

THE ACOLYTES OF THE ARACEAE

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The history of human involvement with the Araceae can be traced back over three millennia. At least three aroids were known to the Pharonic Egyptians and are depicted in the 'Temple of Flowers' at Karnak (Beaux, pers. comm.). Theophrastus recorded Araceae in his treatise (see Prime, 1960), and Hernandez (1651) described a number of tropical aroids and their uses by the Aztec people. European Araceae were described in detail by herbalists such as Fuchs (1542) and Ray (1682) and the uses in folk medicine for the starchy tubers of various *Arum* species are so well established and widespread throughout Europe and Asia Minor that they clearly date from a very early age. Dodoens (1574) included all Araceae then known to him in one group, suggesting that even 400 years ago the aroids were recognized as being an homogeneous assemblage.

Tournefort (1700) created a 'class' without a name in which he grouped three European genera (*Arum*, *Dracunculus* and *Arisarum*), characterized by the possession of a 'monopetalous flower'. This concept of the aroid inflorescence as a flower with a single petal also influenced Linnaeus, who classified the species known to him according to his artificial sexual system (Linnaeus, 1753). However, Jussieu (1789) recognized the 'flower' as an inflorescence comprised of a spike (spadix) of tiny flowers surrounded by an often colourful bract (spathe).

Araceae was established as a natural family by Jussieu (1789). He recognized only a few small, rather broadly conceived genera due to the paucity of good material of taxa from outside Europe. All the climbing species were grouped under the name *Pothos* and most of the terrestrial species were placed in the genera *Arum* and *Dracontium*.

Modern systematic studies of the Araceae began with the work of the Austrian gardener and botanist H.W. Schott. He was the first monographer of the family and the first botanist to make careful comparative studies of aroid inflorescences, flowers and fruits and was thus able to establish the generic foundations of the family. His observations were meticulously documented in his writings and accompanied by an outstanding archive of scientific illustrations (Riedl, 1965a, 1965b). The *Icones Aroidearum*, a collection of over 4,000 superb watercolour and pencil drawn plates of Araceae were prepared under his direction and personal expense. The pencil drawings are of herbarium specimens and material preserved in alcohol from herbaria all over Europe while the watercolour plates were painted by pre-eminent Viennese artists including Liepoldt, Zehner, Seboth, Nickeli and Oberer, from living plants grown at Schönbrunn. These colour plates represent each plant in astonishing detail and thoroughness. The *Icones Aroidearum* are today housed at the Vienna Natural History Museum. About 80 plates (representing the tribe *Lasieae*) are thought to have been lost (Schott, 1984; Riedl & Riedl-Dorn, 1988).

Schott was born on 7 January 1794 at Brünn in Moravia (the present day Czech Republic). At the age of seven he moved to Vienna, where his father had become head gardener at the botanical garden of the University. There he came into contact with the eminent botanists of the day. N.J. von Jacquin stimulated and directed the early interest of the boy to study plants, and a visit from F.W.H.A. von Humboldt made a lifelong impression upon the young Schott. Although he attended lectures in botany, agriculture and chemistry at the University, Schott's first employment was as an assistant gardener under the direction of his father. In 1815 he became gardener at the Belvedere Palace in charge of the collection of Austrian plants. Then two years later, at Jacquin's recommendation, he was chosen to participate in the famous scientific expedition to Brazil which included the botanists C.F.P. von Martius, J.B. von Spix and J.C. Mikan, the zoologist Natterer and the mineralogist Pohl.



H.W. Schott (1794–1865). Photograph circa 1860.

Between 1817 and 1821 Schott worked in Brazil as a member of this team of naturalists and came into intimate contact with a rich tropical flora. His major duty was to establish and direct a garden in Rio de Janeiro to prepare plants for the long journey to Europe. When he returned to Vienna in 1821 he took up gardening again, eventually becoming Director of the botanical and zoological gardens at the Imperial Palace of Schönbrunn, a position he held until his death on 5 March 1865.

Schott's most important written works were the *Genera Aroidearum* (Schott, 1858, 1984; Riedl & Riedl-Dorn, 1988) and the *Prodromus Systematis Aroidearum* (Schott, 1860). Among his many smaller works on Araceae was a series of articles entitled 'Für Liebhaber der Botanik' which he published in the cultural periodical *Wiener Zeitschrift für Kunst, Literatur, Theater und Mode* (Schott, 1829a–g, 1830a–e). These were especially significant because it was here that he published many of his new genera. These papers, though very brief and embedded in a publication of a largely ephemeral nature, are among the most important contributions ever made to aroid systematics. Schott also published many papers on Araceae in the leading journals of his day, for example *Oesterreicher Zeitschrift für Botanik* and *Bonplandia*. A folio work, *Aroideae Maximilianae*, which was based on Schott's descriptions, illustrations and notes was published in 1879, 14 years after his death. This work, edited by J.J. Peyritsch, described species of Araceae collected in eastern Brazil during an expedition in 1859–60 by the Archduke Ferdinand Maximilian, later the Emperor of Mexico.

Schott described many new genera and species and created the first major natural classification of the whole family. His taxonomic concepts were narrow and although many of his genera have withstood the test of time, Engler later synonymized many of his species; however, modern studies suggest that Engler may have been too hasty in many instances. Schott was made a Doctor *honoris causa* and a member of the Kaiserliche Akademie der Wissenschaften for his work in botany and horticulture. He created the basis of Araceae taxonomy, not only for Engler who followed him in studying the family comprehensively, but also for succeeding generations. An important aspect of Schott's work was that he used a combination of herbarium material, living plants and field work in the study of a largely tropical plant group at a time when such a wide-ranging approach was most unusual.

Other significant works on the family published during Schott's lifetime include Kunth's treatment for his *Enumeratio Plantarum* (Kunth, 1841), which was the first post-Linnean treatment at species level, and Blume's *Rumphia* (Blume, 1836, 1837). The latter work was especially important for Asian genera and included very fine coloured plates.

The second great monographer of aroids was H.A. Engler. He published his first major treatment in Martius' *Flora Brasiliensis* (Engler, 1878), followed immediately by a complete monograph at species level in de Candolle's *Monographiae Phanerogamarum* (Engler, 1879). Earlier, Engler had published two important papers on the family. In the first (Engler, 1876) he outlined a new 'natural' system on phylogenetic lines which was substantially different from Schott's classification, especially at the higher taxonomic ranks. The second paper (Engler, 1877) dealt with the shoot architecture of the family and was a pioneering study based on original observations. His account for Beccari's *Malesia* (Engler, 1883a & b) appeared at about the same time as a series of papers in his *Botanische Jahrbücher* which are of great importance in understanding his approach to Araceae systematics (Engler, 1883a & b, 1884a & b). The family treatment for the *Natürlichen Pflanzenfamilien* (Engler, 1889) was his next major contribution.

An important resource for Engler was the large living collection of Araceae at the Botanischer Garten, Berlin-Dahlem, where he was Director for many years. Although Engler carried out little field work, botanists from all over the world sent him material and information. With the founding of *Das Pflanzenreich* in 1900, Engler embarked on his second monograph of the entire family, completed in 1920 with the help of his assistant Krause (Engler 1905, 1908, 1911, 1912, 1915, 1920a, 1920b, 1920c; Engler & Krause 1908, 1920; Krause 1908, 1913). Engler and Krause doubled Schott's total of about 900 species. A novel feature of the treatment for *Das Pflanzenreich* was the large number of fine illustrations, prepared by the draughtsman Pohl; these are mostly original but some were copied from Schott's illustrations.

Engler was born on 25 March 1844 in Sagan, Lower Silesia (modern day Poland), the son of a tradesman; in 1848 his mother took him to the provincial capital of Breslau, where the young Engler grew up. From his early years he took a great interest in natural history and during his University years studied with the famous



H.A. Engler (1844–1930). Photograph taken when Engler was 19.

palaeobotanist and teacher J.H.R. Goepfert; his doctoral thesis was on the genus *Saxifraga*. Following this he was a teacher in Breslau for a short time. In 1869 he became acquainted with A.W. Eichler who had succeeded Martius as editor of the *Flora Brasiliensis* and this contact was to be of great significance for his future career. In April 1871 he was employed as a scientific assistant at the Botanische Sammlungen (herbarium and living collections) in Munich. Here, under the guidance of C.W. von Nägeli's directorship, he remained for eight years until he was 34 years old. The botanic garden and herbarium, together with the library (Bayerische Staatsbibliothek) provided excellent working conditions. These were the creative years during which Engler studied the shoot architecture of the Araceae, produced the first version of his new phylogenetic classification and completed the treatment for the *Flora Brasiliensis*. He widened his circle of contacts with other botanical institutes and botanists, including A. de Candolle at Geneva, who invited Engler to contribute the account of Araceae for the *Monographiae Phanerogamarum* in 1876. This huge task was completed in the phenomenally short time of three years.

In 1879 Engler became a 'professor ordinarius' at the University of Kiel, where he also became Director of the botanical garden and institute. After the death of Göppert in 1884 Engler was appointed to succeed his former professor at the University of Breslau, a post which included the Directorship of the botanic garden. There he began work on *Die Natürlichen Pflanzenfamilien* together with K.A.E. Prantl. In October 1889 Engler moved to Berlin to become the Director of Germany's largest botanical garden and institute. He was by now an extremely able organizer and under his direction a new botanical garden and botanical museum were planned and built at Dahlem, then on the outskirts of Berlin. Started in 1897, the new garden took 12 years to complete, being inaugurated in 1910. In 1902 he journeyed to the Cape Province in South Africa, the Transvaal, East Africa and Egypt. In 1905 he visited South and East Africa again and also the Zambezi region, after which he went to India and Sri Lanka, where he paid particular attention to economic plants and Araceae. His journey then took him to Bogor, Singapore, Malacca, Burma, the Himalaya and Calcutta. In 1913 he went on a world tour that took him to South West Africa, China, Japan, Hawaii, California and New England. He was awarded honorary doctorates by the Universities of Cambridge, Cape Town, Uppsala



H.A. Engler in his later years.

and Geneva and the Gold Medal of the Linnean Society. He retired officially as Director at Berlin on 31 March 1921 but continued his scientific work until his death on 10 October 1930.

Work on Araceae at Berlin continued under K. Krause who published new species collected by various field botanists, especially those working in South America, until 1942. Krause did not take up his studies again after the Second World War and he died in obscurity in 1963. A manuscript that Krause completed in 1942 for the second edition of *Die Natürlichen Pflanzenfamilien* was lost in 1943 when the Berlin Botanical Museum was largely destroyed by war action, bringing Engler's great work to a tragic conclusion.

Joseph Hooker, in Bentham & Hooker's *Genera Plantarum* (Hooker, 1883), followed the classification of Schott (1860). Hutchinson (1934, 1959) also published a system which more closely resembled Schott's than Engler's, probably because he viewed his own work as a revision of Bentham and Hooker's treatise. Essentially Hutchinson translated Schott's treatment into English with some re-arrangements and additions. By reversing Schott's sequence of genera and starting the system with those having bisexual flowers, he gave the impression of a phylogenetic system. Engler's classification was, by contrast, an attempt to portray a true phylogenetic arrangement, without resorting to a linear sequence. As is evident from his writings, he viewed the evolution of his subfamilies as resembling a bush rather than a tree and this concept lies behind his ordering of genera into a series of independent and parallel phylogenetic sequences, particularly clear in his treatment of the *Pothoideae* and the *Lasioideae*.

T. Nakai (1943) published a classification in which he recognized the Pistiaceae, Cryptocorynaceae and Acoraceae as families separate from the Araceae. His work was not followed to a significant degree but it is important as the place of valid publication of a number of suprageneric names.

After 1945 a period of relative inactivity followed, until in the 1950s when G.S. Bunting and later D.H. Nicolson and J. Bogner began working on the family. M. Hotta also began to publish on Araceae in the 1960s and in 1970 he presented a classification for eastern Asian and Malesian genera and a series of studies of vegetative and floral morphology and ecology (Hotta, 1970, 1971, 1982, 1984, 1986a, 1986b; Hotta, Okada & Ito, 1985). Other important studies during this period were those on pollen morphol-

ogy carried out by G. Thanikaimoni (1969) and cytology undertaken by C.J. Marchant (1970, 1971a, 1971b, 1972, 1973). Floristic and revisionary studies in the 1950s and 1960s that should be mentioned are those of H.C.D. de Wit on *Cryptocoryne* (de Wit, 1958, 1959a–i, 1960, 1961a–e, 1970, 1971a & b) and *Lagenandra* (de Wit, 1959d, 1959e), H. Riedl's contributions for *Flora Iranica* (Riedl, 1963) and his revision of *Eminium* (Riedl, 1969), M.T. Madison's treatment of *Monstera* (Madison, 1977), Bunting's revision of *Spathiphyllum* (Bunting, 1960) and the revision of *Aglaonema* published by Nicolson (Nicolson, 1969).

In the 1970s and 1980s the pace of work on the systematics of Araceae accelerated. In 1978 the International Aroid Society was formed in Florida, USA and the journal *Aroideana* founded. Originally under the energetic editorship of Mike Madison, *Aroideana* generated a significant expansion of scientific and horticultural interest in the family and continues to play an important role. International workshops on aroid systematics at Sarasota (1980), Harvard Forest (1984), Berlin (1987) and Moscow (1992) have fostered active collaboration which will undoubtedly continue; the next workshop is planned for 1995 in Kunming, China.

Bogner (1979) updated the Engler classification, adding newly described genera, correcting nomenclature and taking account of new synonymy. Nicolson (1983) published an English translation of Engler's classification, including the accepted genera described since 1920. Bogner & Nicolson (1991) published a revised synoptic key to all the genera, which incorporated a number of important changes from Engler's concepts, particularly in the subfamilies *Pothoideae* and *Lasioideae*. Grayum (Grayum, 1984, 1990, 1992) presented a new phylogenetic classification which is especially notable for recommending the removal of *Acorus* from Araceae, the dismembering of Engler's subfamilies *Lasioideae* and *Aroideae* and a greatly enlarged concept of subfamily *Philodendroideae*.

Important surveys of characters have also been carried out in the last two decades; of particular significance are the studies of J. French (anatomy, also with P. Tomlinson), T. Ray and P. Blanc (shoot morphology), G. Petersen (cytology), M. Grayum (palynology), H.-J. Tillich (seedling morphology), D. Barabé and colleagues (floral anatomy).

New Araceae research centres were started in the 1970s at the Missouri Botanical Garden (T.B. Croat) and the Royal Botanic

Gardens, Kew (S.J. Mayo and later P.C. Boyce). Since then others have developed, for example at Copenhagen (N. Jacobsen), Tokyo (J. Murata), Sydney (A. Hay), Calicut (M. Sivadasan), Kunming (H. Li), Yaoundé (C. Ntépé-Nyame), Leiden (W. Hettterscheid), Moscow (M. Serebryanyi) and in Brazil (M. Nadruz, C. Sakuragui).

Despite the increase in taxonomic activity, most of the genera, especially the larger ones, have not been thoroughly revised since Engler's time and those regions of the world which are richest in Araceae mostly have yet to receive floristic treatments. Notable exceptions are Croat's work on *Anthurium* (Croat 1983, 1986, 1991; Croat & Baker 1979), the largest genus of the family, and Ntépé-Nyame's account for the *Flora du Cameroun*, (Ntépé-Nyame, 1988), the richest region in Africa for aroids.

Field studies, especially in tropical regions, have also grown apace, most notably through the prodigious activities of T.B. Croat, who has built up the world's largest collection of living Araceae at the Missouri Botanical Garden, formed initially as the basis for his monographic work on *Anthurium*. Other active areas include north-eastern Brazil (Mayo), South-east Asia (Boyce, Hay) and Australia (Hay).

The latter part of the twentieth century is proving to be a renaissance for aroid research.

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