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Paraphyly of the genus *Boehmeria* (Urticaceae): a response to Liang et al. 'Relationships among Chinese *Boehmeria* species and the evolution of various clade'

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Abstract

Boehmeria, as currently circumscribed, comprises 52 species and has a pantropical distribution. Liang et al. propose a sectional classification of *Boehmeria* based on the phylogenetic analysis of SNP data for 20 species and an additional 10 subspecific taxa of these at the rank of variety or form. They restrict their sampling to species documented in China. We found many shortcomings in the sampling and analyses which we feel have resulted in a misleading phylogeny for the genus and the economically important fibre-plant, *Boehmeria nivea*. By sampling only Chinese species of this genus for their in-group and using a single distantly related outgroup, Liang et al. have failed to capture the diversity of the genus and so erroneously concluded that it forms a monophyletic group. Previous published research clearly demonstrates that *Boehmeria* is paraphyletic and polyphyletic, comprising at least four monophyletic groupings most closely related to several genera within the Boehmerieae. For these reasons, the sections that Liang et al. (Ind Crops Prod 148:112092, 2020. <https://doi.org/10.1016/j.indcrop.2020.112092>) propose for *Boehmeria* are not effective tools for its classification. The important fibre-plant, *Boehmeria nivea*, should therefore not be considered as part of the genus *Boehmeria* for the purposes of crop breeding, but as sister to *Archiboehmeria*. Breeding programmes for ramie should therefore focus on populations and germplasm of *Archiboehmeria atrata*. We conclude that poor taxon sampling, overlooking relevant molecular and taxonomic literature, internal conflict within their SNP data and the overinterpretation of low support values has resulted in the erroneous conclusion that *Boehmeria* represents a monophyletic or 'natural' genus.

Keywords Monophyly · Paraphyly · Ramie · Systematics · Taxon sampling · *Urtica* · Urticaceae

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Boehmeria Jacq., as currently circumscribed (Wilmot-Dear & Friis 2013), comprises 52 species and has a pantropical distribution (Plants of the World Online 2020). Whilst the greatest diversity of species occurs in Asia, 14 species are known from the Americas (Wilmot-Dear & Friis 1996, 2013) including the type of the genus, *B. ramiflora* Jacq., which is native to Central America and north-western South America (Plants of the World Online 2020).

Boehmeria includes the species of greatest economic value within the nettle family (Urticaceae), *B. nivea*, known as 'ramie'. Ramie is presumed native to China where it has been in cultivation for over 3000 years (Chen et al. 2003). *Boehmeria nivea* was originally described in the nettle genus *Urtica* by Linnaeus (1753) before being transferred to the genus *Boehmeria* by Gaudichaud-Baupré (1830). In (1891) Kuntze transferred the species to the genus *Ramium* but in doing so generated an illegitimate homonym and in the most

recent revision of the genus (Wilmot-Dear & Friis 2013), it remains a species of *Boehmeria*.

Within a systematic framework, subgeneric classifications, such as sections or subgenera, provide a means of recognizing major evolutionary lineages that do not warrant generic rank. Identifying such lineages provides a framework for testing evolutionary hypotheses and in designing plant breeding programmes (Zhang et al. 1998). Indeed, Liang et al. (2020), as justification for their study, state that, ‘*Boehmeria* is the most important natural germplasm bank for deriving commercially viable ramie cultivars’. It is therefore crucial to their study that *Boehmeria nivea* can be assigned to the genus *Boehmeria*. If not, then in designing a breeding programme potentially important sources of germplasm may be overlooked.

Within systematic biology, it is implicit that the genus and sections should represent monophyletic groups. Previous phylogenetic studies based on the analysis of chloroplast, nuclear ribosomal and low-copy nuclear DNA have strongly suggested that *Boehmeria* does not form a monophyletic group (Fig. 1 in Wu et al. 2013; Fig S1 in Wu et al. 2018). Within these studies, *Boehmeria* is recovered as two or four monophyletic groupings most closely related to other genera in the Boehmerieae tribe of the Urticaceae. These include *Boehmeria nivea*, which is recovered as most closely related to *Archiboehmeria*, with strong support, whilst the core of Chinese species were recovered as sister to *Cypholophus*, with moderate to strong support and the Latin American species as sister to *Cypholophus* + Asian *Boehmeria* with strong support, and *Boehmeria depauperata* as sister to Latin American *Boehmeria* + *Cypholophus* + core of Asian *Boehmeria* (Fig S1 in Wu et al. 2018). This strongly suggests that *Boehmeria* is paraphyletic with respect to Asian *Boehmeria*, *Cypholophus*, American *Boehmeria* and *B. depauperata*, and polyphyletic with respect to *B. nivea*.

The selection of a single outgroup by Liang et al. (2020), comprising the most basal member of the Boehmerieae tribe, *Oreocnide*, meant that no effective test of monophyly was undertaken. Their resultant sectional classification combines distantly related taxa that only form a monophyletic group, with very low support, because of the application of an even more distantly related outgroup. In addition, in the presentation of their analyses of SNP data Liang et al. (2020) omit key details. For example, the filtering of homologous loci, a crucial step in the generation of phylogenetic trees from SNP data. In addition, the phylogenetic tree presented is based on neighbour-joining, rather than a maximum likelihood approach, and there seems no clear justification for this. Maximum likelihood approaches are accepted as more reliable for estimating relationships between taxa, than neighbour-joining (Holder & Lewis 2003). Finally, the phylogenetic tree that they support has very low support values on most branches, less than 50% in some cases, suggesting

that they are poor predictions of relationships. Such low support values suggest strong incongruence or conflict within their data and that they have in fact recovered a large polytomy, rather than a resolved tree. That is, that many other groupings and relationships between groupings may be equally plausible, not a basis for a stable classification.

The most obvious risk of using this classification would be with respect to designing a crop breeding programme for ramie. The classification proposed by Liang et al. (2020) would suggest that, outside of *Boehmeria nivea*, the nearest relatives of ramie suitable for inclusion in a crop breeding programme would be from their sections, *Siamensis*, *Duretia*, *Phyllostachys* or *Silvestri*, whereas research published by Wu et al. (2013, 2018) suggests that populations of *Archiboehmeria atrata* are the nearest relatives of *B. nivea*. Using the classification of Liang et al. (2020) would, however, exclude this possibility.

We conclude that poor taxon sampling, a failure to consult the relevant molecular biology and taxonomic literature, internal conflict within their data and the over interpretation of low support values has resulted in the erroneous conclusion that *Boehmeria* represents a monophyletic or ‘natural’ genus and the presentation of an inaccurate estimate of relationships within *Boehmeria*, especially with respect to *Boehmeria nivea*, ‘ramie’.

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Compliance with ethical standards

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

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