

Tribute to Gwilym P. Lewis

Anne Bruneau^A and Colin E. Hughes^B

^AInstitut de recherche en biologie végétale, Université de Montréal, 4101 Sherbrooke Street Est, Montréal, QC, H1X 2B2, Canada.

^BDepartment of Systematic and Evolutionary Botany, University of Zürich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland.

This issue of *Advances in Legume Systematics* is dedicated to Gwilym Peter Lewis in recognition of his long and productive career and significant international contribution to the taxonomy and systematics of Leguminosae.

The young Gwilym Lewis first joined the Royal Botanic Gardens, Kew, as part of the horticultural staff in 1974. There, his enthusiasm for botany was quickly noticed and he was soon recruited and, subsequently, promoted as part of the team of scientists in the herbarium, later going on to become a senior scientist in integrated monography at Kew. This drive, energy and dedication to botany, which were noted at the age of 22, have never left him.

Gwilym has been a key contributor to research at Kew Gardens for nearly 45 years. These four decades have seen monumental changes in legume taxonomy, systematics and evolution, and Gwilym has been an important instigator and contributor to this movement both scientifically and as head of the legume section at Kew, and indeed in many ways, as leader of the legume systematics international research community as a whole in recent years.

In the four decades since Gwilym started his career, our vision of legume relationships has profoundly changed. In the early 1980s, the main legume lineages were thought to have evolved from broad common ancestors, exemplified by simple-flowered extratropical woody Caesalpinioideae (Polhill *et al.* 1981), and were usually portrayed as explicit ancestor-descendant relationships among informal groups of genera. Later in the 1980s, cladistics began to be adopted by legume researchers, the first phylogenetic analyses were presented in *Advances in Legume Systematics* (ALS) Part 3 (e.g. Crisp and Weston 1987; Lavin 1987; Zandee and Geesink 1987), and Jeff Doyle (1987) described the new molecular-biology tools and data and their tremendous potential for resolving evolutionary relationships. These approaches were fully embraced by the legume systematics community, and, in 1995 (ALS 7), 16 new phylogenetic studies across the family, most using molecular data, were published. In the 1990s, the plastid *rbcL* gene was being sequenced to look at higher-level legume relationships (Doyle *et al.* 1997), in 2001, the first full legume plastomes were sequenced, and, in 2008, the full nuclear genome of *Lotus*



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japonicus appeared. By the mid-2000s, the phylogenetic framework and time frame of higher-level legume relationships were broadly established (Wojciechowski *et al.* 2004; Lavin *et al.* 2005; Bruneau *et al.* 2008), and, in 2019, we have now amassed DNA-sequence data for more than 5500 legume species, including nuclear genomes (~25 species) and several hundred plastid genomes (e.g. Egan and Vatanparast 2019), as well as produced a much more comprehensively sampled phylogeny of the family as a whole (Legume Phylogeny Working Group 2017). We are now seeing unprecedented use of these phylogenies to test hypotheses on

the biogeographic history, trajectories of evolutionary diversification, ecological constraints, morphological modifications and evolution of nodulation and polyploidy across the family. None of us could have envisaged 45 years ago that we would be able to amass so much data so quickly and do analyses with such powerful tools.

At the same time as relationships in legumes were being deciphered, species were being described, genera re-defined, and an overhaul of the legume classification was ongoing. In 1974, when Gwilym Lewis began his career, ~650 genera of legumes were known. Today more than 20 000 species and 768 genera are recognised; Gwilym has contributed to describing 58 species and 11 genera^A, and has made a central contribution to generic delimitation and classification across the family as a whole, maintaining a global overview of legume genera over recent decades (Lewis *et al.* 2005, 2013; Legume Phylogeny Working Group 2017). Revisionary taxonomic work has always been an important component of Gwilym's research. He has been involved in several taxonomic revisions, but chief among these is his contribution to our understanding of the *Caesalpinia* group, the focus of his Ph.D., which he completed in 1994 under the supervision of Dr Peter Gibbs at the University of St Andrews, Scotland. This resulted in a major taxonomic account of the *Erythrostemon–Poincianella* group, with more than 60 species (Lewis 1998). Later collaborative work resulted in a new generic system for the entire *Caesalpinia* group, a pantropical clade of 225 species with a complex and confusing taxonomic history (Gagnon *et al.* 2016). Dr Lewis' contribution to legume taxonomy has been recognised by colleagues throughout the world who have named seven species of legumes in his honour and one orchid. It seems that there is nothing that Gwilym likes or does better than detective work to solve a generic mystery. His recent paper reinstating the genus *Steinbachiella* (Lewis *et al.* 2012) is a good example. Reading this paper one gets a sense of Gwilym's enjoyment in figuring out this mystery, starting with an initial suspicion, then a careful search in the library, a search of the herbarium to sleuth out specimens, evidence chanced on, seized upon and expertly pieced together, bringing to bear his encyclopaedic knowledge of legume morphology and genera. Gwilym is in his element on the quest to solve such mysteries and delighted when they are resolved.

In addition to important scientific developments, over the past four decades, effective collaboration across the international legume systematics community has been an important force in advancing research on the family and Gwilym has played an important part in fostering that collaboration. Shortly after Gwilym joined the Kew scientific team, the first International Legume Conference (ILC) was organised by Roger Polhill and Peter Raven and held at Kew Gardens in 1978. In 1981, the first volume of the ALS series was published under the supervision of Polhill and Raven. Gwilym contributed actively to both these activities. When one of the contributors to the Proceedings of this first legume conference defaulted, Gwilym, in a very short

period, wrote, in the words of Roger Polhill 'a lucid, concise insight into the Mimoseae, the springboard for his future confident scientific output' (Lewis and Elias 1981). Since then, 12 other ALS collections have been published, all stemming from International Legume Conferences and other symposia. In 2010, the Legume Phylogeny Working Group was founded in Arizona, and, in 2013, at the sixth ILC in South Africa hosted by Ben-Erik van Wyk and colleagues, a new classification of legumes was discussed and later published in the journal *Taxon* under the authorship of Legume Phylogeny Working Group (2017). Once again, Gwilym was integrally involved in bringing this new classification to fruition.

Throughout his career, Gwilym Lewis has spent considerable periods in the field collecting plants. He started in tropical Asia, but quickly saw the need for fieldwork on legumes in the Neotropics where the greatest diversity in the family is found, and he was determined to work in Brazil. During 6 months in Brazil, in 1981, Gwilym learned Portuguese, collected extensively in Bahia and established a network of colleagues to produce his first major book, the *Legumes of Bahia* (Lewis 1987). Gwilym has never stopped being an active field collector. He has collected nearly 4000 numbers under his own name and facilitated field work for many legume researchers (see <https://bloodhound.shorthouse.net/0000-0003-2599-4577>, accessed 5 May 2019). As impressive as this number may be, it is not so much the number of collections, but their quality, that stands out, and especially the exceptional range of associated material he assembled in the field: including photos of flowers at different stages of anthesis and at different angles, often carefully dissected and arrayed on a black cloth background; fixed flowers; wood samples; root nodules; pollinators; fruits; seeds; and silica-dried leaves for DNA extraction. Gwilym's vision of legume research has always focused on diverse sources of evidence from wood anatomy to phytochemistry, pollen to DNA sequences, garnering the resources of Kew's laboratories and expertise across these diverse fields, and his comprehensive field collections richly augmented by this wealth of associated research material have greatly contributed to this.

Gwilym's knowledge of legumes is encyclopaedic and unsurpassed among living legume specialists. He may be the only person in the world who can come close to being able to identify all 770 or so legume genera and who maintains a global overview. This knowledge underpinned his colossal contribution to the wonderfully illustrated encyclopaedia, *Legumes of the World* (Lewis *et al.* 2005), in collaboration with Brian Schrire, Barbara Mackinder and Mike Lock. Also impressive are his earlier species-level accounts in *Legumes of Bahia* (Lewis 1987) and *Legumes of Ilha de Maracá* (Lewis 1989), documenting the diverse legumes found in key parts of Brazil.

For the past 45 years, Gwilym has also dedicated himself to enriching and curating the legume holdings at Kew and many other herbaria across the Neotropics. The pre-eminence of Kew's legume holdings, which include ~750 000 specimens, 200 000 of which have been added during Gwilym's watch, as the most

^A*Arquita*, *Gelrebia*, *Hererolandia*, *Hultholia*, *Lackeya*, *Maraniona*, *Micklethwaitia*, *Mysanthus*, *Oryxis*, *Paubrasil* and *Tabaroa*, and 58 new species in *Acacia*, *Aeschynomene*, *Bauhinia*, *Caesalpinia*, *Calliandra*, *Canavalia*, *Ceratonia*, *Chamaecrista*, *Cicer*, *Dinizia*, *Eriosema*, *Erythrostemon*, *Inga*, *Lonchocarpus*, *Macropitium*, *Mimosa*, *Moldenhawera*, *Mucuna*, *Orphanodendron*, *Parapiptadenia*, *Piptadenia*, *Poecilanthe*, *Pseudopiptadenia*, *Stylosanthes*, *Tephrosia* and *Zygia*.

comprehensive global collection in the world over the past few decades, can, in large part, be attributed to Gwilym's relentless dedication. He achieved this first through targeted fieldwork in Brazil, Cuba, Argentina, Ecuador, Central America, Mexico and Madagascar, but also through tireless curatorial work, fostering collaboration and successfully encouraging collectors to duplicate their collections and deposit them at Kew. His more than 40 years of curatorial excellence of the legume herbarium collections at Kew, and elsewhere, is another fabulously significant part of Gwilym's legacy.

Gwilym Lewis has supervised numerous undergraduate and graduate students and postdoctoral fellows, but, just as importantly, he has supported and enabled the work of colleagues throughout the world. For many people over several decades, Gwilym seems to always have been present to take the responsibility to teach, guide, train and share information on legumes, making sure legume science is accessible. Gwilym has been the assured leader, for which many students and colleagues worldwide will always be grateful.

Since the beginning of his career, Gwilym Lewis has published 250 papers (67 as lead author), 8 botanical science books (4 as lead author or editor), 24 web publications, one popular book and several popular articles, and his work has been heavily cited. Towards the end of his career, we might expect that Gwilym would slow down, but, in 2018, he published 13 papers, 11 in 2017 and 17 in 2016. He continues to be a very active, knowledgeable and generous colleague whose contributions to legume systematics in the past four decades fully merit recognition and thanks, and to whom we are all grateful.

References

- Bruneau A, Mercure M, Lewis GP, Herendeen PS (2008) Phylogenetic patterns and diversification in the caesalpinoid legumes. *Botany* **86**, 697–718. doi:10.1139/B08-058
- Crisp MD, Weston PH (1987) Cladistics and legume systematics, with an analysis of the Bossiaeeae, Brongniartieae and Mirbelieae. In 'Advances in Legume Systematics'. (Ed. CH Stirton) Part 3, pp. 65–130. (Royal Botanic Gardens, Kew: London, UK)
- Doyle JJ (1987) Variation at the DNA level: uses and potential in legume systematics. In 'Advances in Legume Systematics'. (Ed. CH Stirton) Part 3, pp. 1–30. (Royal Botanic Gardens, Kew: London, UK)
- Doyle JJ, Doyle JL, Ballenger JA, Dickson EE, Kajita T, Ohashi H (1997) A phylogeny of the chloroplast gene *rbcL* in the Leguminosae: taxonomic correlations and insights into the evolution of nodulation. *American Journal of Botany* **84**, 541–554. doi:10.2307/2446030
- Egan A, Vatanparast M (2019) Advances in legume research in the genomics era. *Australian Systematic Botany* **32**(5–6), 459–483. doi:10.1071/SB19019
- Gagnon E, Bruneau A, Hughes CE, de Queiroz LP, Lewis GP (2016) A new generic system for the pantropical Caesalpinia group (Leguminosae). *PhytoKeys* **71**, 1–160. doi:10.3897/phytokeys.71.9203
- Lavin M (1987) A cladistic analysis of the tribe Robinieae (Papilionoideae, Leguminosae). In 'Advances in Legume Systematics'. (Ed. CH Stirton) Part 3, pp. 31–64. (Royal Botanic Gardens, Kew: London, UK)
- Lavin M, Herendeen PS, Wojciechowski MF (2005) Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the Tertiary. *Systematic Biology* **54**, 575–594. doi:10.1080/10635150590947131
- Legume Phylogeny Working Group (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* **66**, 44–77. doi:10.12705/661.3
- Lewis GP (1987) 'Legumes of Bahia.' (Royal Botanic Gardens, Kew: London, UK)
- Lewis GP (1989) 'Legumes of the Ilha de Maracá.' (Royal Botanic Gardens, Kew: London, UK)
- Lewis GP (1998) 'Caesalpinia: a Revision of the *Poincianella*–*Erythrostemon* Group.' (Royal Botanic Gardens, Kew: London, UK)
- Lewis GP, Elias TS (1981) Mimoseae. In 'Advances in Legume Systematics'. (Eds. RM Polhill, P Raven) Part 1, pp. 155–168. (Royal Botanic Gardens, Kew: London, UK)
- Lewis G, Schrire B, Mackinder B, Lock M (2005) 'Legumes of the World'. (Royal Botanic Gardens, Kew: London, UK)
- Lewis GP, Wood JRI, Lavin M (2012) *Steinbachiella* (Leguminosae: Papilionoideae: Dalbergieae), endemic to Bolivia, is reinstated as an accepted genus. *Kew Bulletin* **67**, 789–796. doi:10.1007/s12225-012-9415-z
- Lewis GP, Schrire BD, Mackinder BA, Rico L, Clark R (2013) A 2013 linear sequence of legume genera set in a phylogenetic context: a tool for collections management and taxon sampling. *South African Journal of Botany* **89**, 76–84. doi:10.1016/j.sajb.2013.06.005
- Polhill RM, Raven PH, Stirton CH (1981) Evolution and systematics of the Leguminosae. In 'Advances in Legume Systematics'. (Eds. RM Polhill, P Raven) Part 1, pp. 1–26. (Royal Botanic Gardens, Kew: London, UK)
- Wojciechowski MF, Lavin M, Sanderson MJ (2004) A phylogeny of the legumes (Leguminosae) based on analysis of the plastid *matK* gene sequences resolves many well-supported subclades within the family. *American Journal of Botany* **91**, 1846–1862. doi:10.3732/ajb.91.11.1846
- Zandee M, Geesink R (1987) Phylogenetics and legumes: a desire for the impossible. In 'Advances in Legume Systematics'. (Ed. CH Stirton) Part 3, pp. 131–167. (Royal Botanic Gardens, Kew: London, UK)