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Phylogenetics and Biogeography of Emilia Cass. (Asteraceae, Senecioneae)

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ABSTRACT

A molecular phylogenetic and biogeographic study of the palaeotropical genus *Emilia* Cass., tribe Senecioneae in the Asteraceae, was undertaken as very little was known about these aspects of the genus, which are informative for taxonomic and conservation practices and contribute to our understanding of its evolution. The investigation aimed to: (1) assess the species recognised by Jeffrey (1997) in the large-headed, morphologically variable and widespread *Emilia coccinea* complex using a phenetic approach, and evaluate how applicable the morphological and phenetic species concepts are to this complex; (2) elucidate the phylogenetic relationships of *Emilia* species, genera *Bafutia*, *Emiliella* and closely allied genera in the Senecioneae, using molecular DNA sequence data; (3) examine the pattern and timing of diversification in *Emilia* and correlate this pattern with morphological trends in the genus; and (4) identify centres of diversity and endemism for *Emilia* in southern Africa[1], and compare and assess the following spatial biodiversity indices: species richness (SR), corrected weighted endemism (CWE), phylogenetic diversity (PD), and phylogenetic endemism (PE), and their application to the conservation of *Emilia* in a chosen region (viz. Zimbabwe).

The phenetic study of the *E. coccinea* complex was based on 134 herbarium specimens spanning the altitudinal and geographical ranges of this complex and using multivariate analyses (cluster analysis and ordinations). Parsimony and Bayesian phylogenetic analyses, based on molecular plastid *trn*L-*trn*F and nuclear ITS sequence data, were conducted on a representative sample of *Emilia* species together with other closely related Senecioneae genera to provide the basis for a taxonomic revision of the genus. Phylogenetic relationships of *Emilia* species, including Jeffrey's sectional classification of *Emilia*, the distinctness of the morphologically similar species in the *E. coccinea* complex, and the generic status of similar genera *Bafutia* and *Emiliella* were then evaluated from reconstructed phylogenies. The biogeographic diversification history of *Emilia* was traced using the present distribution of species and a reconstructed nuclear ITS phylogeny. Dated molecular phylogenetic hypotheses constructed using BEAST were used to estimate the time of divergence in *Emilia*, and linked with optimized evolutionary patterns of morphological features to trace evolutionary trends in the genus. Centres of diversity and endemism were mapped and identified in southern Africa

[1] Southern Africa is defined here as the countries south of the Democratic Republic of Congo and Tanzania (Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe).

using distribution data obtained from PRECIS data sets, field work and herbarium specimens. Four spatial biodiversity indices (SR, CWE, PD, and PE), two of which incorporate evolutionary history of the genus (PD, PE), were examined for overlap in southern African countries and also evaluated for potential use in conservation planning in Zimbabwe by assessing the distribution/ranges of the ten Zimbabwean *Emilia* species and their occurrence in currently protected areas that include national parks and botanical reserves. Additionally, the conservation status of the species found in Zimbabwe was assessed using the 'IUCN Red Lists Categories and Criteria'.

Five of the eight species (viz., *Emilia emilioides*, *E. jeffreyana*, *E. praetermissa*, *E. subscaposa*, and *E. vanmeelii*) in the *E. coccinea* complex are phenetically and genetically distinct; *E. lisowskiana* is not distinct as three *E. coccinea sensu stricto* specimens clustered with it in the multivariate analysis and it is unresolved in the molecular analyses. Two species (*E. caespitosa* and *E. coccinea*) are indistinguishable from each other in both the phenetic and molecular analyses as they overlap significantly in many morphological characters, habitats, and co-occur in most areas suggesting that they are either indistinct and should be synonymized, or possibly that they have hybridized in areas where they co-occur. A key with useful combinations of morphological characters separating the eight species in the *E. coccinea* complex is provided.

The molecular phylogenetic analyses revealed that *Emilia* is not monophyletic, and that *Bafutia* and *Emiliella* are nested within it, indicating that these genera do not warrant separate generic status and should be combined with *Emilia*. Jeffrey's sectional classification is not supported by the reconstructed phylogenies and there are no distinguishable morphological patterns evident amongst the clades to warrant the proposal of any meaningful sectional delimitation. *Emilia baumii* and *E. graminea* are grouped outside *Emilia* in both the nuclear and plastic-based molecular analyses and exclusion of these species from the genus is recommended, although additional molecular markers are needed to support this exclusion. Well-supported topological incongruences are revealed between nuclear ITS and plastid *trn*L-*trn*F phylogenies suggesting that hybridization and/or introgression have played a role in the history of *Emilia*, as with many other senecionoid genera.

Emilia, a mainly tropical genus, is hypothesised to have originated in southern Africa during the Mid-Miocene (*ca.* 14.19 Mya) coinciding with a period of global climate cooling

following the mid-Miocene Climatic Optimum (*ca.* 15 Mya). Early diversification occurred northwards into diverse habitats in Africa with further diversification in most *Emilia* clades occurring during the Late Miocene and occupying various habitats such as savannas, grasslands, and forest edges. At least five independent dispersals out of southern Africa to Madagascar, ascribed to long distance wind dispersal, occurred during the Pliocene. The successful diversification of *Emilia* in Africa could have been enhanced by its prevalent annual life form postulated to be either ancestral or evolved early (*ca.* 13.32 Mya) in its history. Narrow leaves, radiate capitula, and non-yellow florets have all arisen independently several times in *Emilia*.

Emilia species are unevenly distributed in southern Africa with the highest number of species occurring in Zambia (12 species), followed by Zimbabwe (10 species) and Malawi (seven species). Centres of greatest diversity for *Emilia* species are found in northern and southern Malawi (including the Nyika and Zomba plateaus respectively) and Zimbabwe (Eastern Highlands and areas surrounding Harare). Two recognized centres of endemism, which are also part of the Austro-temperate Region, viz. the Chimanimani-Nyanga Centre in the Eastern Highlands and the Nyika Plateau Centre, are amongst the centres with the highest diversity of species of *Emilia*. Only six *Emilia* species are endemic or near endemic to southern Africa, a low number compared to other senecionoid genera in the Savanna and Austro-temperate Floras. With the exception of endemism, three of the spatial biodiversity indices (SR, PD, and PE) investigated in this study were congruent thus providing additional conservation information. These three biodiversity indices overlap in some of the following areas: northern Malawi, Harare region and eastern highlands of Zimbabwe and therefore should be prioritized for biodiversity conservation: thus fulfilling one of the mandates of the Convention on Biological Diversity. Phylogenetic diversity and PE provides further conservation information in eastern and north-western Zambia that could have been missed by using SR alone. These phylogenetic indices (PD and PE) should therefore be prioritized in the conservation of *Emilia* species, and other taxa in similar floras, thus mitigating the problems of climate change as areas that have an evolutionary history and contain geographically restricted traits are conserved.

In an assessment of the conservation status of species of *Emilia* in Zimbabwe, three species (*E. limosa*, *E. protracta*, and *E. tenellula*) are rare and/or threatened and are habitat specialists e.g. in swampy areas thus warranting protection and one (*E. baumii*) is Data

Deficient and should be investigated further. The majority of *Emilia* species are categorised as Least Concern. The current protected areas in Zimbabwe cover most areas where 70% of *Emilia* species occur, including those areas with high PD and PE, the exception being the Harare region where populations are unprotected. Conservation efforts should therefore be extended to these unprotected areas. In addition to traditional conservation approaches, it is recommended that conservation prioritization of *Emilia* species in southern Africa and possibly the whole of Africa, as well as other genera with similar distribution patterns in Savanna and/or Austro-temperate Floras, should integrate SR, PD, and PE since phylogenetic indices (PD and PE) provide information on evolutionary history and spatially restricted diversity which are necessary for understanding and maximizing conservation of evolutionary diversity.