

Abstract

Amomum Roxb. s.l. (black cardamom) is a complicated genus in the ginger family Zingiberaceae (subfamily Alpinioideae) that according to some definitions includes groups of species recognized as separate genera, e.g. genus *Elettariopsis* Baker. Phylogenetic studies have so far failed to elucidate both the position of *Amomum* within Alpinioideae and the relationship between *Amomum* and other genera like *Elettariopsis*. In this work, *Amomum* was subjected to a detailed morphological analysis of the largest possible sampling, together with a phylogenetic analysis. *Amomum* was recircumscribed, *Amomum* s.s. and three new genera were established, three genera were resurrected, and genus *Elettariopsis* was merged into *Amomum*. Meanwhile, new species were described and others epitypified.

A well-resolved nuclear-gene phylogeny of *Amomum* s.s. was obtained using next-generation sequencing (Hyb-Seq) and showed the existence of four clades (A, B, C, D) within the genus. Clade D, the former genus *Elettariopsis*, was further divided into three subclades (D1–D3). A chloroplast DNA-based phylogeny supported this structure, but additional phylogenies based on ribosomal DNA were incongruent with it, indicating that the frequently used ITS marker and other rDNA markers may not be suitable for reconstructing deeper phylogenetic nodes.

Genome size is an intensely studied feature of plants with a fundamental impact on their growth, adaptation and speciation. Due to this, it can drive plant diversification and has been successfully used in plant systematics, as it may carry a phylogenetic signal. Genome size is less studied in tropical plants, but *Amomum* as a tropical genus distributed throughout much of the Indomalayan realm and growing in a variety of environments offered itself as a good model for examining genome size dynamics in tropical conditions. The evolution of absolute (2C) genome size in *Amomum* was found to be congruent with *Amomum*'s phylogeny, with 2C genome size gradually rising from the early diverging clade A to the most derived subclade D3 and an overall 4.5-fold 2C genome size range. Interestingly, the gradual increase of GS corresponds with the biogeographical history of the genus, which dispersed from its original location in southern China and northern Indochina (clades A, B and C) southeast over the Isthmus of Kra to Sundaland (subclades D1–D2) and then back north (subclade D3). Chromosomes were counted in selected accessions and two tetraploid species with $2n = 96$ chromosomes were found. These were the first polyploids to be found in *Amomum*; the species *A. cinnamomeum* (subclade D3) had the largest 2C genome size at 15.66 pg, which is also the largest detected genome size in the order Zingiberales to date. The remaining diploids had $2n = 48$ chromosomes.

Within diploids, genome size varied 2.7-fold, which prompted a repeatomic analysis of the genus (i.e. the quantification of the main groups of repetitive sequences in the genome). A subset of species was analysed using the RepeatExplorer pipeline to quantify and compare their repetitive sequences (repeats). Genome size and repeat content were significantly correlated, revealing that repeats were driving the genome size increase; the overall repeat content also carried phylogenetic signal. Repeat lineages of the *Ty1-Copia* superfamily (particularly SIRE) strongly contributed to the genome size increase and were prevalent in *Amomum*'s repeatomes. Most repeat lineages present in *Amomum* were significantly amplified in clade D. Two ancient hybridization events were revealed in *Amomum*: the hybrid origin of clade D, which may have caused repeat proliferation in this clade, and a hybridogenous group of species within this clade. A repeat-based phylogenetic network showed congruency with the nuclear gene phylogeny. Finally, *Amomum* with a repeatome proportion reaching 88% was found to belong among monocot genera with largest repeatome proportions.

Keywords: *Amomum*, Zingiberaceae, genome size, genome evolution, classification, morphology, repetitive DNA, repeatome, phylogeny, next-generation sequencing, ancient hybridization, chromosome count