

## EDITORIAL

# Shaping knowledge on legume morphology

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Morphology has always had a central role in the natural sciences and study of the phenotypical diversity of an organism is pivotal to understanding patterns and processes of the living world. It is through their phenotype that organisms interact with the surrounding environment and with each other and, ultimately, phenotypes are the results of evolution (Wagner, 2001a). In the context of systematics, morphological features were the source of data underpinning taxonomic and most evolutionary hypotheses in the pre-Hennigian era, as well as during the advent of cladistics, before the use of molecular data became widespread. Difficulties in interpreting morphological data and conceptualizing characters (as reflected in the debate on what characters are; see Wagner, 2001b), in contrast to the relative ease in generating large molecular data sets, have led some to propose that morphology should have a limited role in phylogenetics and should only be evaluated in light of DNA-based trees (Scotland, Olmstead & Bennett, 2003). Recent advances, however, are improving our ability to assess comparative morphology.

Initiatives such as MorphoBank (O’Leary & Kaufman, 2011) allow collaborative work via the internet for the scoring of morphological data and building data matrices (e.g. O’Leary *et al.*, 2013). The use of ontologies for comparing semantic description of phenotypes is also a technical advance for the study of morphology (Vogt, Bartolomaeus, & Giribet, 2010; Deans, Yoder, & Balhoff, 2012; Deans *et al.*, 2015). By having a database of annotated phenotypes, one could automatically extract phylogenetic characters

(e.g. Dececchi *et al.*, 2015) and study morphological evolution (e.g. Ramírez & Michalik, 2014). Adoption of a semantic approach could also be a step towards resolution of some problems associated with character formulation (Vogt, 2017). Also, the use of morphological data adds dimensions to studies of biological diversity and establishes a link for the use of both extant and extinct taxa for phylogenetic inference (Jenner, 2004; Wiens, 2004). Of course, and as with any other type of data, including molecular data (Liu *et al.*, 2010), morphology is prone to convergent evolution and must be used with care. Nonetheless, it still has an important role to play in phylogenetics. In the phylogenomic era (Giribet, 2010, 2015), there are examples of concordance between genomic data and morphology, even when such concordance was previously rebutted by small molecular datasets (e.g. Stephens *et al.*, 2015).

In recent years, we have seen a large accumulation of molecular phylogenetic analyses for Fabaceae (e.g. Luckow *et al.*, 2003; Wojciechowski, Lavin & Sanderson, 2004; McMahon & Sanderson, 2006; Bruneau *et al.*, 2008; Simon *et al.*, 2009; Cardoso *et al.*, 2012; Manzanilla & Bruneau, 2012; Cardoso *et al.*, 2013), the third largest family of flowering plants (Lewis *et al.*, 2005; LPWG, 2017). These studies confirmed the monophyly of Fabaceae, but of the three traditional subfamilies, only Faboideae and Mimosoideae were supported as natural groups, with Caesalpinioideae being polyphyletic. This conclusion was initially highlighted by cladistic analysis of DNA (Doyle, 1995) and morphology (Chappill, 1995) and further supported by combined analysis of the two (Herendeen, Bruneau & Lewis, 2003). Although it was clear that the classification of Fabaceae had to be updated, how to do this was

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a matter of debate. Aiming to promote development of legume systematics in a globally co-ordinated approach, the Legume Phylogeny Working Group (LPWG) was created in 2010 (LPWG, 2013) and the group has recently published a new subfamily classification for Fabaceae (as Leguminosae) based on a taxonomically comprehensive *matK* phylogeny, of the family (LPWG, 2017). However, one single marker is not enough: some areas of the phylogenetic tree still lack resolution or robust support (LPWG, 2017) and, although resolution of these issues would benefit from additional molecular data, morphology can also add valuable characters. In this context, the Legume Morphology Working Group (LMWG) was formed in 2014 to create a database of legume morphology and functional traits for the family (Lewis, 2016).

The LMWG is now fully integrated into the LPWG, but its main goals are still alive: (1) to evaluate how comparative morphological studies may help to better understand species groups and poorly-resolved molecular phylogenetic relationships; (2) to identify gaps in our knowledge about legume morphology and co-ordinate efforts to fill these gaps and (3) to promote consistency in legume morphological terminology. The first formal meeting of the LMWG was held in October 2014, during the XI Congresso Latinoamericano de Botánica, held in Salvador, Bahia, Brazil, and was followed by an international morphology symposium and workshop held in November 2015, in Botucatu, São Paulo, Brazil. Most of the papers in the selection on legume morphology presented in this issue of the *Botanical Journal of the Linnean Society* were presented in the Botucatu meeting.

Three contributions are mainly focused on filling gaps in legume morphology. [Marinho \*et al.\* \(2018, this issue\)](#) present a study of osmophores and the floral bouquet in three species and focus on the process of production and release of chemical compounds in the flowers. Their work highlights the existence of a difference between compounds produced in the osmophores and the chemicals actually released during anthesis. This opens the way for more refined studies of the chemical pathways taking place in the osmophores and the relationship between floral bouquet and the pollinators. Setting flowers aside, [Gonzalez and Marazzi \(2018, this issue\)](#) look at the anatomy of extrafloral nectaries (EFNs), which mediate ecologically important ant-plant interactions, and are present in a large number of species in the family. Their contribution includes the description of a novel type of EFN and improves upon EFN terminology. Significantly, the expansion of our knowledge about the histological structure of these nectaries allows better homology assessments of EFNs and other plant organs. [Kochanovski \*et al.\* \(2018, this issue\)](#) also contribute to the elucidation of homology issues among the parts in a zygomorphic flower of a

species belonging to a clade in Detarioideae consisting otherwise of species with actinomorphic flowers. Besides shedding light on the developmental pathways of this atypical zygomorphy, their work opens the way for the formulation of questions related to the origin of this novelty in the clade and its pollination ecology.

The usefulness of morphology in a phylogenetic context is explored in three other papers. [Banks and Lewis \(2018, this issue\)](#) evaluate the phylogenetic relevance of pollen morphology of taxa previously belonging to traditional Caesalpinioideae in the context of the new subfamily classification (LPWG, 2017). A noteworthy finding of these authors is the negative correlation between the number of genera and the number of pollen types in a given subfamily. In other words: the fewer genera in a subfamily, the more pollen types. It would be interesting to see if this relationship holds true after a larger sample of Caesalpinioideae is studied, particularly from within the mimosoid clade (former Mimosoideae). Both [Pinto \*et al.\* \(2018, this issue\)](#) and [Silva \*et al.\* \(2018, this issue\)](#) focus on leaflet anatomy. Besides providing previously unpublished morpho-anatomical and histochemical data, [Pinto \*et al.\*](#) show that leaflet anatomy can be used to characterize clades and could be phylogenetically informative in the context of the resin-producing Detarioideae. [Silva \*et al.\*](#) take a step further and combine anatomical and molecular data to reveal morphological synapomorphies for different nodes of the Dipterygeae clade (Faboideae). Overall, their findings corroborate previous relationships based only on molecular data and are a good example of how a detailed study of morphology can produce phylogenetically informative data.

The last two contributions included in this issue are more focused on evolutionary and ecological aspects of plant phenotypes. [Contreras-Ortiz \*et al.\* \(2018, this issue\)](#) aim to discover the origins of a particular growth form in Andean *Lupinus* L. (Faboideae) and point out that both geography and adaptive convergence play a role in the diversification of the genus. Their contribution makes use of an integrative approach that combines phylogenomic, genetic, ecological and morphological data to better understand evolution in *Lupinus* and to tackle species delimitation problems. [Nogueira \*et al.\* \(2018, this issue\)](#) also use multiple data sources, particularly flower morphology and development, to investigate the occurrence of division-of-labour in flowers of a species of *Chamaecrista* (L.) Moench (Caesalpinioideae). The authors show that even if overall morphology points to the existence of division of labour, this is not corroborated by pollen data. One of their outstanding findings is that interactions with pollinators may occur before anthesis and is not exclusively dependent on features presented only during anthesis.

Overall, the studies presented in this issue cover a wide range of morphological topics and together fit well with the goals established by the former LMWG. Most of the contributions present new data on phenotypic traits and place morphology in a phylogenetic context, either by focusing on understanding character evolution or by evaluating the phylogenetic importance of morphology. Some contributions go beyond the original goals and develop under-studied aspects of biology of Fabaceae or attempt to establish links between morphology, evolution, diversification and ecology. The LPWG is alive and well, and we look forward to future symposia on all aspects of legume biology, especially at the 7<sup>th</sup> International Legume Conference to be held in Sendai, Japan in August–September, 2018.

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