PLANT SYSTEMATICS WORLD

■ JOSEF BOGNER (1939–2020)

Josef Bogner (Fig. 1), who passed away on 23 April this year, was an expert on the taxonomy and biology of monocots, especially aquatic species and Araceae, a family on which he published 199 papers. Josef was born on 29 January 1939 in Gersthofen, about 7 km north of Augsburg in Bavaria. His father and mother produced vegetables and flowers, which may have kindled Josef's love of plants. His formal training, completed in 1956, was as a floral and ornamental plant horticulturist. His exceptionally strong professional interest in this field soon led him abroad. From 1962 to 1963, Josef was a student gardener at the University Botanic Garden of Cambridge (U.K.). In 1966, he completed a degree as a horticultural engineer at the State Research and Teaching Institute for Horticulture at Weihenstephan. His first position was at the famous "Les Cedres" botanic garden in Saint-Jean-Cap-Ferrat (France), and it was there that Josef first began his close involvement with tropical Araceae. Between 1967 and 1969, he carried out two lengthy research trips to East Africa, Madagascar, the Comores, the Seychelles and the Mascarene Islands and began publishing on the family's taxonomy, with five papers coming out in 1968 and 1969, when Josef was 29 (suppl. Table S1 provides a numbered list of JB's 248 publications).

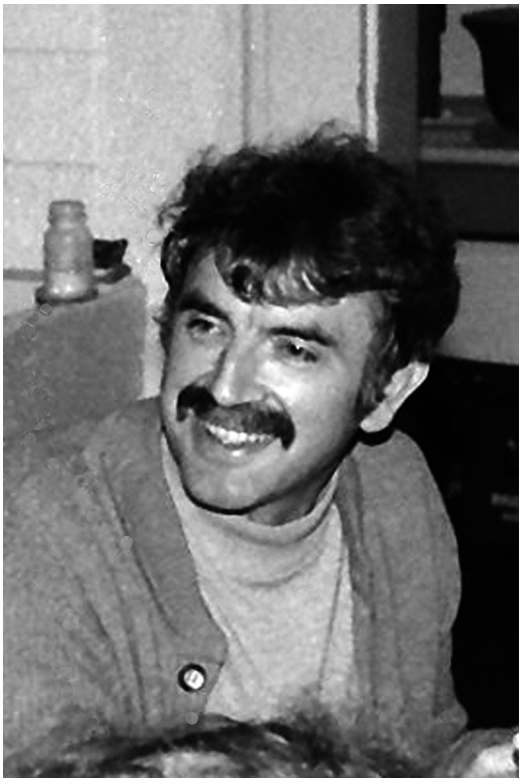

Fig. 1. Josef Bogner in 1981. Photo by Hannes Hertel.

From 1969 to 2002, Josef was employed at the Munich Botanical Garden, ultimately with the rank of Garden Inspector and the responsibility for the extensive glasshouse collections at the Garden. In 1999, Josef received the Bette Waterbury Award for Excellence in Aroid Horticulture at the International Aroid Conference in St. Louis; in 2004, he was awarded the rare honour of a Doctor *honoris causa* of the Ludwig Maximilian University of Munich; in 2005, the "Akademie Preis" of the Bavarian Academy of Sciences given for outstanding scientific achievements by non-academic persons residing in Bavaria; and in 2017, the International Aroid Society's H. W. Schott Award for Excellence in Aroid Research (Croat, 2018).

Over the course of many years, Josef Bogner visited numerous tropical and subtropical regions, including India, Sri Lanka, South China, Bangladesh, Myanmar, Vietnam, Thailand, Sumatra, Peninsular Malaysia, Sarawak, Australia, several West African countries including Gabon and Cameroun, and Venezuela and Brazil in tropical America. His most recent trips were to Colombia (2017) and Brazil (2018). From most of these travels, Josef brought back living plants, seeds and herbarium specimens, almost always in close collaboration with his local colleagues, whom he supported unfailingly then and afterwards in his unpretentious and modest way.

Josef Bogner was an outstanding authority on the monocotyledons and, in particular, he had a uniquely comprehensive and unmatched grasp of Araceae systematics. His deep knowledge of the specialist literature, including palaeobotanical research, enabled him to play a constructive role in stimulating discussions at international scientific meetings. Over and above this, Josef was exceptional

in the way he shared material from his own collections and indeed went to enormous trouble to put them at the disposal of other scientists; his remarkable unselfishness contributed substantially to important advances in Araceae systematics made by others. Sharing his plant materials – in recent years especially for DNA isolation – was second nature to Josef and is among the most important ways in which he linked younger Araceae students with more traditional experts worldwide.

Among the many contributions that Josef Bogner made to the systematics of the Araceae, probably none was more important than his role as a prime mover of radical changes in the family classification, which led eventually to the phylogeny accepted today. At every stage of this process, Josef made major contributions of his own, provided critical material for the research of other systematists and networked across the world to exchange information, data and plant material, and generally enthuse other workers.

Josef was always a stout defender of the "standard" classification of Adolf Engler (1844–1930) who, with help from Kurt Krause, authored the last complete monograph of aroids down to species level in the *Das Pflanzenreich* series (Engler & Krause, 1905–1920). This may have been because Josef was one of the few people able to both read and understand Engler's work fully. His own field explorations and taxonomic studies, supported by his unparalleled skill in cultivating rare or unknown plants, quickly led to a desire to investigate Engler's taxon boundaries with a view to an eventual revision of the classification. Early papers on the genera *Andromycia* (4, the numbers refer to JB's publications in suppl. Table S1) and *Callopsis* (5) already showed this direction of his research, but really important new discoveries appeared with his monograph of the tribe Arophyteae endemic to Madagascar (7). This substantial paper was the result of Josef's field research in Madagascar, during which he recollected previously described taxa and discovered several more himself. This was the taxonomic and nomenclatural revision of a tribe that had been unknown to Engler, and Josef established here his future method for tracking down the rarer genera: field research based on exact location of earlier collections, cultivation of the living plants at the Munich Botanic Garden, soliciting help from colleagues who could supply new data on the plants, especially chromosome numbers and pollen morphology, and from 2000 onward, DNA data, and making permanent herbarium and liquid-preserved collections for posterity.

An important factor in Josef's burgeoning interest in Engler's aroid classification was his friendship with Dan H. Nicolson, who had been investigating the overall classification of the family since the time of his doctoral thesis in the late 1950s and who earlier published a review of aroid classifications (Nicolson, 1960). Dan was also a great admirer of Engler's work, and in the 1960s was concerned with emphasizing its taxonomic superiority over J. Hutchinson's (1959) newer system, which being in English was easier for many researchers around the world to use. Dan played a major role in teaching other aroid taxonomists how to get a "feel" for Engler's eight subfamilies, which while formidable to grasp at first, made intuitive sense with practice. Engler's system was conceived in an evolutionary framework, and his subfamilies were based on the concept of a parallel evolution of taxa with unisexual flowers from bisexual-flowered ancestors (127, 232). The modern phylogenies of the family, which Josef did so much to bring about, differ fundamentally from Engler's view in showing that almost all unisexual-flowered genera belong to a single clade.

From the 1960s to the 1990s, Josef and Dan worked in tandem on the investigation, update and revision of Engler's system in a series of papers, Josef focussing more on targeting poorly known genera in the field, their subsequent cultivation and data gathering and Dan especially on nomenclatural issues, including the revision and typification of all generic and suprageneric names (e.g., Nicolson, 1975, 1984, 1987). Dan also made translations into English of many sections of Engler's *Pflanzenreich* monograph and circulated them to colleagues. In this way, the revision of the family classification began to attract increasing interest from other researchers, beyond the standard revisionary and floristic studies that were also gathering pace around the world (Croat, 2004).

After his Arophyteae revision, Josef published a series of papers on poorly known genera: *Pycnospatha* (12), *Mangonia* (13), *Protarum* (14), *Thomsonia* (19), *Jasarum* (22), *Gonatopus* (24) and *Lagenandra* (25), and a full floristic treatment for Madagascar (16). In 1979, his critical list of aroid genera appeared in the then brand-new journal *Aroideana* (28), and this marked an important step towards the changes to come. This paper was a synopsis of Engler's system, adjusted to include nomenclatural changes and genera described since 1920. Dan Nicolson followed this with a published translation of the Englerian system with updates (Nicolson, 1983, 1988). Further papers by Josef focused on other poorly known genera, e.g., *Aridarum* (30), *Culcasia* (31), *Scaphispatha* (32), *Nephthytis* (34), *Bucephalandra* (35), *Plesmonium* (36), *Pseudohydrosme* (38), *Dracontium* (41), *Hottarum* (48), *Hapaline* and *Phymatarum* (58), and *Stylochaeton* (59).

During this period – late 1970s and 1980s – new research groups had begun working on different aspects of the systematics of the Araceae. Denis Barabé and coworkers and William Carvell began broad surveys of floral structure, Heinz-Dietmar Behnke on sieve-element plastid ultrastructure, James French and Barry Tomlinson on anatomy, Michael Grayum on palynology, Alistair Hay on the origins of the family and especially the Lasioideae, Richard Keating on the vegetative anatomy, Gitte Petersen on cytology, Elke Seubert on seed and embryo structure, Hans-Jürgen Tillich on seedling structure, and Christine Williams and Jeffrey Harborne on flavonoids. Notably, there was a resurgence of interest in shoot architecture, first by Patrick Blanc and then Thomas Ray, which led to the complete translation of Engler's ground-breaking monograph of aroid shoot morphology (Ray & Renner, 1990). Almost all these workers and many others (e.g., C.J. Marchant's [1973] survey of aroid cytology in the early 1970s) were supplied with material for their researches by Josef. What made Josef's contribution so crucial was that he could provide material of taxa that otherwise could not be studied for the characters of interest. In addition, Josef's excellent networking skills and constant urging were invaluable in guiding investigations.

Josef Bogner and Jim French began the breakup of Engler's Pothoideae by transferring *Anadendrum* to the Monsteroideae and promoting it as a new tribe, based on anatomical studies by French and Tomlinson (62). Another telling indication of the "déluge" to come was the story of the genus that commemorates Josef, *Bognera* Mayo & Nicolson. The original specimen was first determined by Dan Nicolson as an unnamed new genus back in 1976. Josef discussed the specimen with various colleagues over several years but no consensus could be reached as to which of Engler's subfamilies

it might belong to. In 1980, it was described by Michael Madison as a new species of *Ulearum* (Aroideae), and in 1984 Nicolson and Mayo decided it should be recognized as a new genus in the Philodendroideae. The solution to the conundrum of its relationships only came when Eduardo Gonçalves discovered in 2002 that DNA placed it near *Dieffenbachia* in an expanded Spathicarpeae (Gonçalves & al., 2007).

The bell truly tolled for the Engler system when Grayum's radical new phylogenetic classification was presented at the second international workshop on aroid systematics at Harvard Forest in 1984. Mike Grayum had pioneered the use of cladistic techniques to work out a phylogenetic classification, basing his study on a comprehensive synthesis of the systematic literature of the family – a truly herculean achievement. This galvanized other researchers towards a general revision of the family classification. Within a few years, three new classifications were published, by Grayum (1990), Hay & Mabberley (1991), and Bogner & Nicolson (101). The latter paper brought to fruition one of the main goals of their long collaboration on the family: a complete and fully updated key to all genera founded on a now much-modified version of Engler's system. This paper was the distillation of their combined expertise over thirty years of work. The pre-molecular phase of aroid systems ended with R. Keating's (2002) monograph of aroid anatomy for which Josef had contributed many critical specimens, and Keating's (2004) family classification.

In the meantime, the head of Kew's Herbarium, Grenville Lucas, encouraged Simon Mayo and Peter Boyce to collaborate with Josef on a fully illustrated account of the genera of the family. The team began serious planning in 1987, and for the next ten years, the project occupied a good deal of Josef's time and effort, although he continued to publish with undiminished vigour on other aroid topics. James French and Robert Hegnauer contributed chapters on anatomy and phytochemistry respectively, and the 106 plates illustrating the critical morphological characters of all the genera were provided by the artist Eleanor Catherine. The classification was based on cladistic analyses of a morphological data matrix. The book was published in 1997 as *The genera of Araceae* (127) and is among Josef's most important scientific achievements. It was awarded the prestigious Henry Allan Gleason Award of the New York Botanical Garden and remains the standard text on the genera of Araceae, although now much out-of-date because it contains neither the duckweeds nor the many new genera published since the mid-1990s. Offshoots of the project were the accounts of Acoraceae and Araceae for *The families and genera of vascular plants* of K. Kubitzki (129, 133).

By the time *The genera of Araceae* was published, the landscape of higher-level angiosperm systematics was undergoing tectonic shifts from new molecular results. In the aroids, this began with Jim French's work (French & al., 1995), which had an impact similar to that of Grayum's earlier studies. It revealed a duckweed, *Lemna*, lodged deep in the aroid clade. The clear separation of *Acorus* from aroids confirmed Grayum's earlier conclusions, but the exclusion of the swamp cabbages of the Orontieae from the rest of the aroids along with the peculiar *Gymnostachys* from Australia was a major new result. Above all, the unisexual-flowered genera all came out in a single clade.

Later, in his paper with Gitte Petersen on aroid cytology (183), Josef included the duckweeds (previously Lemnaceae) formally as subfamily Lemnoideae of Araceae, a satisfying return to Engler's (1879) original idea, even though the latter was based on misleading similarities to the floating aroid *Pistia* in shoot architecture (Ray & Renner, 1990) and seed structure. This move was amply confirmed in the following year by the comprehensive phylogenetic molecular study of Cabrera & al. (193) in which Josef played a prominent role. The new molecular-based phylogenies that were now appearing (see 233 for a survey) acted as a stimulant to Josef to undertake targeted new investigations. In regard to *Pistia* and the duckweeds – and galvanized by extraordinary *Limnobiophyllum* fossils (Kvaček, 1995) that appeared to confirm the *Pistia*-lemnoid relationship – Josef combined studies of extant aquatic Araceae (202) with first-hand study of relevant fossils, especially in collaboration with Zlatko Kvaček. In other cases, too, his palaeobotanical collaborations (e.g., 66, 94, 171, 174, 190, 196, 209, 213, 241) led to startling advances in our knowledge of fossil aroids, among them the realization that the Araceae are one of the oldest groups of angiosperms, with a history stretching back to the early Cretaceous. Josef's vast knowledge of the family played a major role in motivating other palaeobotanists to search for ancient aroids because of his unrivalled ability to assess fossils in the light of the full range of extant diversity, making him the ideal taxonomic collaborator.

Other major issues resulting from molecular phylogenetic results that occupied Josef Bogner in later years were the taxonomic position of the endemic tuberous African genera *Stylochaeton*, *Gonatopus* and *Zamioculcas*, which led to fruitful collaborations with Michael Hesse's palynological research group at the University of Vienna (148) and resulted in the recognition of the subfamily Zamioculcadoideae, a group of critical interest because of its phylogenetic position at the transition between bisexual- and unisexual-flowered clades. Similarly, in the analyses of Cabrera & al. (193) and others, the genus *Calla* emerged in what seemed to be a highly anomalous position. Untiringly he pursued this issue with colleagues, and his efforts were rewarded by important new publications (234; Henriquez & al., 2014).

Since 2003, Josef Bogner's presence was a major factor in the continuation of the long tradition of Araceae research in Munich, where the young Engler first worked out his epoch-making evolutionary aroid classification (Lack, 2000; 232). Josef was very forward-looking, embracing new approaches enthusiastically whenever they offered the chance to solve long-standing anomalies of the classification. In my (SSR's) interactions with Josef from 2000 onwards, he showed intense interest in the possibilities that DNA data offered for exploring the relationships of *Pistia*, *Lemna*, and *Arisaema*, later brought to fruition (Renner & Zhang, 2004; Renner & al., 2004). In collaboration with Renner, Josef guided a new generation of aroid researchers, Natalie Cusimano, Lars Nauheimer, and Aretuza Sousa, whom he never tired of challenging (e.g., Cusimano & al., 2010; Nauheimer & al.; 2012; Sousa & Renner, 2015). These discussions made possible the welding of molecular and molecular-cytogenetic data with a revised version of the morphological data used for the *Genera of Araceae* classification, and led to the publication of what was then the most robust and complete phylogeny of the family (222).

Apart from his intense interest in the general classification of Araceae, Josef produced numerous other publications on the

systematics of the Araceae and other families, many in collaboration with other authors (see the list of his 248 publications in suppl. Table S1). His contributions to the taxonomy of aroids in tropical America, tropical Africa and tropical Asia are manifest and wide-ranging. Last should be mentioned his contribution to the species list of Araceae (152), which is the basis of the various online databases covering the family as a whole.

Until his retirement, Josef lived on the grounds of the Botanical Garden in Munich, afterwards in Gersthofen. He was married to a teacher and accomplished painter, and is survived by his son and his sister. He remained scientifically active, regularly visiting the institute, herbarium, and garden, and indeed talked on the phone to a fellow worker from Peru, another from the Netherlands, and another from Munich just days before his peaceful death in a hospital in Augsburg. Josef's loss is deeply felt by his colleagues at the Garden, the Herbarium, and the university's botanical institute in Munich, and worldwide.

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Supporting information may be found online in the Supporting Information section at the end of the article.

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