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Editorial

The natural history of Annonaceae

This special issue of *Botanical Journal of the Linnean Society* focuses on the systematics and evolution of Annonaceae. Ever since the start of the standardized use of plant family names, with the publication of *Genera plantarum* by de Jussieu (1789), Annonaceae have been an easily identifiable entity. The numerous cultivated species have provided further recognition of the family for centuries. On a local scale, many species are used for their fleshy, edible fruits and others for aromatic, spicy, medicinal or mechanic properties. Perhaps most pleasing, and more widely known, are the essential oil of the Asian species ylang-ylang (*Cananga odorata* (Lam.) Hook.f. & Thomson) and the edible fruits of several species of the Neotropical genus *Annona* L. Halfway through the 17th century, *Annona* spp. had already been widely distributed across the Atlantic and were among the popular fruits cultivated in the first Dutch settlement at the Cape of Good Hope. Trees of *C. odorata* had probably been widely planted in Polynesia and Micronesia before the species was further disseminated to Africa and the New World in colonial times.

The 18th, 19th and early 20th centuries also saw the initial gatherings of Annonaceae in natural history collections. Given the large number of species (*c*. 2400 recognized to date; Rainer & Chatrou, 2006) and the ecological preponderance in tropical rainforests (e.g. Gonmadje *et al*., 2011), a lack of specimens has never been a major problem in Annonaceae systematics. However, remarks about the complexities of the taxonomy and systematics of the family can be found in several publications by expert botanists (Maas, 1983; Schatz & Le Thomas, 1993). Even the most productive and proficient Annonaceae systematist, Robert E. Fries, wrote in his treatment in *Die natürlichen Pflanzenfamilien* (edited by Engler & Prantl) that the 'systematic classification of the Annonaceae poses very large difficulties, when the goal is not only to provide an identification scheme but also to clarify the natural relationships among genera and the phylogeny of the family' (Fries, 1959: 39).

In the early 1980s, and little over 20 years after Fries' last paper, systematic research on Annonaceae was rejuvenated when scholars at the Utrecht Institute of Systematic Botany chose to make the family the focus of their activities and to encourage international research collaboration. This decision was driven by the Neotropical focus of the Institute, the criterion to choose a group of woody plants given the expertise in systematic wood anatomy and the availability of many new plant collections gathered from the 1970s onwards. Over the years, these research efforts would expand to cover the systematics of Annonaceae across the entire distribution area of the family. Moreover, independent research efforts sprouted at several institutes worldwide, each with its own focus regarding geographical areas, clades and life-history characters. The papers in this special issue provide an overview of almost 30 years of research effort.

An important aspect of systematics research in general, and of work on Annonaceae in particular, has been the spreading of taxonomic baseline information to end-users in the shape of floristic treatments, revisions and monographs (e.g. Maas, Westra & Chatrou, 2003; Su & Saunders, 2006; Couvreur, 2009; Weerasooriya & Saunders, 2010) and available databases (e.g. Rainer & Chatrou, 2006; Maas *et al*., 2011). This special issue includes two papers in this tradition: identification keys to all genera (Couvreur *et al*., 2012) and a bibliography enhancing access to the most relevant literature on Annonaceae taxonomy (Erkens, Mennega & Westra, 2012).

During the early days of international, collaborative research on Annonaceae, the theory of phylogenetic systematics was gaining ground and was incorporated into systematic studies of selected genera (e.g. Koek-Noorman, Zandee & Westra, 1988). A number of family-wide inventories accumulated data on macromorphological, anatomical and palynological features (Le Thomas, 1980, 1981; van Setten & Koek-Noorman, 1986, 1992; van Heusden, 1992). The extensive observations that these inventories produced profoundly informed taxonomic revisions and monographs (e.g. Maas & Westra, 1984, 1985, 1992; Kessler, 1988) and the first papers on phylogenetic relationships among genera based on morphological characters (Doyle & Le Thomas, 1994, 1996, 1997).

Phylogenetics is at the heart of this special issue on Annonaceae. After the first paper on phylogenetics of Annonaceae that included DNA sequence data, although in combination with morphological data (Doyle, Bygrave & Le Thomas, 2000), many papers have appeared that have addressed phylogenetic relationships at different taxonomic levels, using different sets of taxa and markers. In line with similar efforts at the level of angiosperms (APG II, 2003; APG III, 2009) and land plants (Chase & Reveal, 2009), genera have been re-circumscribed to comply with the principle of monophyly (e.g. Chatrou, Koek-Noorman & Maas, 2000; Erkens *et al*., 2007; Mols *et al*., 2008; Chatrou *et al*., 2009; Zhou, Su & Saunders, 2009; Zhou *et al*., 2010). Although this process of changing generic delimitations is not complete, phylogenetic patterns are well-enough resolved to update the subfamilial and tribal classification. In this issue, Chatrou *et al*. (2012) present the largest phylogenetic analyses of the family to date, based on a supermatrix including eight plastid markers, and revise the infrafamilial classification. All 108 currently recognized genera are accommodated in this classification.

The new classification will ensure unambiguous communication about clades. The phylogenetic tree on which it is based can, however, be used to address a variety of questions and hypotheses beyond mere classification. It provides the phylogenetic framework for most of the papers presented here. Not only does this maximize the consistency of the special issue and comparability of the papers, but also reciprocally sheds light on characters that have been studied for decades. Do these characters contain any evolutionary signal, when reviewed against the latest phylogenetic insights? Do these insights perhaps shed a different light on the homology assessment of these characters? These questions are addressed in two papers, focusing on pollen morphology (Doyle & Le Thomas, 2012) and wood anatomy (Koek-Noorman & Westra, 2012).

A stimulating complementarity is produced by three papers that focus on pollination biology from different angles. Gottsberger (2012) reviews several decades of fieldwork on the pollination of flowers of Annonaceae, with observations on floral morphology, odour, thermogenesis and pollinating insects. This paper has a focus on pollination syndromes, i.e. the interplay of the various factors. This paper is complemented by Saunders (2012), whose analyses involve optimization of pollinating insects on the phylogenetic tree for three of the four subfamilies, the phylogenetic relationships of which are best resolved. By adopting a rigorous framework of phylogenetic optimizations, correlations between pollinators and flower morphology are discussed. A third paper related to pollination biology reviews the chemical characterization of floral scent (Goodrich, 2012). *Cananga odorata* is best known and cultivated for its odour, but, in the words of the 19th century British botanist Richard Spruce, Annonaceae are 'most novel to the European botanist' because of 'the curious leathery, dull-coloured but often richly-scented flowers' (Spruce, 1908: 41). Goodrich's paper is perhaps the most reductionist of the three papers on pollination biology because of the unraveling of odours into various compounds, yet these results are discussed in the broad context of ecology and phylogenetic relationships.

Annonaceae have been shown to be a good proxy for tropical rainforests as their abundance and richness increases with higher temperature and precipitation (Punyasena, Eshel & McElwain, 2008). To reconstruct the evolution of the tropical rainforest biome requires an understanding of the dynamics of the evolution of its inhabitants, such as Annonaceae. Two papers in this issue address questions related to the dynamics of diversity of Annonaceae over evolutionary timescales. Erkens, Chatrou & Couvreur (2012) test the possible occurrence of evolutionary radiations in Annonaceae and correlations with the origin of characters that may have driven these radiations. Pirie & Doyle (2012) assess the phylogenetic and palaeontological uncertainty involved in the estimation of clade ages. Even although strongly focused on phylogenetic methods, both papers benefit greatly from the knowledge of morphological characters so meticulously accumulated by several generations of Annonaceae systematists.

This issue brings together information on the systematics, evolution and ecology of Annonaceae that has been compiled over the past 30 years or so. However, the research over this period could not have been carried out without the many students of Annonaceae from earlier times who passed on their collections, their knowledge and their fascination for the family, and it is tempting to speculate on future developments in research on Annonaceae. We currently see the application of Annonaceae in novel research on the genetics of ovule development with agronomic potential (Lora *et al*., 2011), conservation of genetic resources (van Zonneveld *et al*., 2012) and speciation processes with relevance to conservation (Couvreur *et al*., 2011). These are just a few examples of a range of research questions, both fundamental and applied, which can be addressed making use of Annonaceae. We hope that future research on Annonaceae will benefit from the compilation of knowledge presented here.

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