

## ABSTRACT OF RECENT PhD DISSERTATIONS

### THE MOSS GENUS *CERATODON*: STUDIES OF EVOLUTIONARY BIOLOGY AND TAXONOMY IN SOUTHERN EUROPE

**Marta Nieto-Lugilde**

**Universidad de Murcia**

**Supervisors: Olaf F. Werner, Rosa M. Ros Espín & Stuart F. McDaniel**

**Date of defense: September 26<sup>th</sup>, 2019**

This research work has been focused from a multidisciplinary point of view with the general objective of studying evolutionary biology and taxonomy in the genus *Ceratodon* in southern Europe. Studies of morphometry, phylogenetic analysis based on DNA sequences and flow cytometry have been combined. Likewise, biogeographical and ecological data have been taken into account.

In order to know the morphology of the species of *Ceratodon* present in the Mediterranean area, the revision of the nomenclatural type of *Ceratodon conicus* and of the synonyms proposed for this name was carried out. To do this, the type specimens were studied and compared with the data from the protologues. The lectotype of *C. conicus* was confirmed, but the material of the isolectotypes did not correspond to the protologue of the species. In addition, the types of the three synonyms *C. cedricola*, *C. dimorphus*, and *C. purpureus* var. *graefii*, were here designated as lectotypes. *Ceratodon purpureus* var. *graefii* was considered synonymous with *C. purpureus* s.l., since its morphological characteristics coincided with those described for this species.

To assess the role of allopatry and the change of ploidy in the divergence of southern European populations from *Ceratodon*, genetic diversity and genome size were examined. Mountainous and lowland areas of the Mediterranean region were sampled, as well as western and central Europe. Phylogenetic and coalescence analyses were performed with the DNA sequences of five nuclear introns and one chloroplast *locus*. The phylogenetic analyses resolved two well differentiated clades, which discriminated

two homogenous groups: one corresponding to the cosmopolitan species *C. purpureus* and another restricted to the mountains of southern Spain. The samples from this local group also had a genome size 25% larger than that of *C. purpureus*, and were exclusively females. Hybrids were also found, and some of them had a genome size equivalent to the sum of the genome of *C. purpureus* and that of specimens from southern Spain, suggesting that they were formed by allopolyploidy. All these data suggest that a new species of *Ceratodon* arose from a process of peripatric speciation, which potentially implied a change in the size of the genome and a strong deviation in the sex ratio.

The effect of environmental variation on the taxonomy of the genus *Ceratodon* was evaluated through a biometric analysis based on 22 morphological characters, both in plants collected in the field and in plants grown *in vitro*. These data were compared with those of the phylogenetic analysis based on their DNA sequences and those of the genome size. The results showed that the expression of several gametophytic traits changed between the samples collected in the field and the samples cultured *in vitro*, which confirmed that environmental variability complicates taxonomic inferences, and suggested that some characters should be used with caution in distinguishing among species. However, consistent with the genetic and flow cytometry data, a clear biometric discontinuity was found between some plants collected from southern Spain, and those from other parts of the world. The integrative approach unequivocally supported the recognition of a new species, which was formally described under the name of *Ceratodon amazonum*. The results also suggested that the previously recognized *C. conicus* is a recombinant between *C. purpureus* and *C. amazonum*. For this reason it was considered as a nothospecies, for which an epitype was designated because the lectotype is demonstrably ambiguous.

Finally, the demographic and evolutionary history of *C. purpureus*, *C. amazonum* and the recombinant *C. ×conicus* was reconstructed with the data generated with nine genetic markers, something that has been done in a few bryophyte species. A speciation event was confirmed approximately 1.7 million years ago and evidence of asymmetric gene flow between the parents *C. purpureus* and *C. amazonum* was found, which favored the introgression of the cosmopolitan species in the isolated south of Europe. It was also estimated that *C. ×conicus* was formed by multiple hybridization events between the parents.

On balance this thesis highlights the current gaps in knowledge about the diversity of bryophytes and the mechanisms that generate it, even in common and widely distributed species, and demonstrates that wild cosmopolitan species have the potential to reveal the various genetic causes of speciation. It also confirms that the phenomena of hybridization and polyploidy are mechanisms that also intervene in the bryophyte speciation.