persicaria pubescens*	706	Therophyte	Annual	Noncarnivorous	20
Caryophyllales	Polygonaceae	*Persicaria virginiana*	1907	Hemicryptophyte	Perennial	Noncarnivorous	4
Caryophyllales	Polygonaceae	*Polygonum arenastrum*	723	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Polygonum aviculare*	1099	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Polygonaceae	*Polygonum rurivagum*	1099	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Portulacaceae	*Portulaca oleracea*	1225	Therophyte	Annual	Noncarnivorous	59
Caryophyllales	Simmondsiaceae	*Simmondsia chinensis*	721	Phanerophyte	Perennial	Noncarnivorous	1
Caryophyllales	Tamaricaceae	*Myricaria germanica*	1436	Chamaephyte	Perennial	Noncarnivorous	64
Caryophyllales	Tamaricaceae	*Tamarix africana*	1614	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Actinidiaceae	*Actinidia arguta*	1516	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Actinidiaceae	*Actinidia deliciosa*	2176	Phanerophyte	Perennial	Noncarnivorous	1

Ericales	Actinidiaceae	*Actinidia eriantha*	743	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Actinidiaceae	*Actinidia chinensis*	758	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Actinidiaceae	*Actinidia kolomikta*	680	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Actinidiaceae	*Actinidia polygama*	768	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Balsaminaceae	*Impatiens balsamina*	1296	Therophyte	Annual	Noncarnivorous	1
Ericales	Balsaminaceae	*Impatiens capensis*	831	Therophyte	Annual	Noncarnivorous	4
Ericales	Balsaminaceae	*Impatiens glandulifera*	812	Therophyte	Annual	Noncarnivorous	59
Ericales	Balsaminaceae	*Impatiens noli-tangere*	579	Therophyte	Annual	Noncarnivorous	59
Ericales	Balsaminaceae	*Impatiens omeiana*	3182	Cryptophyte	Perennial	Noncarnivorous	1
Ericales	Balsaminaceae	*Impatiens pallida*	391	Therophyte	Annual	Noncarnivorous	4
Ericales	Balsaminaceae	*Impatiens parviflora*	1868	Therophyte	Annual	Noncarnivorous	59
Ericales	Clethraceae	*Clethra acuminata*	1115	Phanerophyte	Perennial	Noncarnivorous	15
Ericales	Ebenaceae	*Diospyros discolor*	1171	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Ebenaceae	*Diospyros kaki*	2484	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Ebenaceae	*Diospyros malabarica*	1433	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Ebenaceae	*Diospyros montana*	1614	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Ericaceae	*Andromeda polifolia*	962	Chamaephyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Arctostaphylos uva-ursi*	1218	Chamaephyte	Perennial	Noncarnivorous	1
Ericales	Ericaceae	*Calluna vulgaris*	522	Chamaephyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Empetrum nigrum*	631	Chamaephyte	Perennial	Noncarnivorous	1
Ericales	Ericaceae	*Erica carnea*	655	Chamaephyte	Perennial	Noncarnivorous	1
Ericales	Ericaceae	*Erica manipuliflora*	528	Chamaephyte	Perennial	Noncarnivorous	37
Ericales	Ericaceae	*Erica tetralix*	420	Chamaephyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Gaultheria procumbens*	1540	Chamaephyte	Perennial	Noncarnivorous	4
Ericales	Ericaceae	*Gaylussacia baccata*	587	Phanerophyte	Perennial	Noncarnivorous	4
Ericales	Ericaceae	*Chimaphila umbellata*	8900	Chamaephyte	Perennial	Noncarnivorous	4
Ericales	Ericaceae	*Moneses uniflora*	8353	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Monotropa hypopitys*	2690	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Monotropa uniflora*	29242	Hemicryptophyte	Perennial	Noncarnivorous	4
Ericales	Ericaceae	*Orthilia secunda*	7920	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Pyrola elliptica*	4694	Hemicryptophyte	Perennial	Noncarnivorous	4
Ericales	Ericaceae	*Pyrola chlorantha*	4769	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Pyrola minor*	3485	Hemicryptophyte	Perennial	Noncarnivorous	59

Ericales	Ericaceae	*Pyrola rotundifolia*	3288	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Rhododendron brachycarpum*	724	Phanerophyte	Perennial	Noncarnivorous	37
Ericales	Ericaceae	*Rhododendron tomentosum*	1029	Chamaephyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Vaccinium arboreum*	499	Phanerophyte	Perennial	Noncarnivorous	54
Ericales	Ericaceae	*Vaccinium corymbosum*	1032	Chamaephyte	Perennial	Noncarnivorous	54
Ericales	Ericaceae	*Vaccinium crassifolium*	538	Chamaephyte	Perennial	Noncarnivorous	54
Ericales	Ericaceae	*Vaccinium darrowii*	533	Chamaephyte	Perennial	Noncarnivorous	54
Ericales	Ericaceae	*Vaccinium myrsinites*	1032	Chamaephyte	Perennial	Noncarnivorous	54
Ericales	Ericaceae	*Vaccinium myrtillus*	526	Chamaephyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Vaccinium pallidum*	538	Chamaephyte	Perennial	Noncarnivorous	54
Ericales	Ericaceae	*Vaccinium stamineum*	494	Chamaephyte	Perennial	Noncarnivorous	54
Ericales	Ericaceae	*Vaccinium tenellum*	636	Chamaephyte	Perennial	Noncarnivorous	1
Ericales	Ericaceae	*Vaccinium uliginosum*	1267	Chamaephyte	Perennial	Noncarnivorous	59
Ericales	Ericaceae	*Vaccinium vitis-idaea*	975	Chamaephyte	Perennial	Noncarnivorous	59
Ericales	Fouquieriaceae	*Fouquieria splendens*	518	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Lecythidaceae	*Barringtonia racemosa*	1319	Phanerophyte	Perennial	Noncarnivorous	36
Ericales	Marcgraviaceae	*Marcgravia rectiflora*	3007	Hemicryptophyte	Perennial	Noncarnivorous	56
Ericales	Marcgraviaceae	*Norantea guianensis*	10186	Phanerophyte	Perennial	Noncarnivorous	56
Ericales	Marcgraviaceae	*Souroubea exauriculata*	3037	Phanerophyte	Perennial	Noncarnivorous	56
Ericales	Polemoniaceae	*Collomia grandiflora*	2034	Therophyte	Annual	Noncarnivorous	1
Ericales	Polemoniaceae	*Microsteris gracilis*	2758	Therophyte	Annual	Noncarnivorous	67
Ericales	Polemoniaceae	*Navarretia squarrosa*	1286	Therophyte	Annual	Noncarnivorous	1
Ericales	Polemoniaceae	*Phlox adsurgens*	6132	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox alyssifolia*	5090	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox amoena*	5873	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox amplifolia*	7242	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox austromontana*	3868	Hemicryptophyte	Perennial	Noncarnivorous	67
Ericales	Polemoniaceae	*Phlox buckleyi*	10890	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox divaricata*	5819	Hemicryptophyte	Perennial	Noncarnivorous	4
Ericales	Polemoniaceae	*Phlox drummondii*	5980	Therophyte	Annual	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox floridana*	10685	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox glaberrima*	6817	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox muscoides*	3716	Hemicryptophyte	Perennial	Noncarnivorous	67

Ericales	Polemoniaceae	*Phlox nana*	4998	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox paniculata*	6797	Hemicryptophyte	Perennial	Noncarnivorous	4
Ericales	Polemoniaceae	*Phlox pattersonii*	7242	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox pulcherrima*	10998	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox pulchra*	7017	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox pungens*	7804	Hemicryptophyte	Perennial	Noncarnivorous	67
Ericales	Polemoniaceae	*Phlox roemeriana*	6377	Hemicryptophyte	Perennial	Noncarnivorous	27
Ericales	Polemoniaceae	*Phlox stansburyi*	4528	Hemicryptophyte	Perennial	Noncarnivorous	67
Ericales	Polemoniaceae	*Phlox stolonifera*	5257	Hemicryptophyte	Perennial	Noncarnivorous	67
Ericales	Polemoniaceae	*Phlox woodhousei*	3839	Hemicryptophyte	Perennial	Noncarnivorous	67
Ericales	Polemoniaceae	*Polemonium caeruleum*	5580	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Polemoniaceae	*Polemonium reptans*	5917	Hemicryptophyte	Perennial	Noncarnivorous	4
Ericales	Primulaceae	*Aegiceras corniculatum*	841	Phanerophyte	Perennial	Noncarnivorous	36
Ericales	Primulaceae	*Anagallis arvensis*	1144	Therophyte	Annual	Noncarnivorous	59
Ericales	Primulaceae	*Anagallis foemina*	1704	Therophyte	Annual	Noncarnivorous	59
Ericales	Primulaceae	*Androsace elongata*	802	Therophyte	Annual	Noncarnivorous	59
Ericales	Primulaceae	*Androsace septentrionalis*	517	Therophyte	Annual	Noncarnivorous	59
Ericales	Primulaceae	*Ardisia crenata*	2592	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Bonellia frutescens*	592	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Cyclamen coum*	6635	Cryptophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Cyclamen graecum*	2256	Cryptophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Cyclamen hederifolium*	2917	Cryptophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Cyclamen persicum*	1550	Cryptophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Cyclamen purpurascens*	3230	Cryptophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Glaux maritima*	1274	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Hottonia palustris*	765	Hydrophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Jacquinia aculeata*	1042	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Lysimachia nummularia*	1373	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Lysimachia punctata*	2033	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Lysimachia thyrsiflora*	1297	Helophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Lysimachia vulgaris*	3727	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Myrsine africana*	1203	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Myrsine umbellata*	3242	Phanerophyte	Perennial	Noncarnivorous	6

Ericales	Primulaceae	*Primula elatior*	472	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Primula farinosa*	1469	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Primula meadia*	2725	Hemicryptophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Primula minima*	1452	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Primula veris*	417	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Primula vulgaris*	460	Hemicryptophyte	Perennial	Noncarnivorous	1
Ericales	Primulaceae	*Samolus valerandi*	515	Hemicryptophyte	Perennial	Noncarnivorous	59
Ericales	Primulaceae	*Soldanella alpina*	1741	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella angusta*	1638	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella calabrella*	1765	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella carpatica*	1697	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella hungarica*	1643	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella chrysosticta*	1897	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella marmarossiensis*	1648	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella minima*	1672	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella montana*	1653	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella oreodoxa*	1677	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella pindicola*	1814	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella pusilla*	1667	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella rugosa*	1599	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella sacra*	1756	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Soldanella villosa*	1462	Cryptophyte	Perennial	Noncarnivorous	61
Ericales	Primulaceae	*Trientalis borealis*	1516	Cryptophyte	Perennial	Noncarnivorous	4
Ericales	Primulaceae	*Trientalis europaea*	2499	Cryptophyte	Perennial	Noncarnivorous	1
Ericales	Roridulaceae	*Roridula gorgonias*	186	Chamaephyte	Perennial	Carnivorous	1
Ericales	Sapotaceae	*Madhuca longifolia*	966	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Sapotaceae	*Mimusops elengi*	274	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Sapotaceae	*Planchonella eerwah*	526	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Sarraceniaceae	*Darlingtonia californica*	2411	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Heliamphora heterodoxa*	1167	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Heliamphora minor*	1170	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Heliamphora nutans*	1110	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Heliamphora pulchella*	1198	Hemicryptophyte	Perennial	Carnivorous	

Ericales	Sarraceniaceae	*Sarracenia alata*	3375	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Sarracenia flava*	3532	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Sarracenia leucophylla*	3424	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Sarracenia minor*	3585	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Sarracenia oreophila*	3597	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Sarracenia psittacina*	3494	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Sarracenia purpurea*	3413	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Sarraceniaceae	*Sarracenia rubra*	3444	Hemicryptophyte	Perennial	Carnivorous	
Ericales	Styracaceae	*Pterostyrax psilophyllus*	866	Phanerophyte	Perennial	Noncarnivorous	1
Ericales	Styracaceae	*Styrax officinalis*	641	Phanerophyte	Perennial	Noncarnivorous	37
Ericales	Theaceae	*Camellia angustifolia*	2323	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia atrothea*	3002	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia crassicolumna*	2939	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia grandibracteata*	2924	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia kwangsiensis*	2866	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia leptophylla*	2196	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia ptilophylla*	3183	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia sinensis*	2841	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia tachangensis*	2919	Phanerophyte	Perennial	Noncarnivorous	23
Ericales	Theaceae	*Camellia taliensis*	2890	Phanerophyte	Perennial	Noncarnivorous	23
Lamiales	Acanthaceae	*Acanthus ilicifolius*	925	Chamaephyte	Perennial	Noncarnivorous	36
Lamiales	Acanthaceae	*Acanthus mollis*	953	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Acanthaceae	*Avicennia marina*	507	Phanerophyte	Perennial	Noncarnivorous	36
Lamiales	Acanthaceae	*Justicia procumbens*	1001	Hemicryptophyte	Perennial	Noncarnivorous	20
Lamiales	Acanthaceae	*Peristrophe japonica*	3492	Hemicryptophyte	Perennial	Noncarnivorous	20
Lamiales	Bignoniaceae	*Amphilophium carolinae*	1800	Phanerophyte	Perennial	Noncarnivorous	48
Lamiales	Bignoniaceae	*Amphilophium crucigerum*	763	Phanerophyte	Perennial	Noncarnivorous	48
Lamiales	Bignoniaceae	*Campsis radicans*	489	Phanerophyte	Perennial	Noncarnivorous	4
Lamiales	Bignoniaceae	*Cuspidaria convoluta*	1653	Phanerophyte	Perennial	Noncarnivorous	48
Lamiales	Bignoniaceae	*Dolichandra unguis-cati*	1311	Phanerophyte	Perennial	Noncarnivorous	48
Lamiales	Bignoniaceae	*Handroanthus impetiginosus*	500	Phanerophyte	Perennial	Noncarnivorous	9
Lamiales	Bignoniaceae	*Handroanthus ochraceus*	500	Phanerophyte	Perennial	Noncarnivorous	9
Lamiales	Bignoniaceae	*Handroanthus serratifolius*	666	Phanerophyte	Perennial	Noncarnivorous	9

Lamiales	Bignoniaceae	*Jacaranda mimosifolia*	568	Phanerophyte	Perennial	Noncarnivorous	9
Lamiales	Bignoniaceae	*Kigelia africana*	1697	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Bignoniaceae	*Parmentiera cereifera*	645	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Bignoniaceae	*Sparattosperma leucanthum*	510	Phanerophyte	Perennial	Noncarnivorous	9
Lamiales	Bignoniaceae	*Tabebuia heterophylla*	510	Phanerophyte	Perennial	Noncarnivorous	9
Lamiales	Bignoniaceae	*Tecoma stans*	784	Phanerophyte	Perennial	Noncarnivorous	9
Lamiales	Byblidaceae	*Byblis gigantea*	495	Chamaephyte	Perennial	Carnivorous	
Lamiales	Byblidaceae	*Byblis liniflora*	884	Therophyte	Annual	Carnivorous	
Lamiales	Calceolariaceae	*Calceolaria mexicana*	1333	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Haberlea rhodopensis*	1369	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Primulina baishouensis*	870	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina bicolor*	1037	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina bipinnatifida*	875	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina brachytricha*	846	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina bullata*	924	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina cordifolia*	998	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina danxiaensis*	1149	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina depressa*	1012	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina dongguanica*	914	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina eburnea*	846	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina fimbrisepala*	1051	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina glandulosa*	1046	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina gueilinensis*	958	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina guihaiensis*	1002	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina hedyotidea*	763	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina heterotricha*	680	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina hochiensis*	866	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina huaijiensis*	548	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina chizhouensis*	924	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina juliae*	1227	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina langshanica*	880	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina latinervis*	1115	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina laxiflora*	665	Hemicryptophyte	Perennial	Noncarnivorous	28

Lamiales	Gesneriaceae	*Primulina leiophylla*	939	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina leprosa*	1012	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina liboensis*	968	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina liguliformis*	822	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina linearifolia*	577	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina lobulata*	949	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina longgangensis*	680	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina longicalyx*	1007	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina longii*	1007	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina lunglinensis*	1037	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina lungzhouensis*	1012	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina luochengensis*	645	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina lutea*	1105	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina mabaensis*	1125	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina macrodonta*	880	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina medica*	993	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina mollifolia*	1061	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina nandanensis*	949	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina napoensis*	929	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina obtusidentata*	1115	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina ophiopogoides*	675	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina orthandra*	900	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina parvifolia*	719	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina pinnatifida*	1115	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina pseudoeburnea*	841	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina pteropoda*	714	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina qingyuanensis*	963	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina renifolia*	812	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina repanda*	1022	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina ronganensis*	949	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina rongshuiensis*	958	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina sclerophylla*	851	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina shouchengensis*	1012	Hemicryptophyte	Perennial	Noncarnivorous	28

Lamiales	Gesneriaceae	*Primulina sinensis*	1149	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina spinulosa*	719	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina subrhomboidea*	914	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina subulata*	880	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina swinglei*	792	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina tabacum*	885	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina tenuifolia*	1027	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina tenuituba*	1051	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina tiandengensis*	836	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina tribracteata*	1042	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina varicolor*	983	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina verecunda*	875	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina villosissima*	998	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina wentsaii*	797	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina xiuningensis*	1169	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina xiziae*	914	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina yangchunensis*	836	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Primulina yungfuensis*	1007	Hemicryptophyte	Perennial	Noncarnivorous	28
Lamiales	Gesneriaceae	*Sinningia aggregata*	282	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia eumorpha*	255	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia guttata*	335	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia harleyi*	251	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia macrophylla*	375	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia pusilla*	358	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia richii*	315	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia speciosa*	281	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Sinningia tubiflora*	372	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Gesneriaceae	*Streptocarpus andohahelensis*	2316	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus baudertii*	919	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus brevipilosus*	918	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus cyaneus*	856	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus daviesii*	845	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus dunnii*	1022	Hemicryptophyte	Perennial	Noncarnivorous	41

Lamiales	Gesneriaceae	*Streptocarpus glandulosissimus*	515	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus grandis*	1261	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus hilsenbergii*	558	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus inflatus*	515	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus johannis*	844	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus kentaniensis*	857	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus micranthus*	909	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus muscosus*	612	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus pallidiflorus*	549	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus papangae*	1294	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus primulifolius*	906	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus rexii*	929	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus saxorum*	595	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus shumensis*	846	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus stomandrus*	565	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus thompsonii*	581	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus variabilis*	1478	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus venosus*	600	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus vestitus*	619	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Gesneriaceae	*Streptocarpus wendlandii*	1235	Hemicryptophyte	Perennial	Noncarnivorous	41
Lamiales	Lamiaceae	*Agastache rugosa*	518	Hemicryptophyte	Perennial	Noncarnivorous	34
Lamiales	Lamiaceae	*Ajuga chamaepitys*	901	Therophyte	Annual	Noncarnivorous	59
Lamiales	Lamiaceae	*Ajuga reptans*	1090	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Betonica officinalis*	4091	Hemicryptophyte	Perennial	Noncarnivorous	60
Lamiales	Lamiaceae	*Blephilia hirsuta*	1320	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Lamiaceae	*Bystropogon canariensis*	538	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Callicarpa americana*	763	Phanerophyte	Perennial	Noncarnivorous	10
Lamiales	Lamiaceae	*Callicarpa japonica*	743	Phanerophyte	Perennial	Noncarnivorous	10
Lamiales	Lamiaceae	*Callicarpa mollis*	704	Phanerophyte	Perennial	Noncarnivorous	10
Lamiales	Lamiaceae	*Callicarpa pedunculata*	655	Phanerophyte	Perennial	Noncarnivorous	10
Lamiales	Lamiaceae	*Callicarpa rubella*	680	Phanerophyte	Perennial	Noncarnivorous	10
Lamiales	Lamiaceae	*Clerodendrum trichotomum*	1131	Phanerophyte	Perennial	Noncarnivorous	68
Lamiales	Lamiaceae	*Clinopodium acinos*	530	Therophyte	Annual	Noncarnivorous	59

Lamiales	Lamiaceae	*Clinopodium gracile*	832	Hemicryptophyte	Perennial	Noncarnivorous	20
Lamiales	Lamiaceae	*Clinopodium thymifolium*	425	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Clinopodium vulgare*	440	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Lamiaceae	*Elsholtzia ciliata*	557	Therophyte	Annual	Noncarnivorous	34
Lamiales	Lamiaceae	*Galeopsis angustifolia*	512	Therophyte	Annual	Noncarnivorous	59
Lamiales	Lamiaceae	*Galeopsis speciosa*	957	Therophyte	Annual	Noncarnivorous	59
Lamiales	Lamiaceae	*Galeopsis tetrahit*	1429	Therophyte	Annual	Noncarnivorous	59
Lamiales	Lamiaceae	*Glechoma hederacea*	803	Hemicryptophyte	Perennial	Noncarnivorous	24
Lamiales	Lamiaceae	*Glechoma longituba*	896	Hemicryptophyte	Perennial	Noncarnivorous	24
Lamiales	Lamiaceae	*Hyssopus officinalis*	489	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Isodon inflexus*	499	Hemicryptophyte	Perennial	Noncarnivorous	34
Lamiales	Lamiaceae	*Lamium album*	1076	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Lamium amplexicaule*	1262	Therophyte	Annual	Noncarnivorous	37
Lamiales	Lamiaceae	*Lamium barbatum*	1087	Hemicryptophyte	Perennial	Noncarnivorous	20
Lamiales	Lamiaceae	*Lamium maculatum*	1205	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Lamium moschatum*	1518	Therophyte	Annual	Noncarnivorous	37
Lamiales	Lamiaceae	*Lamium purpureum*	1076	Therophyte	Annual	Noncarnivorous	1
Lamiales	Lamiaceae	*Lavandula angustifolia*	5526	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Lavandula buchii*	494	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Lavandula multifida*	499	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Leonurus cardiaca*	678	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Lycopus europaeus*	383	Helophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Lycopus exaltatus*	401	Helophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Lycopus uniflorus*	831	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Lamiaceae	*Meehania urticifolia*	569	Hemicryptophyte	Perennial	Noncarnivorous	24
Lamiales	Lamiaceae	*Melissa officinalis*	782	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Melittis melissophyllum*	465	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Mentha aquatica*	1284	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Mentha arvensis*	1023	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Mentha australis*	748	Hemicryptophyte	Perennial	Noncarnivorous	26
Lamiales	Lamiaceae	*Mentha canadensis*	1286	Hemicryptophyte	Perennial	Noncarnivorous	26
Lamiales	Lamiaceae	*Mentha gattefossei*	308	Hemicryptophyte	Perennial	Noncarnivorous	26
Lamiales	Lamiaceae	*Mentha japonica*	753	Hemicryptophyte	Perennial	Noncarnivorous	26

Lamiales	Lamiaceae	*Mentha longifolia*	376	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Mentha pulegium*	330	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Mentha requienii*	489	Hemicryptophyte	Perennial	Noncarnivorous	26
Lamiales	Lamiaceae	*Mentha spicata*	728	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Mentha suaveolens*	426	Hemicryptophyte	Perennial	Noncarnivorous	26
Lamiales	Lamiaceae	*Micromeria herpyllomorpha*	372	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Micromeria hyssopifolia*	352	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Micromeria varia*	367	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Minthostachys mollis*	822	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Minthostachys spicata*	803	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Monarda fistulosa*	929	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Lamiaceae	*Nepeta cataria*	636	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Lamiaceae	*Ocimum basilicum*	2377	Therophyte	Annual	Noncarnivorous	51
Lamiales	Lamiaceae	*Ocimum selloi*	1491	Phanerophyte	Perennial	Noncarnivorous	51
Lamiales	Lamiaceae	*Ocimum tenuiflorum*	450	Hemicryptophyte	Perennial	Noncarnivorous	51
Lamiales	Lamiaceae	*Origanum compactum*	748	Hemicryptophyte	Perennial	Noncarnivorous	40
Lamiales	Lamiaceae	*Origanum elongatum*	729	Hemicryptophyte	Perennial	Noncarnivorous	40
Lamiales	Lamiaceae	*Origanum onites*	714	Hemicryptophyte	Perennial	Noncarnivorous	40
Lamiales	Lamiaceae	*Origanum syriacum*	802	Chamaephyte	Perennial	Noncarnivorous	37
Lamiales	Lamiaceae	*Origanum vulgare*	636	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Perilla frutescens*	1395	Therophyte	Annual	Noncarnivorous	68
Lamiales	Lamiaceae	*Phlomis umbrosa*	2543	Hemicryptophyte	Perennial	Noncarnivorous	34
Lamiales	Lamiaceae	*Phlomoides tuberosa*	1978	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Prunella asiatica*	724	Hemicryptophyte	Perennial	Noncarnivorous	34
Lamiales	Lamiaceae	*Prunella grandiflora*	619	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Prunella vulgaris*	636	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Pycnanthemum virginianum*	2592	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Lamiaceae	*Salvia aethiopis*	639	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Salvia broussonetii*	421	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Salvia canariensis*	484	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Salvia fruticosa*	817	Phanerophyte	Perennial	Noncarnivorous	37
Lamiales	Lamiaceae	*Salvia glutinosa*	946	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Salvia microstegia*	611	Hemicryptophyte	Perennial	Noncarnivorous	37

Lamiales	Lamiaceae	*Salvia multicaulis*	1100	Chamaephyte	Perennial	Noncarnivorous	37
Lamiales	Lamiaceae	*Salvia nemorosa*	468	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Salvia officinalis*	474	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Salvia ringens*	597	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Salvia sclarea*	567	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Salvia splendens*	831	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Salvia viridis*	421	Therophyte	Annual	Noncarnivorous	37
Lamiales	Lamiaceae	*Salvia viscosa*	1105	Hemicryptophyte	Perennial	Noncarnivorous	37
Lamiales	Lamiaceae	*Satureja cuneifolia*	1100	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Satureja montana*	2714	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Scutellaria baicalensis*	377	Hemicryptophyte	Perennial	Noncarnivorous	8
Lamiales	Lamiaceae	*Scutellaria viscidula*	424	Hemicryptophyte	Perennial	Noncarnivorous	68
Lamiales	Lamiaceae	*Stachys alpina*	765	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Stachys byzantina*	642	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Stachys palustris*	1397	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Stachys recta*	810	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Stachys sylvatica*	1103	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Tectona grandis*	465	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Teucrium canadense*	734	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Lamiaceae	*Teucrium heterophyllum*	1120	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Teucrium chamaedrys*	1530	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Teucrium montanum*	582	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Teucrium scorodonia*	1149	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Thymus pulegioides*	608	Chamaephyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Thymus serpyllum*	503	Chamaephyte	Perennial	Noncarnivorous	59
Lamiales	Lamiaceae	*Thymus vulgaris*	758	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Vitex negundo*	1587	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Lamiaceae	*Ziziphora clinopodioides*	549	Chamaephyte	Perennial	Noncarnivorous	37
Lamiales	Lentibulariaceae	*Genlisea aurea*	64	Hemicryptophyte	Perennial	Carnivorous	19
Lamiales	Lentibulariaceae	*Genlisea glandulosissima*	169	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Genlisea guianensis*	298	Helophyte	Perennial	Carnivorous	14
Lamiales	Lentibulariaceae	*Genlisea hispidula*	1417	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Genlisea lobata*	1200	Therophyte	Annual	Carnivorous	63

Lamiales	Lentibulariaceae	*Genlisea margaretae*	168	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Genlisea pygmaea*	161	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Genlisea repens*	77	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Genlisea subglabra*	1471	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Genlisea uncinata*	995	Hemicryptophyte	Perennial	Carnivorous	19
Lamiales	Lentibulariaceae	*Genlisea violacea*	460	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula agnata*	651	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula bohemica*	590	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula caerulea*	1178	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula ehlersiae*	978	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula gracilis*	518	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula grandiflora*	424	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula gypsicola*	501	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula lusitanica*	665	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula moranensis*	713	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Pinguicula rotundiflora*	547	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia alpina*	159	Epiphyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia amethystina*	382	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia asplundii*	202	Epiphyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia aurea*	193	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia australis*	200	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia biloba*	150	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia bisquamata*	308	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia caerulea*	706	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia dichotoma*	246	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia endresii*	133	Epiphyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia flaccida*	349	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia geminiloba*	287	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia geminiscapa*	191	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia gibba*	103	Hydrophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia graminifolia*	377	Helophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia chrysantha*	404	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia inflata*	313	Hydrophyte	Perennial	Carnivorous	63

Lamiales	Lentibulariaceae	*Utricularia intermedia*	203	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia juncea*	106	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia livida*	239	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia longifolia*	97	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia macrorhiza*	193	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia minor*	190	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia nana*	561	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia nelumbifolia*	349	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia nephrophylla*	247	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia praelonga*	162	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia prehensilis*	526	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia pubescens*	232	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia reniformis*	292	Helophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia resupinata*	169	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia sandersonii*	204	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia subulata*	340	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia tricolor*	262	Hemicryptophyte	Perennial	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia uliginosa*	116	Therophyte	Annual	Carnivorous	63
Lamiales	Lentibulariaceae	*Utricularia vulgaris*	199	Hydrophyte	Perennial	Carnivorous	63
Lamiales	Linderniaceae	*Craterostigma plantagineum*	1027	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Linderniaceae	*Torenia baillonii*	166	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Martyniaceae	*Proboscidea louisiana*	474	Therophyte	Annual	Noncarnivorous	1
Lamiales	Oleaceae	*Fraxinus americana*	851	Phanerophyte	Perennial	Noncarnivorous	65
Lamiales	Oleaceae	*Fraxinus angustifolia*	870	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Oleaceae	*Fraxinus excelsior*	954	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Oleaceae	*Fraxinus nigra*	880	Phanerophyte	Perennial	Noncarnivorous	4
Lamiales	Oleaceae	*Fraxinus ornus*	963	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Oleaceae	*Fraxinus pennsylvanica*	861	Phanerophyte	Perennial	Noncarnivorous	65
Lamiales	Oleaceae	*Fraxinus quadrangulata*	709	Phanerophyte	Perennial	Noncarnivorous	65
Lamiales	Oleaceae	*Ligustrum quihoui*	1392	Phanerophyte	Perennial	Noncarnivorous	68
Lamiales	Oleaceae	*Ligustrum vulgare*	1364	Phanerophyte	Perennial	Noncarnivorous	59
Lamiales	Oleaceae	*Nyctanthes arbor-tristis*	1200	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Oleaceae	*Olea europaea*	1907	Phanerophyte	Perennial	Noncarnivorous	1

Lamiales	Oleaceae	*Syringa josikaea*	1535	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Oleaceae	*Syringa oblata*	1692	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Oleaceae	*Syringa pinnatifolia*	1487	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Oleaceae	*Syringa pubescens*	1428	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Oleaceae	*Syringa reticulata*	1555	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Oleaceae	*Syringa villosa*	1555	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Oleaceae	*Syringa vulgaris*	1648	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Oleaceae	*Syringa wolfii*	1535	Phanerophyte	Perennial	Noncarnivorous	33
Lamiales	Orobanchaceae	*Bartsia alpina*	727	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Orobanchaceae	*Bellardia latifolia*	553	Therophyte	Annual	Noncarnivorous	37
Lamiales	Orobanchaceae	*Bellardia trixago*	905	Therophyte	Annual	Noncarnivorous	7
Lamiales	Orobanchaceae	*Euphrasia minima*	631	Therophyte	Annual	Noncarnivorous	7
Lamiales	Orobanchaceae	*Euphrasia picta*	550	Therophyte	Annual	Noncarnivorous	59
Lamiales	Orobanchaceae	*Euphrasia rostkoviana*	510	Therophyte	Annual	Noncarnivorous	59
Lamiales	Orobanchaceae	*Euphrasia stricta*	981	Therophyte	Annual	Noncarnivorous	59
Lamiales	Orobanchaceae	*Lathraea squamaria*	561	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Orobanchaceae	*Melampyrum nemorosum*	3935	Therophyte	Annual	Noncarnivorous	59
Lamiales	Orobanchaceae	*Melampyrum sylvaticum*	4117	Therophyte	Annual	Noncarnivorous	59
Lamiales	Orobanchaceae	*Nothobartsia asperrima*	758	Therophyte	Annual	Noncarnivorous	7
Lamiales	Orobanchaceae	*Odontitella virgata*	2088	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Orobanchaceae	*Odontites bocconei*	680	Hemicryptophyte	Perennial	Noncarnivorous	16
Lamiales	Orobanchaceae	*Odontites corsicus*	557	Therophyte	Annual	Noncarnivorous	16
Lamiales	Orobanchaceae	*Odontites luteus*	621	Therophyte	Annual	Noncarnivorous	16
Lamiales	Orobanchaceae	*Odontites maroccanus*	1491	Therophyte	Annual	Noncarnivorous	16
Lamiales	Orobanchaceae	*Odontites pyrenaeus*	533	Therophyte	Annual	Noncarnivorous	16
Lamiales	Orobanchaceae	*Odontites vernus*	557	Therophyte	Annual	Noncarnivorous	1
Lamiales	Orobanchaceae	*Odontites viscosus*	1100	Therophyte	Annual	Noncarnivorous	16
Lamiales	Orobanchaceae	*Odontites vulgaris*	458	Therophyte	Annual	Noncarnivorous	59
Lamiales	Orobanchaceae	*Orobanche caryophyllacea*	3485	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Orobanchaceae	*Orobanche cernua*	1418	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Orobanchaceae	*Orobanche gracilis*	1621	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Orobanchaceae	*Orobanche hederae*	2275	Therophyte	Annual	Noncarnivorous	1
Lamiales	Orobanchaceae	*Orobanche minor*	1789	Therophyte	Annual	Noncarnivorous	1

Lamiales	Orobanchaceae	*Orobanche picridis*	2724	Therophyte	Annual	Noncarnivorous	1
Lamiales	Orobanchaceae	*Orobanche pinorum*	2269	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Orobanchaceae	*Rhinanthus alectorolophus*	1065	Therophyte	Annual	Noncarnivorous	59
Lamiales	Orobanchaceae	*Rhinanthus minor*	1168	Therophyte	Annual	Noncarnivorous	59
Lamiales	Paulowniaceae	*Paulownia tomentosa*	587	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Pedaliaceae	*Ceratotheca sesamoides*	513	Therophyte	Annual	Noncarnivorous	2
Lamiales	Pedaliaceae	*Sesamum alatum*	1648	Therophyte	Annual	Noncarnivorous	1
Lamiales	Pedaliaceae	*Sesamum capense*	1186	Therophyte	Annual	Noncarnivorous	1
Lamiales	Pedaliaceae	*Sesamum indicum*	949	Therophyte	Annual	Noncarnivorous	1
Lamiales	Pedaliaceae	*Sesamum triphyllum*	523	Therophyte	Annual	Noncarnivorous	1
Lamiales	Phrymaceae	*Erythranthe glabrata*	391	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Phrymaceae	*Erythranthe guttata*	377	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Phrymaceae	*Mazus pumilus*	1560	Therophyte	Annual	Noncarnivorous	20
Lamiales	Phrymaceae	*Mimulus ringens*	636	Helophyte	Perennial	Noncarnivorous	4
Lamiales	Phrymaceae	*Phryma leptostachya*	1100	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Plantaginaceae	*Antirrhinum majus*	633	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Bacopa monnieri*	914	Helophyte	Perennial	Noncarnivorous	31
Lamiales	Plantaginaceae	*Campylanthus salsoloides*	743	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Collinsia heterophylla*	2005	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Collinsia verna*	1809	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Cymbalaria muralis*	484	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Plantaginaceae	*Digitalis grandiflora*	1102	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Digitalis purpurea*	914	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Plantaginaceae	*Digitalis thapsi*	1017	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Plantaginaceae	*Digitalis trojana*	1369	Hemicryptophyte	Perennial	Noncarnivorous	11
Lamiales	Plantaginaceae	*Globularia meridionalis*	787	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Globularia salicina*	411	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Globularia vulgaris*	435	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Gratiola officinalis*	1331	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Hippuris vulgaris*	584	Helophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Isoplexis canariensis*	973	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Isoplexis chalcantha*	993	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Kickxia elatine*	1321	Therophyte	Annual	Noncarnivorous	59

Lamiales	Plantaginaceae	*Kickxia spuria*	802	Therophyte	Annual	Noncarnivorous	7
Lamiales	Plantaginaceae	*Lagotis integrifolia*	2623	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Linaria vulgaris*	774	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Littorella uniflora*	5518	Therophyte	Annual	Noncarnivorous	59
Lamiales	Plantaginaceae	*Misopates orontium*	430	Therophyte	Annual	Noncarnivorous	7
Lamiales	Plantaginaceae	*Penstemon albertinus*	655	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon albidus*	782	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon ambiguus*	504	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon angustifolius*	856	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon attenuatus*	1149	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon azureus*	1159	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon barbatus*	802	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon cobaea*	763	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon comarrhenus*	875	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon confertus*	1276	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon confusus*	778	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon cyananthus*	895	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon davidsonii*	484	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon digitalis*	3130	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon dissectus*	460	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon dolius*	782	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon eatonii*	724	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon fendleri*	592	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon fremontii*	719	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon fruticosus*	474	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon grinnellii*	685	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon harbourii*	748	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon humilis*	597	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon labrosus*	773	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon laricifolius*	557	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon lentus*	812	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon leonardii*	474	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon linarioides*	499	Hemicryptophyte	Perennial	Noncarnivorous	1

Lamiales	Plantaginaceae	*Penstemon lyallii*	582	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon montanus*	650	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon newberryi*	518	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon nitidus*	910	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon ophianthus*	807	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon ovatus*	680	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon palmeri*	689	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon personatus*	494	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon pinifolius*	582	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon procerus*	616	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon pseudoputus*	866	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon pseudospectabilis*	709	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon radicosus*	694	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon rostriflorus*	567	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon secundiflorus*	807	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon serrulatus*	523	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon smallii*	553	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon speciosus*	743	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon strictiformis*	763	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon strictus*	802	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon thompsoniae*	645	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon triphyllus*	484	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon virens*	817	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon watsonii*	621	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon whippleanus*	636	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Penstemon wilcoxii*	699	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Picrorhiza kurrooa*	1726	Hemicryptophyte	Perennial	Noncarnivorous	**43**
Lamiales	Plantaginaceae	*Plantago afra*	1127	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago albicans*	1907	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago arborescens*	474	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago arenaria*	1112	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago atrata*	2805	Hemicryptophyte	Perennial	Noncarnivorous	**59**
Lamiales	Plantaginaceae	*Plantago coronopus*	844	Hemicryptophyte	Perennial	Noncarnivorous	1

Lamiales	Plantaginaceae	*Plantago crassifolia*	1443	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago famarae*	489	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago lagopus*	1223	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago lanceolata*	1192	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Plantago major*	696	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago maritima*	1049	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Plantago media*	2420	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Plantago ovata*	513	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago raoulii*	4846	Hemicryptophyte	Perennial	Noncarnivorous	66
Lamiales	Plantaginaceae	*Plantago reniformis*	655	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago rugelii*	489	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Plantaginaceae	*Plantago serraria*	880	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Plantago spathulata*	4416	Hemicryptophyte	Perennial	Noncarnivorous	66
Lamiales	Plantaginaceae	*Plantago subulata*	1360	Hemicryptophyte	Perennial	Noncarnivorous	62
Lamiales	Plantaginaceae	*Plantago triandra*	5135	Hemicryptophyte	Perennial	Noncarnivorous	66
Lamiales	Plantaginaceae	*Plantago uniflora*	5518	Therophyte	Annual	Noncarnivorous	59
Lamiales	Plantaginaceae	*Plantago virginica*	591	Therophyte	Annual	Noncarnivorous	20
Lamiales	Plantaginaceae	*Plantago webbii*	543	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Scoparia dulcis*	724	Chamaephyte	Perennial	Noncarnivorous	18
Lamiales	Plantaginaceae	*Veronica acinifolia*	606	Therophyte	Annual	Noncarnivorous	7
Lamiales	Plantaginaceae	*Veronica agrestis*	714	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica allionii*	741	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica anagallis-aquatica*	515	Helophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica anagalloides*	516	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica armena*	372	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica arvensis*	405	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica austriaca*	1786	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica barrelieri*	786	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica baumgartenii*	489	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica beccabunga*	839	Helophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica bellidioides*	1046	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica bollonsii*	1013	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica bombycina*	396	Hemicryptophyte	Perennial	Noncarnivorous	37

Lamiales	Plantaginaceae	*Veronica bozakmanii*	1915	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica calycina*	1493	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica catarractae*	1041	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica ciliata*	1359	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica cinerea*	313	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica colostylis*	1205	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica copelandii*	812	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica crinita*	784	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica crista-galli*	675	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica cymbalaria*	742	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica densiflora*	1627	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica densifolia*	1135	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica dieffenbachii*	1168	Phanerophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica donii*	734	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica erinoides*	736	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica filiformis*	352	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica gentianoides*	1135	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica glauca*	391	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica hederifolia*	1379	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica chamaedrys*	1696	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica incana*	777	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica jacquinii*	900	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica javanica*	266	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica lanceolata*	1085	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica lavaudiana*	827	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica leiocarpa*	1575	Hemicryptophyte	Perennial	Noncarnivorous	37
Lamiales	Plantaginaceae	*Veronica longifolia*	699	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica lyallii*	1134	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica lycica*	430	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica macrantha*	1280	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica macrostemon*	1639	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica melanocaulon*	1088	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica micrantha*	1051	Hemicryptophyte	Perennial	Noncarnivorous	7

Lamiales	Plantaginaceae	*Veronica missurica*	1291	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica montana*	831	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica multifida*	375	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica officinalis*	881	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica ochracea*	2905	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica oltensis*	1678	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica opaca*	635	Therophyte	Annual	Noncarnivorous	59
Lamiales	Plantaginaceae	*Veronica orbiculata*	1386	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica orchidea*	792	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica orientalis*	377	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica ornata*	1674	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica panormitana*	356	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica pectinata*	933	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica peregrina*	929	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica perfoliata*	1516	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica persica*	703	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica planopetiolata*	2392	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica plebeia*	1108	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica polifolia*	623	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica polita*	419	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica prostrata*	720	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica pusilla*	523	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica rotunda*	1477	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica salicifolia*	1025	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica saturejoides*	861	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica scutellata*	925	Helophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica senex*	1158	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica serpyllifolia*	383	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Plantaginaceae	*Veronica schmidtiana*	547	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica speciosa*	1110	Chamaephyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica spicata*	823	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica sublobata*	1268	Therophyte	Annual	Noncarnivorous	59
Lamiales	Plantaginaceae	*Veronica syriaca*	627	Therophyte	Annual	Noncarnivorous	39

Lamiales	Plantaginaceae	*Veronica thessalica*	914	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica thymifolia*	558	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica trichadena*	381	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica triloba*	597	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica triphyllos*	576	Therophyte	Annual	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica urticifolia*	303	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronica vendettadeae*	626	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica verna*	528	Therophyte	Annual	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronica vindobonensis*	880	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Veronicastrum axillare*	2076	Hemicryptophyte	Perennial	Noncarnivorous	39
Lamiales	Plantaginaceae	*Veronicastrum virginicum*	1281	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Plantaginaceae	*Wulfenia carinthiaca*	1320	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Scrophulariaceae	*Buddleja davidii*	1340	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Scrophulariaceae	*Buddleja globosa*	839	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Scrophulariaceae	*Buddleja lindleyana*	919	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Scrophulariaceae	*Dermatobotrys saundersii*	1096	Chamaephyte	Perennial	Noncarnivorous	
Lamiales	Scrophulariaceae	*Limosella aquatica*	621	Therophyte	Annual	Noncarnivorous	59
Lamiales	Scrophulariaceae	*Myoporum mauritianum*	1900	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Scrophulariaceae	*Scrophularia auriculata*	875	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Scrophulariaceae	*Scrophularia glabrata*	1007	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Scrophulariaceae	*Scrophularia grandiflora*	949	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Scrophulariaceae	*Scrophularia herminii*	1252	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Scrophulariaceae	*Scrophularia lyrata*	1560	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Scrophulariaceae	*Scrophularia ningpoensis*	3028	Cryptophyte	Perennial	Noncarnivorous	68
Lamiales	Scrophulariaceae	*Scrophularia nodosa*	675	Cryptophyte	Perennial	Noncarnivorous	1
Lamiales	Scrophulariaceae	*Scrophularia scorodonia*	1032	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Scrophulariaceae	*Scrophularia sublyrata*	1086	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Scrophulariaceae	*Verbascum phlomoides*	348	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Scrophulariaceae	*Verbascum virgatum*	704	Hemicryptophyte	Perennial	Noncarnivorous	7
Lamiales	Verbenaceae	*Aloysia citrodora*	719	Phanerophyte	Perennial	Noncarnivorous	1
Lamiales	Verbenaceae	*Lantana camara*	2692	Chamaephyte	Perennial	Noncarnivorous	1
Lamiales	Verbenaceae	*Lippia alba*	1144	Chamaephyte	Perennial	Noncarnivorous	50
Lamiales	Verbenaceae	*Lippia aristata*	914	Chamaephyte	Perennial	Noncarnivorous	12

Lamiales	Verbenaceae	*Lippia brasiliensis*	2103	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia corymbosa*	807	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia diamantinensis*	1653	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia duartei*	1663	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia filifolia*	1110	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia florida*	1154	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia glandulosa*	1100	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia hederifolia*	1237	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia hermannioides*	1125	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia lupulina*	1120	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia origanoides*	1100	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia pseudothea*	1002	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia rosella*	1061	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia rotundifolia*	1663	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia rubella*	1086	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia salviifolia*	1134	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia sidoides*	944	Chamaephyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Lippia velutina*	958	Phanerophyte	Perennial	Noncarnivorous	12
Lamiales	Verbenaceae	*Phyla lanceolata*	538	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Verbenaceae	*Verbena hastata*	587	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Verbenaceae	*Verbena officinalis*	292	Hemicryptophyte	Perennial	Noncarnivorous	59
Lamiales	Verbenaceae	*Verbena rigida*	1161	Hemicryptophyte	Perennial	Noncarnivorous	1
Lamiales	Verbenaceae	*Verbena urticifolia*	489	Hemicryptophyte	Perennial	Noncarnivorous	4
Lamiales	Verbenaceae	*Volkameria inermis*	843	Chamaephyte	Perennial	Noncarnivorous	36
Oxalidales	Cephalotaceae	*Cephalotus follicularis*	1984	Hemicryptophyte	Perennial	Carnivorous	
Oxalidales	Ealeocarpaceae	*Crinodendron patagua*	293	Phanerophyte	Perennial	Noncarnivorous	1
Oxalidales	Oxalidaceae	*Averrhoa carambola*	235	Phanerophyte	Perennial	Noncarnivrous	1
Oxalidales	Oxalidaceae	*Oxalis acetosella*	2403	Hemicryptophyte	Perennial	Noncarnivorous	59
Poales	Bromeliaceae	*Aechmea aquilega*	528	Epiphyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Aechmea filicaulis*	815	Epiphyte	Perennial	Noncarnivorous	58
Poales	Bromeliaceae	*Aechmea nudicaulis*	372	Epiphyte	Perennial	Noncarnivorous	13
Poales	Bromeliaceae	*Aechmea ramosa*	655	Epiphyte	Perennial	Noncarnivorous	13
Poales	Bromeliaceae	*Ananas bracteatus*	440	Hemicryptophyte	Perennial	Noncarnivorous	1

Poales	Bromeliaceae	*Ananas comosus*	538	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Ayensua uaipanensis*	421	Chamaephyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Billbergia euphemiae*	430	Epiphyte	Perennial	Noncarnivorous	13
Poales	Bromeliaceae	*Billbergia horrida*	372	Epiphyte	Perennial	Noncarnivorous	13
Poales	Bromeliaceae	*Billbergia nutans*	368	Epiphyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Billbergia pallidiflora*	504	Epiphyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Billbergia tweedieana*	450	Epiphyte	Perennial	Noncarnivorous	13
Poales	Bromeliaceae	*Brocchinia acuminata*	372	Epiphyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Brocchinia reducta*	372	Hemicryptophyte	Perennial	Carnivorous	
Poales	Bromeliaceae	*Brocchinia tatei*	381	Epiphyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Bromelia antiacantha*	391	Hemicryptophyte	Perennial	Noncarnivorous	13
Poales	Bromeliaceae	*Catopsis morreniana*	562	Epiphyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Cryptanthus bahianus*	367	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Cryptanthus beuckeri*	713	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Deuterocohnia longipetala*	362	Chamaephyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Deuterocohnia lorentziana*	846	Chamaephyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Deuterocohnia meziana*	587	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Deuterocohnia schreiteri*	391	Chamaephyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Dyckia brevifolia*	983	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia distachya*	910	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia estevesii*	782	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Dyckia floribunda*	773	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Dyckia granmogulensis*	1066	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia choristaminea*	870	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia maritima*	1012	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia marnier-lapostollei*	954	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia monticola*	1017	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia pseudococcinea*	1027	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Dyckia pulquinensis*	1164	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Edmundoa lindenii*	645	Epiphyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Encholirium horridum*	768	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Encholirium irwinii*	851	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Encholirium magalhaesii*	949	Hemicryptophyte	Perennial	Noncarnivorous	42

Poales	Bromeliaceae	*Encholirium scrutor*	958	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Fascicularia bicolor*	513	Hemicryptophyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Fosterella penduliflora*	910	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Fosterella villosula*	910	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Fosterella windischii*	445	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Greigia sphacelata*	763	Hemicryptophyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Guzmania monostachia*	577	Epiphyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Guzmania variegata*	577	Epiphyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Hechtia argentea*	793	Hemicryptophyte	Perennial	Noncarnivorous	58
Poales	Bromeliaceae	*Nidularium billbergioides*	479	Epiphyte	Perennial	Noncarnivorous	13
Poales	Bromeliaceae	*Ochagavia elegans*	548	Chamaephyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Orthophytum saxicola*	313	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia albiflos*	680	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Pitcairnia atrorubens*	587	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia burle-marxii*	699	Hemicryptophyte	Perennial	Noncarnivorous	42
Poales	Bromeliaceae	*Pitcairnia feliciana*	293	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia flammea*	626	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia grafii*	655	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia heterophylla*	430	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia piepenbringii*	587	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia rectiflora*	587	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia recurvata*	587	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia riparia*	557	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia spicata*	597	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia villetaensis*	616	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Pitcairnia yaupi-bajaensis*	548	Hemicryptophyte	Perennial	Noncarnivorous	45
Poales	Bromeliaceae	*Puya coerulea*	499	Hemicryptophyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Puya mirabilis*	430	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Puya raimondii*	553	Phanerophyte	Perennial	Noncarnivorous	45
Poales	Bromeliaceae	*Puya stenothyrsa*	460	Hemicryptophyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Quesnelia arvensis*	430	Epiphyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Racinaea ropalocarpa*	621	Hemicryptophyte	Perennial	Noncarnivorous	17
Poales	Bromeliaceae	*Tillandsia stricta*	577	Epiphyte	Perennial	Noncarnivorous	13

Poales	Bromeliaceae	*Tillandsia usneoides*	1232	Epiphyte	Perennial	Noncarnivorous	1
Poales	Bromeliaceae	*Vriesea scalaris*	528	Epiphyte	Perennial	Noncarnivorous	13
Poales	Typhaceae	*Sparganium angustifolium*	577	Helophyte	Perennial	Noncarnivorous	21
Poales	Typhaceae	*Sparganium emersum*	510	Helophyte	Perennial	Noncarnivorous	59
Poales	Typhaceae	*Sparganium erectum*	513	Helophyte	Perennial	Noncarnivorous	1
Poales	Typhaceae	*Sparganium natans*	480	Hydrophyte	Perennial	Noncarnivorous	59
Poales	Typhaceae	*Typha angustifolia*	225	Helophyte	Perennial	Noncarnivorous	58
Poales	Typhaceae	*Typha domingensis*	259	Helophyte	Perennial	Noncarnivorous	21
Poales	Typhaceae	*Typha latifolia*	224	Helophyte	Perennial	Noncarnivorous	59
Poales	Typhaceae	*Typha laxmannii*	254	Helophyte	Perennial	Noncarnivorous	59
Poales	Typhaceae	*Typha shuttleworthii*	230	Helophyte	Perennial	Noncarnivorous	59

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