Chapter 1

A history of research in Compositae: early beginnings to the Reading Meeting (1975)

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INTRODUCTION

The magnitude of the work of the great students of the Compositae in the 19th and early 20th centuries is astonishing, both in the quality and scope of their research, as well as in the great number of systematic treatments and floras they produced. Their achievements go beyond exceptional, however, when they are seen in the context of the technology that these workers had available at the time.

What follows is an attempt to gather and tie together many scattered pieces of information on their lives, work, and ideas, and to pay tribute to those individuals who have made outstanding contributions to the field. We are grateful to these men of science; their work has enabled us to see and understand the most diverse and successful plant family on Earth. This chapter covers notable synantherologists up to the 1975 conference held at Reading; a two-volume work that resulted from this meeting was published in 1977 (Heywood et al. 1977). The scientists are discussed in chronological order of the date of their major contribution(s) to our understanding of Compositae.

PRE-TOURNEFORT ERA

Compositae are such a well-defined, diverse, and conspicuous group in most areas of the world that it is perhaps not surprising to discover that even early authors such as Theophrastus (ca. 371 to 287 BC) had at least some idea about the naturalness of the group (Greene 1983: 184). As early as the mid 16th century Jean Ruel (1474–1537), a French botanist, is credited with many original observations on plants and the coining of copious new morphological terminology. He presented a description of several Compositae, clearly identifying the capitulum as being composed of several florets of different types: "*Anthemidi è rotundis capitulis flores prominent in orbem foliati, alios intus aureos flores continentibus*" ["Anthemis has its rounded capituli encircled by leafy flowers, and within these yellow ones"] (Ruel 1536, cited by Greene 1983). However, a deeper insight on the true nature of the Compositae did not come until well into the 17th century with the work of Joseph Pitton de Tournefort, Sébastien Vaillant, and Johann Le Francq van Berkhey.

Before presenting an introduction to the lives and works of these three important botanists, it seems appropriate to include a brief note on three other botanists, who albeit did not contribute to advancing the understanding of Compositae systematics, are nonetheless credited with coining the two alternative names for the family.

Michel Adanson was born April 7, 1727 in Aix-en-Provence. In 1729 the family moved to Paris. In 1763 Adanson published his *Familles des Plantes* in which he described several plant families, one of them named

Compositae. However, after the resolution adopted at the Vienna Congress in 2005 (Article 13.1, McNeill et al. 2006), the starting date for the names of families was set to August 4, 1789 (date of publication of Jussieu's *Genera Plantarum*; Jussieu 1789) and the priority of the name fell to Giseke who had published the name independently in his *Praelectiones* in 1792. Adanson died in Paris, on August 3, 1806. Biographic information on Adanson can be found in Cuvier (1861) and Bailly (1992: 127–196); see Stafleu and Cowan (1976) for a thorough list of works on the life and works of Adanson.

Paul Dietrich Giseke was born in Hamburg on December 8, 1741, the son of a merchant. He studied Medicine at Göttingen University and received his degree in 1767. Interested in the Natural System of plants, he wrote to Linnaeus for advice. Linnaeus answered that he could not give the characters of the natural orders but could explain them in person. In 1771, Giseke traveled to Uppsala where Linnaeus gave him and four other students a private lecture on these ideas; he had only done this once before, in 1764. Another student in this group was Johann Christian Fabricius (1748–1808), who later became famous as an entomologist. Fabricius and Giseke had both made records of Linnaeus' lectures, and Giseke (1792) combined them in his *Praelectiones in Ordines Naturales Plantarum* [Lectures on the natural orders of plants]. The text, partly a dialogue between the professor and his students, shows the clear insight of Linnaeus in the principles of a natural system: he recommended individuals to not use single characters to define a group (taxon)

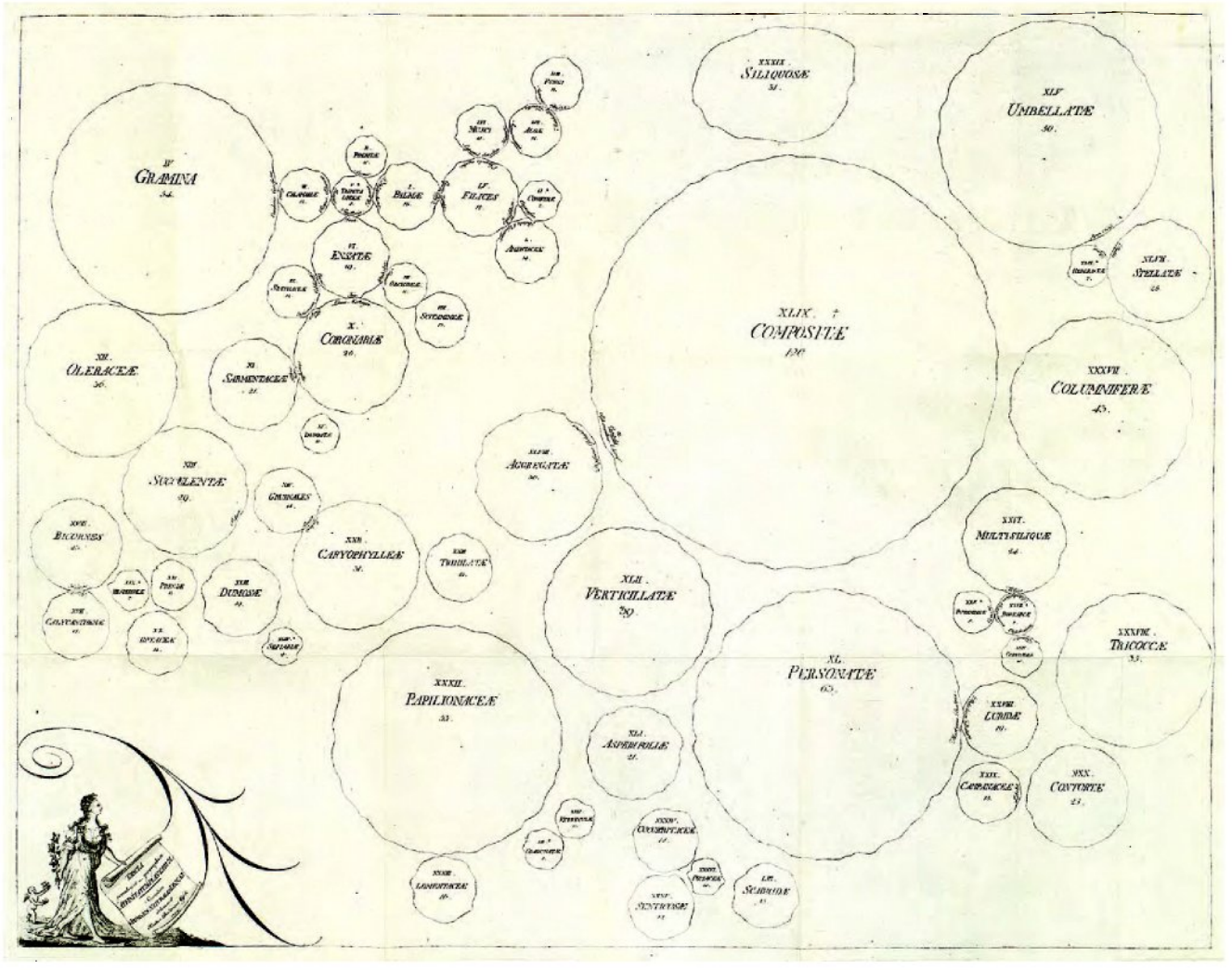


Fig. 1.1. Giseke's "Tabula genealogico-geographica affinitatum plantarum secundum ordines naturales Linnaei", where he expresses in a novel graphic mode the relationships among the plant families as envisaged by Linnaeus. The size of the circles is indicative of the number of genera considered for each order. Note the conspicuousness of Compositae. This plate, dated 1789, was also published separately and represents the first record for the name Compositae. [Taken from Giseke's *Caroli A Linne Praelectiones in Ordines Naturales Plantarum*, reproduced with the kind permission of the Linnean Society, London.]

but rather a combination of them. Compositae is taken from *Compositi* in Linnaeus' *Philosophia Botanica* (1751, cf. page 29), which in turn can be traced back to Ray's (1682) "Herbae Florae Composito". The subdivision of the family in the *Praelectiones* is the same as in Linnaeus (1751).

Probably the most interesting feature of Giseke's book is the "Tabula genealogico-geographica affinitatum plantarum secundum ordines naturales Linnaei [quam] delineavit Paulus Dietericus Giseke 1789" (Genealogical-geographical table [plate] of the relationships among plants according to Linnaeus's natural orders drawn by Paul Dietrich Giseke 1789) (Fig. 1.1), published also prior to and separately from the text. In a surprisingly modern style this copper engraving shows the Linnaean orders as circles of different sizes in relationship to the number of genera they were believed to comprise and arranged according to their presumed affinities, among them Giseke's Compositae, in fact as the circle with the largest diameter (the actual number of genera is indicated in the circle itself, which for Compositae is 120). It is a remarkable fact that Giseke is not known to have validated a single name within Compositae and is therefore listed in this contribution with some hesitation among the more important synantherologists.

When Giseke returned to Hamburg he was employed as a physician, and he became a professor of physics (meaning natural history) and poetry at the famous gymnasium of Hamburg. Giseke died on April 26, 1796 in his native town. The biographical notes on Giseke presented here were largely adapted from Schröder (1854), Schuster (1928), Hedge (1967), and Stafleu (1971).

Finally, we would like to briefly mention Ivan Ivanovich [Ivanovič] Martynov, the author responsible for coining the name Asteraceae, accepted under the current Botanical Code as the alternative name for Compositae. Little is known about the life and work of this Russian botanist born in 1771. In 1820, Martynov published a sort of botanical dictionary presenting information on terminology and nomenclature both in Latin and Russian. In this publication, *Tekhno-Botanicheskii Slovar*, Martynov (1820) validated the names of 99 plant families, Asteraceae among them, mostly through a Latinization of French names and making reference to validly published descriptions. Martynov died in 1833.

For a thorough list of all valid and invalid names applied to Compositae, see Hoogland and Reveal (2005).

JOSEPH PITTON DE TOURNEFORT (1656–1708)

Joseph Pitton de Tournefort (Fig. 1.2) was born in 1656, in the region of Aix-en-Provence. Tournefort had been interested in Botany since his youth, but his father had him pursue religious studies. When Tournefort was 22, the death of his father freed him from his religious endeavors, and from then on he devoted himself entirely to Botany. Often he collected plants in the southeast of France with Plumier. In 1679 he went to Montpellier where he followed Magnol's teaching. In 1700, Tournefort's most famous contribution, the *Institutiones Rei Herbariae*, was published (Tournefort 1700). It was an expanded Latin translation of an earlier French version entitled *Éléments de Botanique*. The *Institutiones* presented generic descriptions for more than 1500 genera of plants and displayed the encyclopedic knowledge that Tournefort had gained not only through the study of herbarium specimens but also through extensive traveling and collecting in Europe and SW Asia. Caesalpino influenced him in regard to using seeds and fruits in his classification, although he relied greatly on corollas for the definition of the main groups. Tournefort had no understanding of the role of the structures of both the androecium and gynoecium (Greene 1983). He did not believe in sexuality of plants, and this was a source of friction with Vaillant. However, the first use of the term 'pistyl' in its present sense is

Fig. 1.2. Joseph Pitton de Tournefort (1656–1708). [Engraving by L. Desrochers; courtesy of Hunt Institute.]

attributed to him, and he is recognized as one of the major contributors to the standardizing of botanical terminology in the 18th century (Stearn 1992).

With regard to his understanding of Compositae, Tournefort (1700) saw the group as a class divided into three families: *(1)* "Fleur à fleurons" (composed of species with discoid and probably disciform heads), *(2)* "Fleur à demi-fleurons" (composed of species bearing ligulate capitula), and *(3)* "Fleur radiée" (species with radiate heads). In his treatment, Tournefort included 35 detailed illustrations depicting some important groups of his native Europe, clearly showing he knew that the heads were formed by several florets, and in some cases different types of florets (Fig. 1.3). Appointed "démonstrateur et professeur de l'intérieur et de l'extérieur des plantes" at the Jardin du Roi in Paris, Tournefort died only seven months later on 28 November 1708 after a serious traffic accident in September in rue Coupeau [now rue Lacépède] near the garden. The biographic notes on Tournefort presented here were adapted from Duprat (1957), Greene (1983), and Bailly (1992: 59–126).

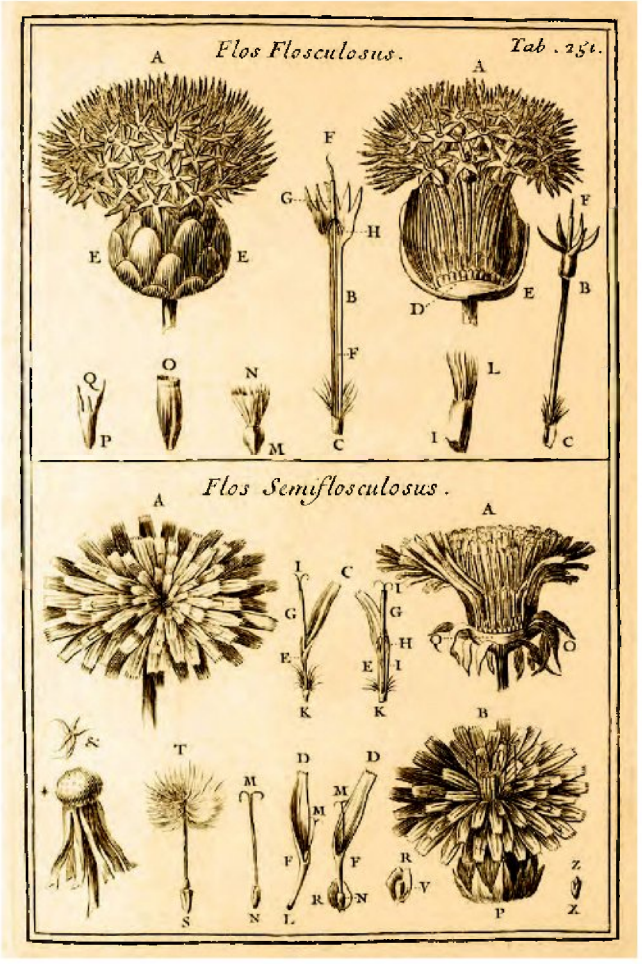


Fig. 1.3. Compositae as seen by Tournefort, in one of the 35 plates devoted to the family in *Institutiones Rei Herbariae*, showing impressive detail and accuracy. [Anonymous engraving taken from vol. 3, plate 251, courtesy of Smithsonian Institution, Cullman Library; for original figure legends, see Appendix C.]

SÉBASTIEN VAILLANT (1669–1722)

Another botanist, who made interesting contributions to the field, during what we call the 'pre-Cassini era', was Sébastien Vaillant. Vaillant (Fig. 1.4) was born on May 26, 1669 in Vigny, northwest of Paris. According to some accounts, Vaillant at age five started his own little garden in a patch of the family estate given to him by his father to grow plants he collected in the countryside around the house. One year later he was sent to study Latin and religion, where he was a very dedicated student. Apparently the strict discipline enforced by the instructors caused Vaillant to fear failure, so to avoid punishment he would use various techniques (e.g., putting a nail inside his night hat) so that he would sleep less comfortably and wake up earlier, in order to have more time to study. His dedication eventually led him to excel in all the subjects and to gain recognition from his tutors.

Vaillant's father, seeing the great progress that his son had made, sent him to learn music at Pontoise, an activity that Vaillant seems to have particularly enjoyed, quickly mastering the pipe organ and substituting for his master in public performances. During his free time as a musician Vaillant visited the local hospital and became increasingly interested in surgery. Later he decided to become a surgeon. He succeeded in his medical studies and after a few years of practicing surgery he met Tournefort and started studying botany. After a few classes in which he was shown plants and their names, he decided to dedicate himself entirely to botany, rapidly gaining a thorough understanding of the local flora that would eventually lead to his (posthumous) publishing of the *Botanicon Parisiense* (Vaillant 1727). In 1708, he obtained a position as "sous-démonstrateur de l'extérieur des plantes" at the Jardin du Roi, and it seemed he was very much appreciated as a teacher considering that his lectures were at six in the morning and attended by hundreds of listeners.

Vaillant is remembered as a strong supporter of sexuality in plants, and he apparently contributed to the spreading of these ideas in his lectures on the subject at the Jardin du Roi. A lecture on the structure and function of flowers held in 1717 was published one year later (Vaillant 1718) both in Latin and in French (see the translation in Bernasconi and Taiz 2002). This work was an important stimulus for the young Linnaeus, who would eventually base his classification system on the sexual organs of plants. In his treatment of Compositae (Vaillant 1719–1723),

Vaillant stressed the sex of individual florets but also used other characters derived from the phyllaries, receptacles, and pappus. He coined several new terms and presented magnificent illustrations of different parts of the heads and florets (Fig. 1.5). Vaillant divided Compositae into three groups; in addition to Cichorieae recognized by Tournefort, he identified Cardueae ("Cynarocéphales") and the rest of Compositae known at his time formed the remaining group known as "Corymbifères". Vaillant's contributions to Compositae made him the last serious contributor to the field before Cassini.

Sébastien Vaillant died in Paris on May 26, 1722, after suffering for several years from severe asthma, notably aggravated by excessive work. The biographic notes on Vaillant presented here were adapted from Hermann Boerhaave's preface to *Botanicon Parisiense* (Boerhaave 1727), from Small (1917), and Greuter et al. (2005). Additional information on Vaillant can be found in Rousseau (1970) and Bernasconi and Taiz (2002).

Fig. 1.4. Sébastien Vaillant (1669–1722). [Anonymous engraving taken from *Botanicon Parisiense*, courtesy of Missouri Botanical Garden Library © 1995–2009.]

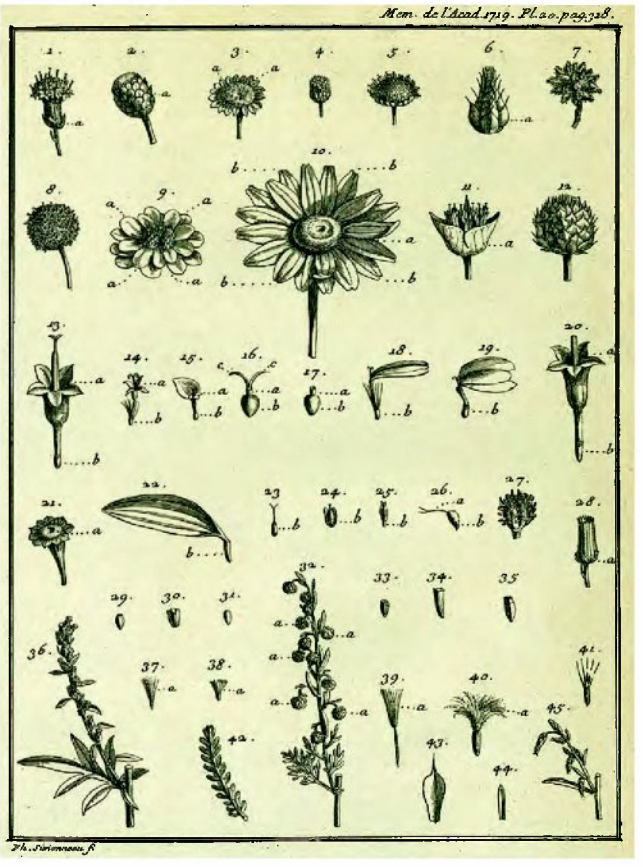


Fig. 1.5. Illustration showing different traits of "Corymbifères", the largest of the three groups in which Vaillant divided the Compositae. [Engraving by Ph. Simonneau f. taken from Vaillant's second contribution to Compositae in 1721, courtesy of Mertz Library at NYBG; for original figure legends, see Appendix C.]

JOHANNES LE FRANCQ VAN BERKHEY (1729–1812)

A short note on the Dutch naturalist Johannes Le Francq van Berkhey [Berkheij] seems appropriate since he was the first to write a book exclusively on the general features of Compositae. Berkhey was born on January 23, 1729 in Leiden and studied medicine there. His book, *Expositio Characteristica Structurae Florum qui Dicuntur Compositi* (1760) seems to be an expanded edition of his dissertation. In his *Expositio*, Berkhey (1760) described in great detail the characters of the capitula and flowers in Compositae, and their variability is shown in nine excellent copper plates (Fig. 1.6) based on his own sketches. Although the book shows good insight into the morphology of

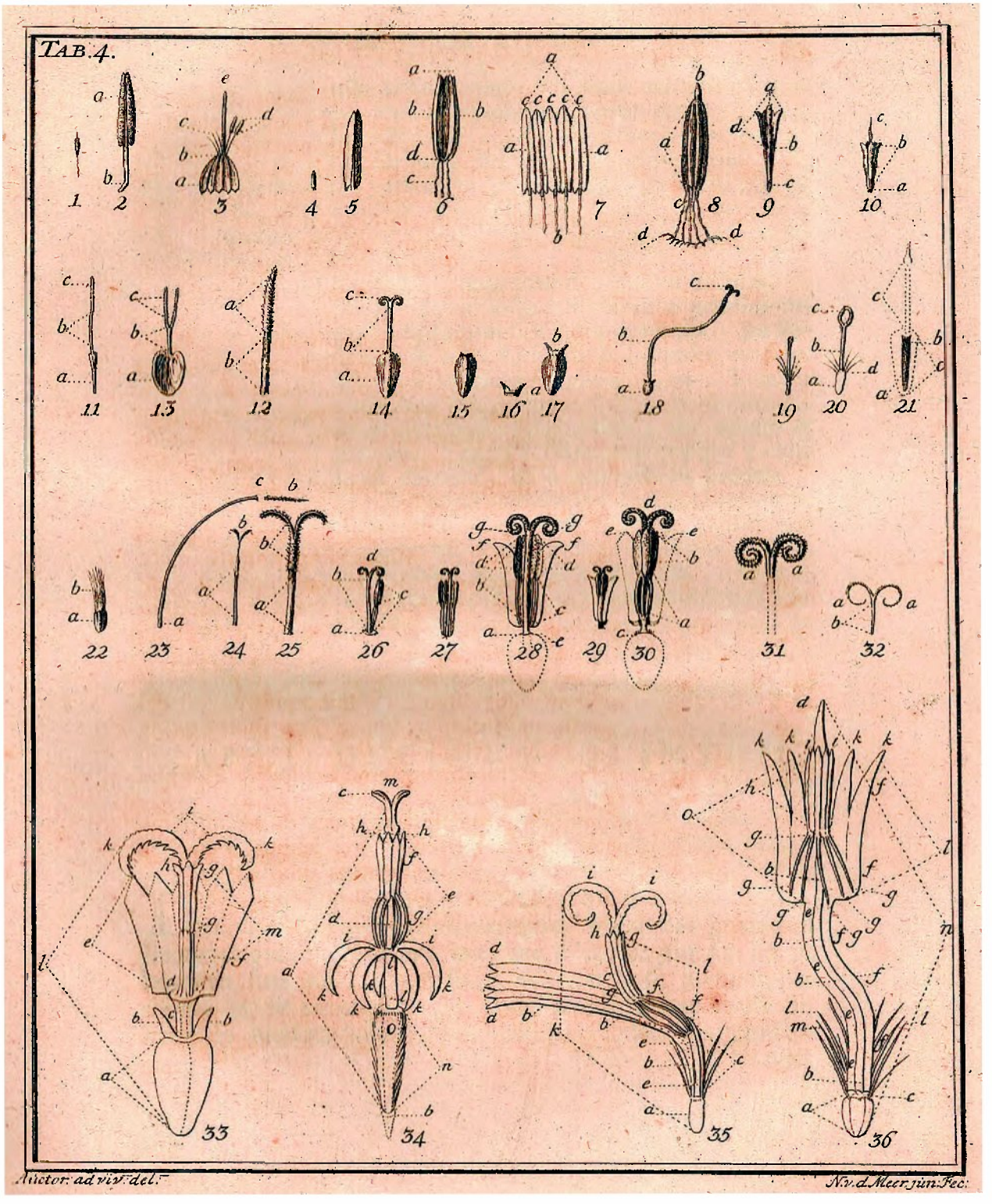


Fig. 1.6. Berkhey's *Expositio Characteristica Florum qui Dicuntur Compositi*, published in 1760 holds the status of the first book ever published exclusively about Compositae. This illustration, one of the nine magnificent plates depicting the family's morphological diversity known to him by the mid-1700s, shows Berkhey's acute level of understanding of Compositae. Berkhey's work inspired and challenged Cassini, who admitted he would have to work hard to surpass the Dutch naturalist. [Courtesy of Botanic Garden and Botanical Museum Berlin-Dahlem; for original figure legends, see Appendix C.]

the family, showing also some of the characteristic differences of the styles, it does not develop the ideas any further. Berkhey's *Expositio* was a rather rare publication, but it was known to Cassini who eulogized it generously amid some objective and constructive criticisms (Cassini 1818a). The *Expositio* inspired, and at the same time challenged Cassini's genius and he set himself to produce a more comprehensive treatise, which would eventually be destined to be more far-reaching than Berkhey's own. In Cassini's own words: "il [Berkhey] a rendu ma tâche difficile, parce que j'ai dû m'imposer l'obligation de le surpasser" (he [Berkhey] has made my task harder, because I had to impose on myself the obligation of surpassing him; Cassini 1818a).

Berkhey was a man of many talents, being known also as an artist and a poet. He was also a lecturer at the university of Leiden and wrote the monumental *Natuurlijke Historie van Holland* [Natural History of the Netherlands] in nine volumes, which unfortunately was never finished (e.g., two volumes including the part on plants were not published). Some unfortunate events towards the end of his life caused him to spend his later years in poverty and partially secluded from academic life. Berkhey died on March 13, 1812 in The Hague (The Netherlands).

The African genus *Berkheya* F. Ehrhart from the Arctotideae was named after him. This brief sketch on Berkhey was adapted from Aa (1859) and Zagwijn (2004); a wealth of information on the life and work of Berkhey can be found in Arpots (1990), and San Pío Aladrén (2007).

ALEXANDRE-HENRI-GABRIEL DE CASSINI (1781–1832)

Information on Cassini's life and work is scarce. Three of the few accounts are notable: a short biography written by Gossin (1834), an acquaintance from Cassini's judiciary circle, and located at the beginning of the third volume of Cassini's *Opuscules Phytologiques*; Cassini's own remarks at the beginning of the first volume of the *Opuscules* (Cassini 1826); and in footnotes in other works by Cassini (Cassini 1834). Cassini's work on Compositae is a masterpiece. His descriptions of organs are still valid and, for most cases, still interpreted in the same way he described and illustrated them almost 200 years ago. He is the true founder of detailed, rigorous, and systematic studies of Compositae. His modesty and respect for other botanists' works are shown repeatedly throughout his own works, but it is also evident from the comments of scientists who knew him.

It is thanks to King and Dawson (1975) and King et al. (1995a, b) that we have easy access to the amazing array of scientific works of Cassini which, for diverse reasons, appeared scattered in publications of various sorts, some of them rare and under restricted access today. These authors, working on an idea originally suggested by José Cuatrecasas, compiled most of Cassini's scattered publications in five volumes and presented them in three contributions entitled *Cassini on Compositae* I, II, and III.

A member of an illustrious family of French astronomers, Alexandre-Henri-Gabriel de Cassini (Fig. 1.7) was born on May 9, 1781, in the Royal Astronomic Observatory in Paris, the residence of his family since it was built, and four generations had lived there from the time his family had moved from its native Savoy to Paris during the reign of Louis XIV. When the revolution started, he was sent to Savoy to live with his uncle where he studied at the College of Nobles in Turin (today Italy, then the Kingdom of Sardinia). After the revolution, he returned to France, and between 1794 and 1798 he retreated to the family estate in the countryside in Thury (department of Oise) to study under his father.

It was during this time that Cassini developed his profound interest in Nature. Soon after he started observing his surroundings, young Cassini realized that he could not find in the current literature answers to many of his questions, and so he started to make observations, descriptions, and drawings of the plants, animals and fossils that were around him. Later on, following family tradition, he went to Paris to study astronomy. However, his zeal for natural history, especially botany, did not diminish, and during this time he studied botanical books, visited the Jardin des Plantes, and botanized around Paris.

According to Cassini, his lack of private fortune forced him to find an occupation that would allow him to make a living. He began to study law in 1804. He soon attracted the attention of M. Pigeau, one of his professors, who took him as an assistant and eventually a co-worker. Cassini started his career in the French judiciary system as Judge of First Instance and made his way through the system to the highest position, President of the Chamber. Under King Louis Philippe, Cassini was made 'Pair de France', then one of the most prestigious honorary positions in the country.

Cassini developed his ideas on Compositae during his leisure time. Through his *Opuscules* we learn why he eventually took up Botany from among the different fields of learning. In Cassini's own words: "The mineral kingdom was not varied and offered little interest where I lived. I also reluctantly abandoned very soon the study of animals, which interested me the most but caused me terrible disgust, because of the torments and suffering that had to be inflicted on these unhappy creatures. Therefore, I focused my entire attention on the living but insensitive beings that were so abundant around me, very variable and graceful, and that I could

Fig. 1.7. Alexandre-Henri-Gabriel de Cassini (1781–1832). [Engraving by Ambroise Tardieu; courtesy of the Department of Botany, Smithsonian Institution.]

mutilate, dissect and destroy without inspiring pity in me" [*Opuscules Phytologiques*, vol. 1, page ix]. He started studying Compositae in 1810.

In February 1812, Cassini married Agatha de Riencourt to whom he would remain loyally attached. He dedicated the genera *Agathaea* and *Riencourtia*, as a proof of his "*love, esteem, respect, and gratitude*" [*Opuscules Phytologiques* 1, page xv].

Cassini believed that, in order to truly understand the *système naturel*, it was necessary to study all the organs of a plant throughout all the species in the family without exception, and through all the phenological stages. Only after this gargantuan work has been completed could the true order of the plant groups be established. Therefore, Cassini envisaged studying one organ at a time (probably influenced by Adanson). He stated that once all the organs for Compositae were carefully described, it would be possible to tell which characters defined the groups more clearly. Cassini started his *Mémoires* with the description of the style because, according to him, this character was one of the best to infer the natural groups of Compositae. He acknowledged the fact that earlier botanists such as Jussieu, Richard, and Adanson all noticed the importance of this character, but he felt they had failed to extract all possible information from it. Cassini even presented a critique of the description of the styles by these botanists.

In April 1812, Cassini's "Observations sur le style et le stigmate des Synanthérés" was presented at one of the meetings of the Académie des Sciences. This work (Cassini 1813a) was greatly praised by Jussieu and Mirbel. Cassini believed (correctly) that the style was one of the characters with which the natural groups in Compositae could be identified. In this work, Cassini presented the descriptions of the shape and variations of the style throughout the whole family, setting a landmark in the study of the family. Cassini had a methodical way of recording his observations, giving a precise account of the genera and species he had observed in order to reach his conclusions. In a series of seminal papers that started with the one on styles and stigmas, Cassini would describe during the following seven years (Cassini 1813a–c, 1814, 1816a, b, 1817, 1818a, b, 1819a, b) the characters derived from stamens, corollas, achenes, and pappus (Fig. 1.8). In one of these papers, Cassini (1817) would lay out his first three principles governing the classification of Compositae, which he would expand the next year (Cassini 1818b) to include two extra principles. In this later paper, Cassini stated:

"1. The Compositae form so tight an assemblage, that it is absolutely impossible to divide it into a small number of large natural groups, and so in order to divide it naturally it is necessary to recognize 20 small groups or tribes.

2. The characters dividing these natural tribes are those that are based on the style, plus the stigma and sweeping hairs, stamens, corolla, and the ovary; other organs can only suggest generic characters.

3. The hermaphroditic flowers possess all the diagnostic characters that define the tribe they belong to.

4. It is impossible to assign diagnostic characters to the natural tribes except for those common in the family.

5. Many Compositae offer a mix of characters that are present in several different tribes."

In the course of the series of papers mentioned above, the survey of the different organs and the understanding of the whole group progressed at a steady rate, which lead Cassini to gradually improve his classification. At the beginning (Cassini 1813a–c) he adopted a rather conservative approach, taking up from Jussieu's classification a division of the family into three groups: Lactucées, Astérées, and Carduacées, dividing however, Astérées into nine sections. In his final classification scheme (Cassini 1819a) he would recognize 20 tribes (Table 1.1).

Most of the tribes recognized by Cassini still hold their status and are defined by the same characteristics he described near 200 years ago. Note how Cassini's placement of tribes agrees to a certain extent with current classification (in Fig. 1.9, circles in green represent tribes in a clade with lowermost branch containing Senecioneae; circles in orange represent lower branches of the tree, from Barnadesioideae to Corymbieae). Although not a novel idea, Cassini correctly placed Calyceraceae (Boopidées) as one of the closest relatives to Compositae; even his placement of the other relative, Campanulaceae, is not that far from reality, as it is currently placed in the same order Asterales. Cassini took the original idea of placing the families (or tribes in this case) in a linear sequence from Mirbel; however, to reconcile that Vernoniées and Lactucées, according to him closely related, ended up at the extremes of the linear sequence, he placed them in a circle. To show other relationships among the different tribes, he added additional lines to his diagram. The rooting of Cassini's scheme was misplaced, but in general tribes that are closely related were placed near each other. The lines connecting adjacent tribes (e.g., Centauriées and Carduacées) denote a very close relationship, more than mere contiguity would imply. Similarly, lines connecting more distant tribes denote more distant resemblances. Although when describing the figure, Cassini (1818b) mentioned Boopidées (Calyceraceae) and Goodenoviées (Goodeniaceae) as the two closely associated families, eventually he ended up publishing his figure placing Campanulaceae instead of Goodeniaceae. Cassini was not explicit on the reasons explaining why these families were placed close to Vernonieae and Lactuceae; however it seems likely that the discoid heads and the highly dissected actinomorphic corollas of mainstream Vernonieae played

a major part in his assignment of a relationship towards Calyceraceae. The zygomorphic corollas of Lactuceae, in addition to the presence of latex, so characteristic in this group, most assuredly pointed a sort of natural idea of relationship between this tribe and Campanulaceae or Goodeniaceae. According to Cassini the reasons behind his decision of placing Lactuceae side by side with Vernonieae, lay on the similar style (not shared with any other tribe) and the members of Vernonieae (*Gorteria*) with zygomorphic corollas that would set a natural transition between both groups.

A note of interest is that although Compositae was his main interest and the topic of most of his printed publications, Cassini also sought to apply his method of systematics to Gramineae, and he published miscellaneous works on other botanical topics.

In 1827, Cassini was elected and appointed *Académicien libre* at the Académie Royale des Sciences. When a cholera epidemic struck Paris in 1832, Cassini became infected and soon there was no hope for him. Alexandre-Henri-Gabriel de Cassini died on April 16, 1832, having been survived by his devoted wife and his caring father. As King and

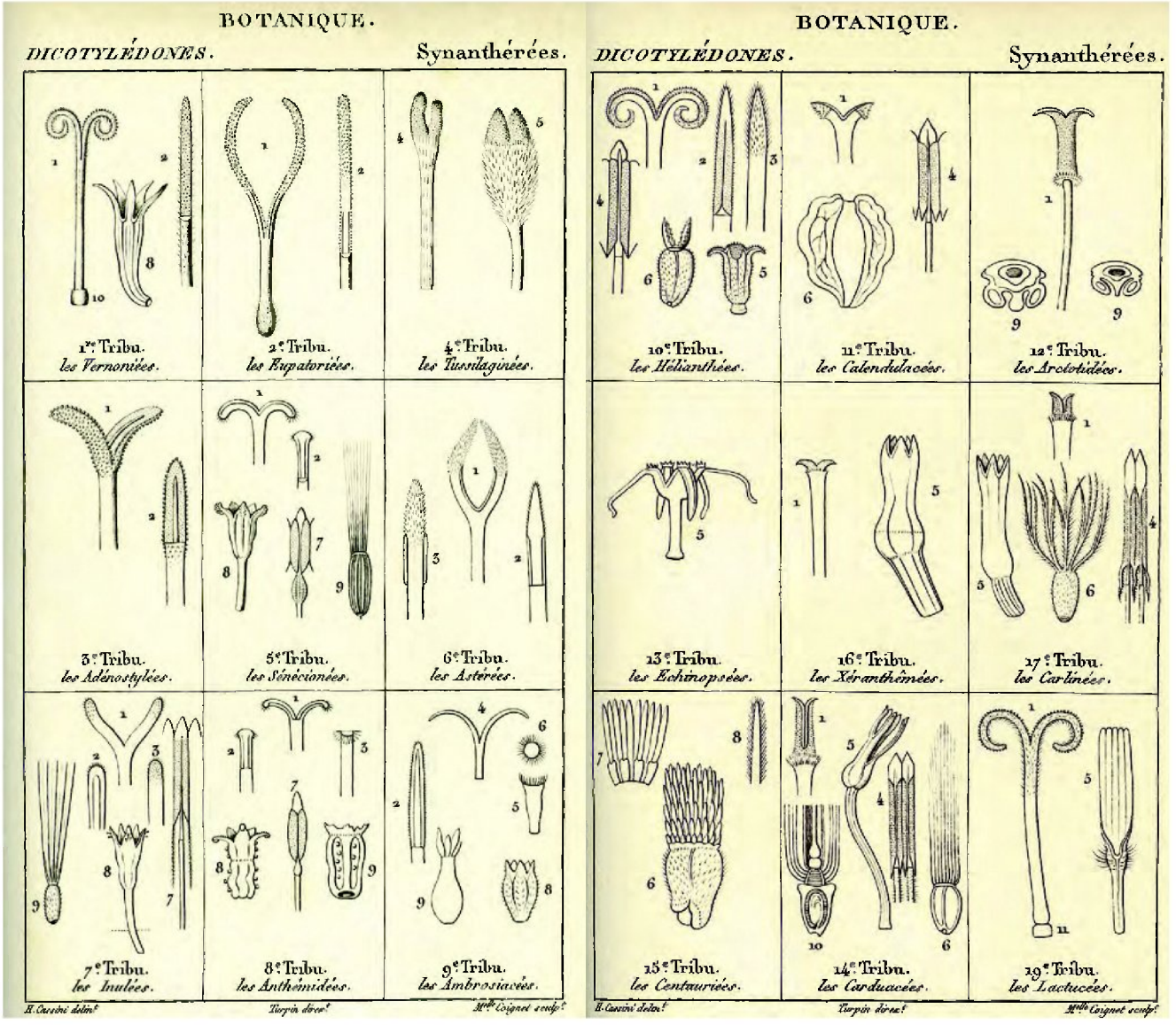


Fig. 1.8. Compositae as seen by Cassini, showing with remarkable skill and accuracy the defining traits of the tribes he recognized, most of which are still valid and defined by the same morphological traits. [Drawings by Cassini, engraving by Coignet, taken from *Opuscules Phytologiques*, vol. 1; courtesy of the Department of Botany, Smithsonian Institution; for original figure legends, see Appendix C.]

Dawson (1975) rightfully stated, because Cassini did not survive his father, he did not acquire the title of Count, which has often been assigned to him incorrectly.

Cassini's detailed descriptions of the styles, anthers, corollas, and achenes of Compositae led him to classify a complex group, which although recognized in the past, was internally in a state of chaos. When Cassini compiled some of the scattered articles that had appeared in different journals and the *Dictionnaire*, he authored the first books published on the classification of Compositae: *Opuscules Phytologiques* vols. 1 and 2, in 1826, only preceded as a book entirely dedicated to Compositae by the general book on the family by Berkhey in 1760. Cassini's generic concepts were rather narrow and comprised only a few closely allied species; also the materials he based his descriptions on correspond in some cases with plants taken from gardens, a situation that sometimes present problems for determination, which in turn can make typifications difficult. This, however, does not diminish the value of his studies; in many cases his genera eventually became sections of larger genera.

On the introduction to the (posthumously published) third installment of his *Opuscules* (Cassini 1834), dated May 9 of 1831, a rather somber Cassini proclaimed his definitive departure from the study of Compositae. The disputes with other botanists as well as the non-acceptance of his method by the current establishment and the indifference and dismissal of his classification by other

Table 1.1. During a period of six years, Cassini presented his classification of Compositae in a series of classic papers. From the table one sees the impact that his progressive study of more organs had on his classification. The modern flavor of his classification can be seen, which contains more than 15 tribes still recognized.

1813a–c 11 sects. + 1 unclassified	1814 12 sects. + 1 unclassified	1816 17 tribes + 1 unclassified	1817 19 tribes	1819a, b 20 tribes
Lactucées	Lactucées	Lactucées	Lactucées	Lactuceae
		Labiatiflores		
Carduacées	Carduacées	Carduacées	Carduinées	Carduineae
		Carlinées	Carlinées	Carlineae
			Centauriées	Centaurieae
		Xéranthémées		
		Echinopsées	Echinopsées	Echinopseae
Arctotides	Arctotides	Arctotidées	Arctotidées	Arctotideae
		Calendulacées	Calendulées	Calenduleae
				Tagétineae
Hélianthes	Hélianthes	Hélianthées	Hélianthées	Héliantheae
	Ambrosiacées**	Ambrosiacées	Ambrosiacées	Ambrosieae
Chrysanthèmes	Chrysanthèmes	Anthémidées	Anthémidées	Anthémidées
Inules	Inules	Inulées	Inulées	Inuleae
Solidages	Solidages	Astérées	Astérées	Astereae
		Sénécionées	Sénécionées	Sénécioneae
			Nassauviées	Nassauvieae
			Mutisiées	Mutisieae
Tussilages	Tussilages	Tussilaginées	Tussilaginées	Tussilagineae
			Adénostylées	Adénostyleae
Eupatoires	Eupatoires	Eupatoriées	Eupatoriées	Eupatorieae
Vernonies	Vernonies	Vernoniées	Vernoniées	Vernonieae
Hétérogynes*	Hétérandres*	Synanthérées non-classées*		

* Transitory (including unclassified species or genera); ** included as an addendum in the text discussion.

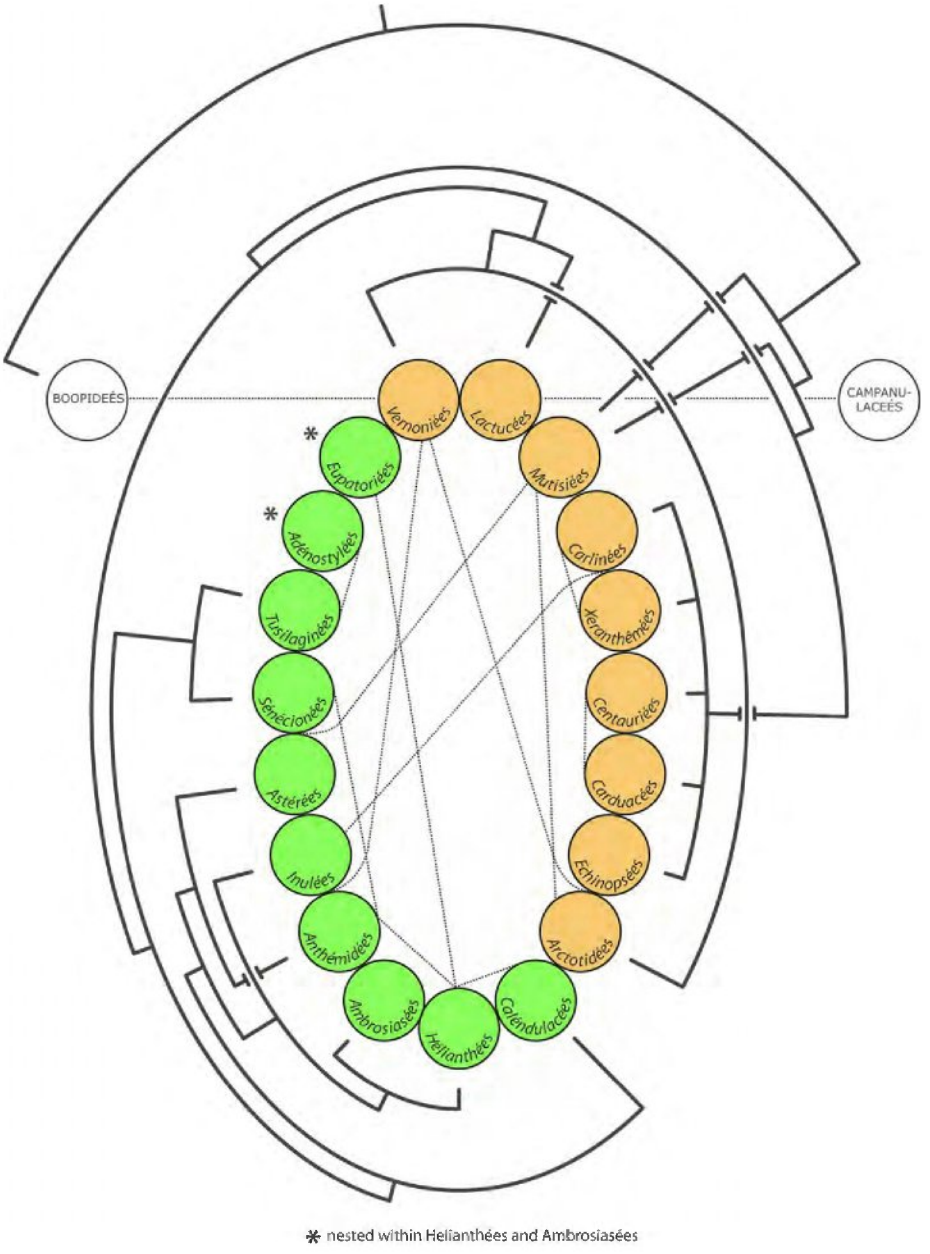


Fig. 1.9. Compositae classification by Cassini vs. current classification (cf. explanation in the text). [Modified from Cassini's *Opuscules Phytologiques*, vol. 1; circular tree adapted from the general tree for the family presented in Chapter 44.]

leading synantherlogists of his time (e.g.: Kunth and Lessing) most assuredly tired this remarkable man who withdrew from studies on the family.

Cassini's classification (Fig. 1.9) has been confirmed, to a considerable extent, by modern techniques (i.e., chromosome counts, phytochemistry, SEM & TEM examinations, and DNA sequencing), a clear reminder of all that can be done with careful observation and a simple microscope. Cassini is commemorated by the generic name *Cassinia* R. Br. (Compositae). The biographic notes on Cassini presented here were adapted from Gossin (1834) and Cassini (1826, 1834).

CHRISTIAN FRIEDRICH LESSING (1809–1862)

Christian Friedrich Lessing was born on August 10, 1809 in Polnisch-Wartenberg (now Syców, Poland), which at that time was part of the Kingdom of Prussia, and remained a part of Germany until 1945. Little is known about the life of this precocious Prussian botanist. We know that his brother, Carl Friedrich Lessing, was a celebrated painter and his grandfather, Karl Gotthelf Lessing, was the brother of the famous poet and philosopher Gotthold Ephraim Lessing and that Christian Friedrich pursued medical studies in Berlin and graduated in 1832.

Beginning as a schoolboy, he had a great love for botany and enjoyed roaming the countryside much to the dismay of his father. In his youth he was a stammerer, a condition that excluded him from many positions in public life.

Lessing's contributions to the understanding of Compositae appeared as a series of papers published in the journal *Linnaea* from 1829 to 1834, the first one completed when he was still a teenager. However, the publication for which he is best known is that of a separate work on the family, which included the second classification system proposed for Compositae (after Cassini's in 1813): *Synopsis Generum Compositarum Earumque Dispositionis Novae Tentamen Monographiis Multarum Capensium Interjectis*, which appeared in July–August 1832 (Lessing 1832). He assembled the material for this work in part during his travels, and notably from the rich collection of plants in the botanical garden and the herbarium in Berlin, specifically through study of the collections of Vahl, Bergius, Ecklon, Kunth, Thunberg and others. Importantly for South American workers, Lessing had access to collections by Sellow, which resulted in the description of several new genera from that continent.

In the *Synopsis*, Lessing (1832) presented his classification of Compositae, including a total of fourteen pages dedicated to characters that defined the family. Lessing stressed the importance of the style in the classification, depicting this character in four impressive illustrations on the diversity of this feature. He recognized only eight tribes.

Other papers by Lessing refer to Compositae deposited in the Berlin herbarium (Lessing 1829, 1830a, c, d, 1831d), Compositae of the Romanzoff expedition

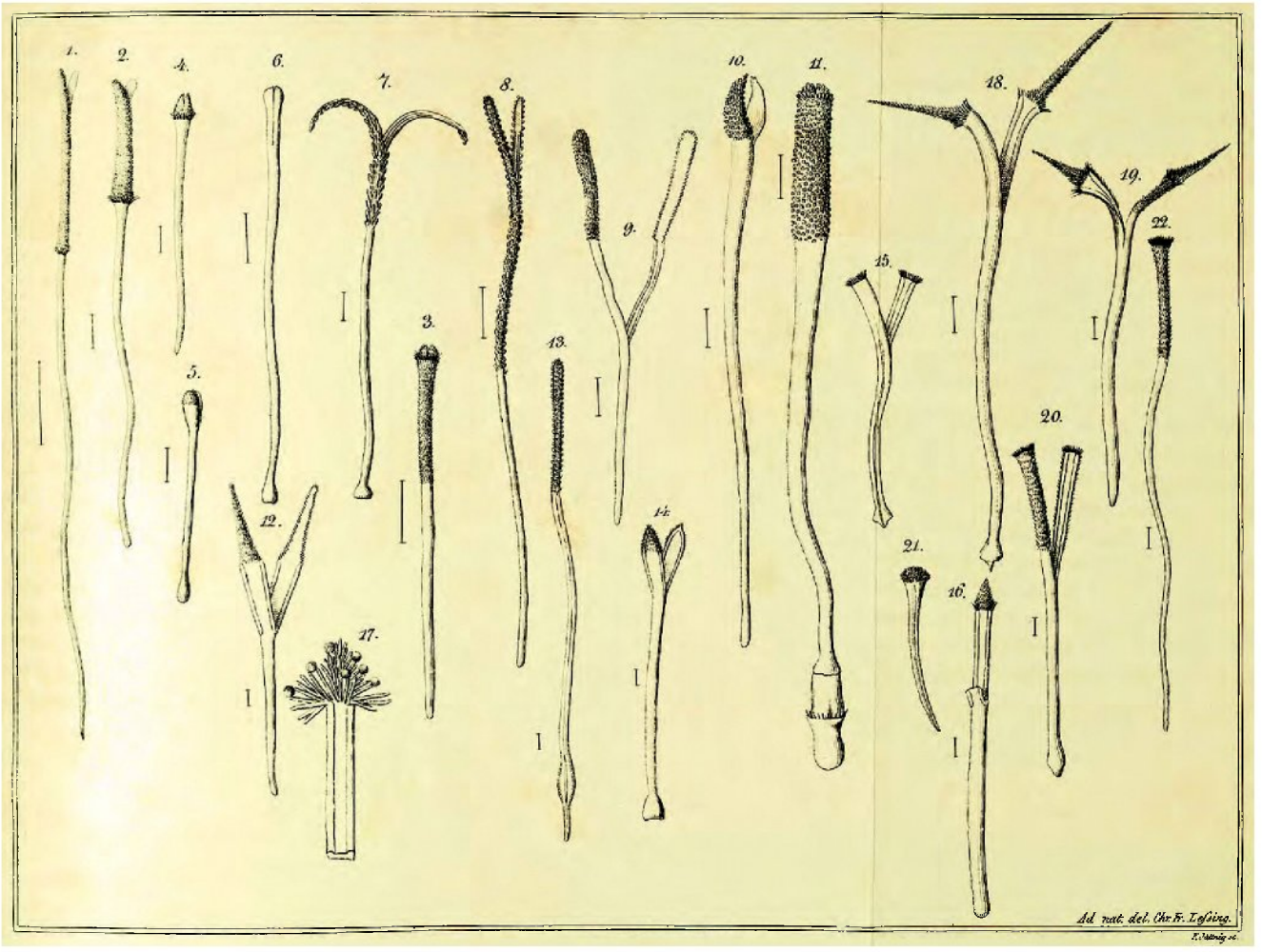
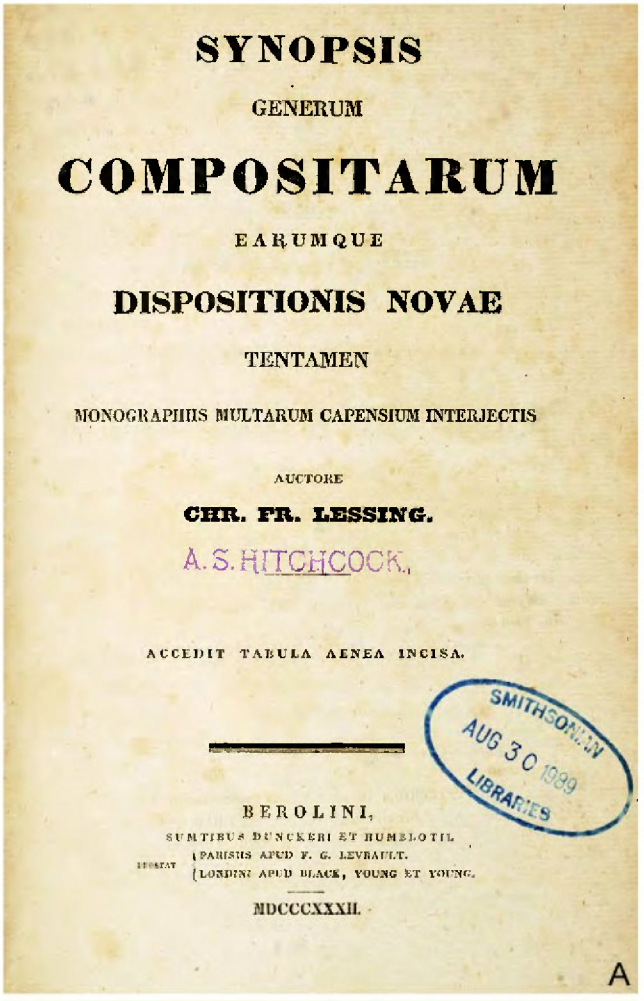


Fig. 1.10. Compositae as seen by Lessing, showing detailed morphology of styles, the character upon which he largely based his classification. [Drawings by Lessing, engraving by F. Jättnig, taken from Lessing's *Synopsis Generum Compositarum Earumque Dispositionis Novae Tentamen Monographiis Multarum Capensium Interjectis*, 1832; courtesy of Smithsonian Institution, Cullman Library; for original figure legends, see Appendix C.]

(Lessing 1831a–c), and Compositae from the collections of Schiede and Deppe in Mexico (Lessing 1830b). All these papers show a rigorous and detailed treatment of the plants considered. However, two notable characteristics of these publications deserve special mention. First, he included dichotomous keys for the identification of some genera and species; these keys are the first of their kind for the identification of genera in Compositae. Second, the illustrations (Fig. 1.10) he presented for the different characters defining the genera and the tribes are remarkable and only equaled by those of Hoffmann, which appeared almost 60 years later. Reading Lessing's work, it is evident that he based his own treatments on the findings of Cassini. However, it was remarkable that he accomplished such a large amount of work in such a short period of time.


SYNOPSIS

GENERUM

COMPOSITARUM

EARUMQUE

DISPOSITIONIS NOVAE

TENTAMEN

MONOGRAPHIIS MULTARUM CAPENSIUM INTERJECTIS

AUCTORE

CHR. FR. LESSING.

A.S. HITCHCOCK.

ACCEDIT TABULA AENEA INCISA.

BEROLINI,

SUMTIBUS DUNCKERI ET HUMBLOTII.

PARISIIS APUD F. G. LEVRAULT.

LONDINI APUD BLACK, YOUNG ET YOUNG.

MDCCCXXXII.

A

B

Fig. 1.11. A Title page of Lessing's 1832 book on Compositae; **B** Lessing's handwriting. [A, courtesy of Smithsonian Institution, Cullman Library; B, taken from *Webbia* 32: 14. 1977.]

In 1830 Lessing traveled for seven months in the Scandinavian countries and collected specimens, somehow managing to produce a published account of his travels, including the description of the geography and vegetation, and a flora of the places he had visited. All of this was published in a 300-page volume (Lessing 1831e).

Soon after publication of his Doctoral thesis, and his book on Compositae in 1832 (Fig. 1.11A), Lessing obtained a travel stipend from Alexander von Humboldt, and went to St. Petersburg, Russia, apparently with the intention of making his future living there. This same year, he went on a longer journey to Asiatic Russia, this time thanks to the support of the Prussian and Russian states. He then explored the flora of the southern Urals and the adjoining steppes. The results of this journey (Lessing 1834) would end up being Lessing's last printed contribution; he was only 25 years old.

In these first two years in Russia, Lessing became acquainted with Prince Pastievitch who hired him as a personal physician for his gold washing operations for a period of fourteen years. It was because of this activity that Lessing ended up in Krasnojarsk, Siberia. During this time in Siberia, Lessing learned the business of gold washing in detail and this new skill along with the success of his medical practice led him to resign his position with Prince Pastievitch and start his own gold-washing operation in the Altai. He was initially successful and joined with two Russian businessmen in order to expand his operations. This decision would later result in the loss of most of his fortune and he was left with only some real estate in Krasnojarsk. He withdrew to his remaining properties and resumed his medical profession.

Eventually he was given up as lost by his family as well as his botanical friends. According to some reports he became a beer brewer in his later years. This highly gifted man fell victim to the harsh conditions of Siberian life and the selfishness of false friends. All who knew him described his character as exceptionally noble. Christian Friedrich Lessing died on March 13, 1862 in Krasnojarsk, Russia.

At the beginning of his first publication (Lessing 1829) was the quote "Magno amore in familiam Synantherearum captus atque summorum virorum auxiliis gaudens, clar. Adalb. de Chamisso et D.F.L. de Schlechtendal, qui herbaria ditissima, et sua ipsorum et regia, eximia cum benevolentia et atque confidentia mihi aperuerunt statui hanc familiam fractare, nescius quousque ducar" [Seized by a great love of the family of Compositae I have undertaken to cope with this family. I was glad to have the support of excellent men, the famous Adalb. de Chamisso and D.F.L. de Schlechtendal. With extraordinary benevolence and confidence they opened to me their own

herbaria as well as the Regius herbarium, which are very rich. I do not know how far this will lead me"] and we find it inexplicable that after having so profusely declared his passion for Compositae that he should have abandoned it altogether. We can only speculate about the reasons that might have caused this highly gifted young botanist to distance himself from the study of Compositae and his family and friends. It is possible that losses in his gold mining speculations, and also his need to make a living in such a desolate region, may be the main reasons, but why did he remain in Siberia? All his papers appeared in a very short period, but after 1834 he never authored another paper on any subject.

Lessing is commemorated by the generic name *Lessingia* Cham. (Compositae). The biographic notes on Lessing presented here were adapted from Anonymous (1864), Wunschmann (1883), Herder (1888), and Buchholtz (1909). By far the most detailed report on his life is in a massive book by Buchholtz (1909) on the history of the Lessing family. Buchholtz had access to the archives and cites extensively from letters to the family and to the Secretary of the State (Minister) Altenstein. Our efforts to locate an image depicting Lessing failed, and we found only his handwriting (Fig. 1.11B). According to the information available to us and collected from Buchholtz (1909), Lessing refused his wife's wish to have him photographed.

CARL (KARL) HEINRICH SCHULTZ BIPONTINUS (1805–1867)

Born on 30 June 1805 in Zweibrücken, then Deux-Ponts, Department Mont-Tonnère, France, Carl Heinrich Schultz (Fig. 1.12) was the second son of the apothecary Carl Friedrich Schultz and his wife Marie Caroline. Since Schultz is an extremely common surname Carl Heinrich later on added the epithet "Bipontinus" (two bridges), referring to Bipontinum, the Latin name of his birthplace, hence the standardized author abbreviation "Sch.Bip."

Carl Heinrich grew up in a well-to-do family; among his uncles were Dr. Carl Ferdinand Schultz, physician in Zweibrücken, Dr. Fleschütz, physician-in-ordinary to Princess Therese of Saxony-Hildburghausen, Queen of Bavaria, and the famous Dr. Johann Gottlieb Fichte, professor of philosophy at Berlin University and its first rector. When Carl Heinrich entered the gymnasium in Zweibrücken, the Congress of Vienna had reshuffled Central Europe and his native town had become part of the Kingdom of Bavaria.

At age 20, Carl Heinrich moved to Erlangen, then also belonging to the Kingdom of Bavaria, where he started to study medicine and joined the Burschenschaft Germania. Because of the infamous Carlsbad Decrees, which had banned all student fraternities, this was both illegal and dangerous, in particular since the Germania clearly aimed for a political unification of the German speaking area and used the strictly forbidden colors black-red-gold. However, Carl Heinrich remained unharmed and later moved to Munich University where he not only continued his political activities but also finished his medical studies as early as 1829 and published a medical thesis. After having passed his biennium practicum with his uncle in Zweibrücken and as an assistant at the Hôtel de Dieu in Paris, Carl Heinrich passed his approbation examination in Munich and opened his practice in the Bavarian capital.

Nothing indicates that he took part in the Hambacher Fest, a festival celebrated in late May 1832 near Neustadt an der Weinstraße, then belonging to the Kingdom of Bavaria, with about 30,000 participants from all ranks of society, workmen, students and members of parliament. Although disguised as non-political county fair, liberty, civil rights and national unity were demanded with highly critical texts published in the local press. Political pamphlets printed in Zweibrücken and elsewhere were sent in some number to Carl Heinrich in Munich who rather unwisely made them freely available and even sold the rest to a bookseller. Back from an excursion to the Tyrol in Munich he was arrested, charged for high treason and in December 1832 found guilty of having attempted high treason as well as of committing an insult against his Majesty the King in the second degree. The sentence was severe: imprisonment of the second class for an unlimited period of time, then effectively sixteen years. A career seemed to have come to an end, in particular since Carl Heinrich' s name was listed in the Black Book of revolutionaries kept in Munich. In short he suffered a fate similar to that of the key figures of the Hambacher Fest.

The family's network of contacts plus the huge sum of 5000 guilders helped to speed up the release of Carl Heinrich, who after three years in jail returned in 1836 to his native Zweibrücken. He had learned his lesson, sent a letter of apology to the minister of the interior in Munich, and refrained from any further political activity. The same year Carl Heinrich was appointed physician of the hospital in Deidesheim, a small town in the Bavarian part of the Palatinate. For the rest of his life he maintained this position that came with an official residence in hospital. On 15 June 1837, Carl Heinrich married Carolina Giessen, the daughter of the owner of a local vine-growing estate, and had two sons and two daughters with her. He settled down in Deidesheim as a respected physician with a busy practice. His workload fluctuated depending on epidemics and the number of visits to the sick, infirm and dying, but otherwise peaceful years followed.

After a remarkably active life Carl Heinrich Schultz Bipontinus died on December 17, 1867 in Deidesheim, then Kingdom of Bavaria, and was buried in the local cemetery, survived by his two sons and younger daughter. He was also survived by his elder brother Friedrich Wilhelm, an apothecary and botanist in Wissembourg who had earlier fled his native town because of political reasons, his younger brother Wilhelm Eugen, an apothecary in Zweibrücken, and his elder sister Caroline Sophie.

Carl Heinrich seems to have developed an early taste for the natural sciences in Zweibrücken, which was further developed by the botanist Wilhelm Daniel Joseph Koch at Erlangen University. The excursion to the Tyrol was clearly a botanical one, later described in print. However, the focus on synantherology developed only later, in prison, with Julius Hermann Schultes the younger, physician in Munich, acting as his key contact. It is hard to believe but true that Carl Heinrich had not only books and letters sent into his confinement, but even Compositae achenes that he managed to raise in the prison court, a fact substantiated by a label in FI stating "culta in aula carceris regii monacensis Schultz Bip." [grown in the court of the Royal Prison in Munich]. Carl Heinrich was also permitted to send letters from prison to his botanical friends, the red lines in the four corners of the paper are evidence of the scrutiny of the censor. Even more surprising is the fact that Carl Heinrich had his first papers published while still an inmate of the infamous Fronsveste in Munich, dealing with Cichorieae, notably Hypochaeridinae.

Fig. 1.12. Carl (Karl) Heinrich Schultz Bipontinus (1805–1867). [Photograph taken from Portrait Collection, courtesy of Botanic Garden and Botanical Museum Berlin-Dahlem.]

When finally released he continued with synantherology, apparently as a hobby and alternative to his busy practice. Based in the tiny town of Deidesheim, Carl Heinrich could not rely on an institutional infrastructure but rather had to build up his own herbarium and library. This he started by asking fellow botanists for duplicates and by maintaining an extensive correspondence with many of his colleagues and the main collectors of his time, among them Willibald Lechler, Gilbert Mandon, Eduard Rüppell, the Schlagintweits, Friedrich Sello, Jules Pierre Verraux, Hugh Algernon Weddell, to name a few. Remarkably, Carl Heinrich also grew very many species from seed in a garden at Deidesheim, possibly the hospital's, and had herbarium specimens prepared from them. Little is known about his travels; he visited Vienna in 1856, London in 1866 and must have been to the Royal Herbarium in Berlin since his private herbarium contained very many fragments from specimens kept in the latter institution, including some taken from the Willdenow Herbarium. There is evidence that he also attended several meetings of naturalists in Central Europe where he lectured, mainly on Compositae.

Carl Heinrich studied the whole geographic and taxonomic range of this family, in particular Cichorieae, and published widely and extensively, mainly in journals, e.g., *Flora*, *Linnaea*, *Bonplandia* and *Jahrbuch der Pollichia*. An important contribution to the systematics of Anthemideae was his paper "Über die Tanaceteen" (Schultz Bipontinus 1844), dedicated to his mentor and friend Koch containing a new circumscription of genera such as *Chrysanthemum* L. and *Matricaria* L. using mainly fruit characters.

Several of the generic names he coined have stood the test of time; among his larger genera are *Critoniopsis* Sch. Bip., *Fleischmannia* Sch. Bip. and *Tripleurospermum* Sch. Bip. However, many other names remained unpublished and were validated by subsequent workers, which results in a long list of names having "Sch. Bip. ex" as author citation, e.g., *Laggera* Sch. Bip. ex Koch. The reason for this is not entirely clear, but the busy practice seems to have been an important cause. Overwhelmed by the steady flow of collections reaching him from all over the world, he often only published preliminary lists of names. Carl Heinrich's suprageneric and infrageneric entities are a nightmare for the monographer, being often both chaotic and confused. His single account for a flora is the treatment of Compositae for the *Histoire Naturelle*

des Iles Canaries published between 1844 and 1850 in several installments by Philip Barker Webb and Sabine Berthelot in Paris. An extensive series of letters by Carl Heinrich to Webb on this subject is kept at the Museo di Storia Naturale in Florence, all now available on the Internet but not yet analyzed. Similarly very many more letters by Carl Heinrich, mostly in French or Latin, still await further study, e.g., those kept in the Conservatoire Botanique in Geneva, the Pfälzische Landesbibliothek in Speyer and elsewhere. Carl Heinrich published little outside Compositae. Clearly he simply did not have the time to write a magnum opus like his colleagues placed in more comfortable circumstances. With the exception of his paper "Beitrag zum Systeme der Cichoriaceen" (Schultz Bipontinus 1866), a critical synopsis of Cichorieae aiming at a global approach, his contributions refer as a rule to a single genus or a small group of genera.

After Koch's death in 1849, his chair at Erlangen University became vacant. In order to impress the selection panel Carl Heinrich seems to have quickly validated the generic name *Erlangea* Sch.Bip., and indeed the senate proposed him as full professor to the ministry responsible for university affairs in Munich. However, the ministry of the interior vetoed this move because of Carl Heinrich's political past and the whole affair came to nothing. In 1840, Carl Heinrich was among the cofounders of an association named Pollichia, which continues to the present day as the Palatinate's society to promote the study of natural history and the preservation of the country. Since 1843, he was a fellow of the famous Leopoldina, the Imperial Academy of Natural History and Medicine then based in Breslau (Wrocław) with the cognomen Henri Comte Cassini. He was made an Adjunkt [member] in 1853 and in 1865 received the order of St. Michel first class of the Kingdom of Bavaria. Late in life Carl Heinrich distributed a series of exsiccate under the title "Cichoriaceotheca", with sets in several major institutions.

Upon his death Carl Heinrich's library was sold to a bookseller in Frankfurt and broken up, while his priceless herbarium, probably the most comprehensive collection of Compositae then in existence, passed to his elder son Carl Heinrich, a wine merchant in Deidesheim. He sold it to Ernest Saint-Charles Cosson in Paris who seems to have kept it intact. In 1904, Ernest Saint-Charles's grandson Ernest Armand Durand presented his grandfather's and Carl Heinrich's collections to the Muséum National d'Histoire Naturelle in Paris where it was integrated into the Herbier Général. The specimens from Carl Heinrich were mounted with a note "Herb. Schultz Bip." added to the sheet along with all his manuscripts and annotations; this trove of information is not yet fully appreciated by many synantherologists. Specimens annotated by Carl Heinrich in his characteristic hand are often difficult to decipher; they are found in many herbaria, in particular Florence, where Webb's collections from the Canary Islands are preserved.

Carl Heinrich is commemorated by the generic name *Bipontia* S.F. Blake = *Soaresia* Sch.Bip., nom. cons. (Compositae). The biographic notes on Schultz presented here were adapted from Anonymous (1868), Becker (1932), Poeverlein (1905), Remling (1847), Spilger (1942), and Strebel (1955).

GEORGE BENTHAM (1800–1884)

Son of Samuel Bentham, a well-known British naval architect, George Bentham (Fig. 1.13) was born in Plymouth, England, on September 22, 1800. When Bentham was only five, his father was asked to build vessels for the British navy in Russian dockyards so the family moved to St. Petersburg. While in Russia, George Bentham quickly learned Russian and French, and also became interested in music. When war broke out between Russia and England in 1807, the family swiftly returned to England where they lived till 1814.

Bentham never attended school, and his education (and that of his brothers) was carried out at home through private tutors as well as his parents, who always engaged their children in varied cultural activities. It is perhaps because of this circumstance, which Bentham later regretted, that he remained a rather shy individual for the rest of his life.

After Napoleon was defeated by the allies and peace returned to continental Europe, the Benthams moved to France. Now that George's father had retired, they decided to enjoy the better climate of the continent, and at the same time they would offer their children a better education, since living abroad was much more affordable than in their own country.

The portraits of Bentham depicting him with a rather sober expression can be misleading in terms of showing his true character. Throughout his life he enjoyed getting together with friends after work and attending concerts and plays. Apparently Bentham was fond of music and theater, and even a performer of both. He seems to have particularly enjoyed the long festivities of the French Carnivals during his youth, hardly missing a single dance.

In 1817, Bentham's mother introduced him to botany when she bought De Candolle's *Flore Française* (Lamarck and De Candolle 1805) to understand the plants surrounding their recently acquired estate in southern France. Bentham was struck by the synthetic way in which the information to identify the plants was presented, and immediately started to use De Candolle's flora to identify the plants near his house. In Bentham's words, "I had not the slightest idea of what was meant by any of the commonest botanical terms. All these I had to work out

from the introduction, and I spent the whole morning over the *Salvia*...."

Bentham's mother was also responsible for introducing young George into drying and preserving specimens, and he did a considerable amount of collecting during the rest of his time in France. In later years, Bentham received copious amounts of specimens from almost anywhere, becoming involved with several floristic treatments around the world. He corresponded with nearly all botanists of his time, and he visited most European colleagues at least once.

In 1826, Bentham had decided he would dedicate his life to law and science, the first to make a living and the second for recreation. That same year the family returned to England. Bentham devoted himself to the study of law and to help his uncle in his writings on logic, relegating botany for evening hours or other spare time. However, after getting married in 1833 he soon found out that it was unlikely that they would have children, and since their income was sufficient for a moderate life style, Bentham left law, and dedicated himself exclusively to botany.

Fig. 1.13. George Bentham (1800–1884). Portrait taken just before Bentham started his major undertaking, the *Genera Plantarum*. Notice Bentham's signature at the bottom and year the picture was taken. [Photograph courtesy of Hunt Institute.]

It is impossible to present a full account of Bentham's published accomplishments in this short chapter. Among his major contributions, the most well-known one is probably *Genera Plantarum* published in co-authorship with Joseph Dalton Hooker over a span of almost 20 years. This work, together with the unfinished *Prodromus* edited by the two De Candolles (De Candolle and De Candolle 1824–1873), Kunth's *Enumeratio* (Kunth 1833–1850) and Engler and Prantl's *Die natürlichen Pflanzenfamilien* (Engler and Prantl 1887–1915) ranks among the four most important taxonomic productions of the 19th century. Bentham also contributed to De Candolle's *Prodromus* (De Candolle and De Candolle 1824–1873), most notably treatments of Ericaceae, Labiatae, and Scrophulariaceae among several other minor groups during the years 1838 to 1864. In addition, mention should be made of Bentham's participation in yet another important botanical enterprise of the 19th century, Martius' *Flora Brasiliensis* with the treatment of Leguminosae from 1859 to 1876.

If this short list of only the major botanical enterprises with which Bentham was directly involved is not sufficient proof of his impressive efficiency and unparalleled capacity, along with the already-mentioned publications, we can add that he produced, in a period of fifteen years, *Flora Australiensis* (Bentham 1863–1878), a monumental treatment of some 8400 species extending over 4000 pages arranged in six massive volumes, all without a co-author.

Bentham's treatment of Compositae in the *Genera* (Bentham 1873a) is considered a classic and an unavoidable reference for any researcher of the family. Together, with Hoffmann's treatment, they constitute the two most important references at the generic level for the family extending over more than a hundred years. As a companion to his treatment, he also published a paper on the classification, history and geographical distribution of the family (Bentham 1873b). In this interesting paper, Bentham presented an account of his system and acknowledged that his system was in a way similar to that of Cassini's, having used basically the same characters, stating however that he had arrived at these conclusions independently.

Joseph Dalton Hooker (Fig. 1.14), friend and colleague in the herculean undertaking of the *Genera Plantarum*, said of Bentham: "It is difficult to give an idea of the

Fig. 1.14. Hooker and companions on a field trip in the Rockies, La Veta Pass, Colorado, 1877, 9000 feet. Left to right seated: Sir Joseph Dalton Hooker, Professor Asa Gray, Mrs. Strachey, Mrs. Asa Gray, Dr. Robert H. Lambourne, Major-General Richard Strachey and Dr. F.V. Hayden. Mr. James Stenson is standing between Dr. Lambourne and General Strachey. Although Bentham was mainly responsible for Compositae in the *Genera*, as well as for many other groups, he remarked that all changes or new proposals in the *Genera* were done in consultation with his co-author. Asa Gray (1810–1888) was one of the pillars upon which North American Botany was erected. Although Gray's field of action encompassed the whole plant realm, he started his work as a botanist on Compositae and contributed with many works on the family. A thorough account on the life and work of Asa Gray is found in Dupree (1959). [Photograph reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.]

prodigious amount of systematic and descriptive work in phanerogamic botany that Bentham accomplished. In the *Genera Plantarum* there is hardly an order of any importance that he did not more or less remodel. His labours on the Compositae, Gramineae, Cyperaceae, and Orchidaceae are especially noticeable … His treatises on the Leguminosae are no less exhaustive and valuable; and there is not a temperate or tropical region of the globe whose floras have not been largely elucidated by him … Of his amiable disposition and his sterling qualities of head and heart it is impossible to speak too highly, though cold in manner and excessively shy in disposition, he was the kindest of helpmates and most disinterested of labourers for others."

The capacity for work that Bentham showed throughout his lifetime is one of monumental proportions as evidenced by his published record and Hooker's comment. A very inspiring note on this, however, can be found in one anecdote mentioned by Jackson in his biography of Bentham: "On Saturday, 8th August, he [Bentham] finished the work on Orchidaceae for the *Genera*, half-an-hour before the close of his day's work. Most men would have put down their pen with a sight of relief and attempted nothing fresh for the moment; not so Bentham. Without a moment's hesitation he begged one of the assistants to bring him the unnamed and doubtful specimens belonging to the next part of his task [the Cyperaceae], on which he at once commenced."

After living a long and eventful life, George Bentham died in London on September 10, 1884, just a few months after the completion of the *Genera Plantarum*.

Bentham (1873b) said of Compositae, "[They] are at once the largest, the most distinct, and the most uniform, and therefore the most natural, of all orders of Pharenogamous plants … the principal changes I have proposed in the general methods of Lessing and De Candolle [on Compositae] were determined upon and worked out long before I was aware that they were in a great measure a return to that of Cassini. The confusion which his multiplication of names had produced, and the unusual terminology of his descriptions, had excited in my mind a prejudice against him, until, after completing my work of detail, I came to study his generalizations, which showed how much better his views of affinities coincided with mine than those of his successors." Bentham will always be remembered as one of the greatest botanists of all times, and he was responsible for bringing Cassini's earlier works to the attention of the Compositae community. The biographic notes on Bentham presented here were adapted from Filipiuk (1997) and Jackson (1906).

KARL AUGUST HOFFMANN (1853–1909)

Karl August "Otto" Hoffmann was born on October 25, 1853, in Beeskow, Brandenburg, Prussia. We know very little about the life of this talented Prussian botanist who in 1872 went to Berlin University to study mathematics and natural history. Later on, he attended Göttingen University for his graduate studies; he received his Doctorate degree in February 1876, though not in botany, his thesis was on "spherical curves", a mathematical subject. Hoffmann's strong interest in mathematics during his time as a student did not deter him from devoting important time to botany. He did much more on the subject than merely attend the official field excursions, clearly defining the future of his academic botanical endeavors.

Hoffmann's contributions to botany had one striking similarity with that of Cassini's: his scientific activities, and specifically his studies on Compositae, were undertaken during whatever "spare" time he had left from his main occupation. In Hoffmann's case, he was a high school teacher. He started as a private teacher in Dresden and, beginning in October 1877 until the end of his life, he taught at the prestigious Friedrichswerdersche Gymnasium in Berlin.

He collaborated with his mentor, Wilhelm Vatke, in the study of the voluminous material from J.M. Hildebrandt from Madagascar. Later on, Hoffmann worked on some other families from the rich collections of Rutenberg, also from Madagascar. He then continued to study material collected by Major von Mechow and Teusz from the interior of Angola.

However, it is in Compositae that Hoffmann produced most of his work, and in which, within a few years, he gained a deep knowledge. He benefited from the copious material he received from travelers such as Dusen, who collected in Patagonia and Tierra del Fuego, and Chevalier, who sent him specimens collected in Sudan, but also from his own hard work.

Hoffmann published several papers on the family, but his major contribution was the treatment of Compositae in the monumental *Die natürlichen Pflanzenfamilien*, edited by Engler and Prantl (Hoffmann 1890–1894). Hoffmann's classification was very similar to that of Bentham's, but his work included new information generated since Bentham's treatment was published. His treatment also differed from that of Bentham in the impressive inclusion of 108 notably detailed figures illustrating the diversity across the family (Fig. 1.15A, B). Hoffmann's work included 806 genera and constituted the last treatment at the generic level for Compositae for a hundred years until the cladistic treatment of Bremer (1994) and the revision edited by Anderberg et al. (2007).

Hoffmann published numerous individual papers as well, and in a later publication he discussed the differences between his classification and that of Bentham. Further data were published as two "Nachträge" to the *Die natürlichen Pflanzenfamilien* (1897, 1900). Due to a lack of time, he was not able to contribute to "Nachtrag III" edited by R. Pilger in 1908. Hoffmann donated his extensive and well-curated herbarium to the Berlin Herbarium. The well-known traveler and explorer-botanist R. Schlechter named a genus from western Africa, *Hoffmanniella* (Compositae), after Hoffmann.

Hoffmann was also an extraordinarily talented musician, a good husband, and an understanding father. He died on September 11, 1909 following an appendicitis operation, almost certainly in Berlin. An image of Hoffmann still remains elusive despite looking up several sources and consulting several colleagues around the globe. The biographic notes on Hoffmann presented here were adapted from Ascherson (1910).

BENJAMIN LINCOLN ROBINSON (1864–1935)

Benjamin Lincoln Robinson (Fig. 1.16) was born in Bloomington, Illinois on November 8, 1864, the youngest of eight children. He was one year younger than his brother, the historian James Harvey Robinson. He had an early interest in natural history, entered Williams College in 1883, and transferred to Harvard College in 1884, graduating in 1887. He married Margaret Louis

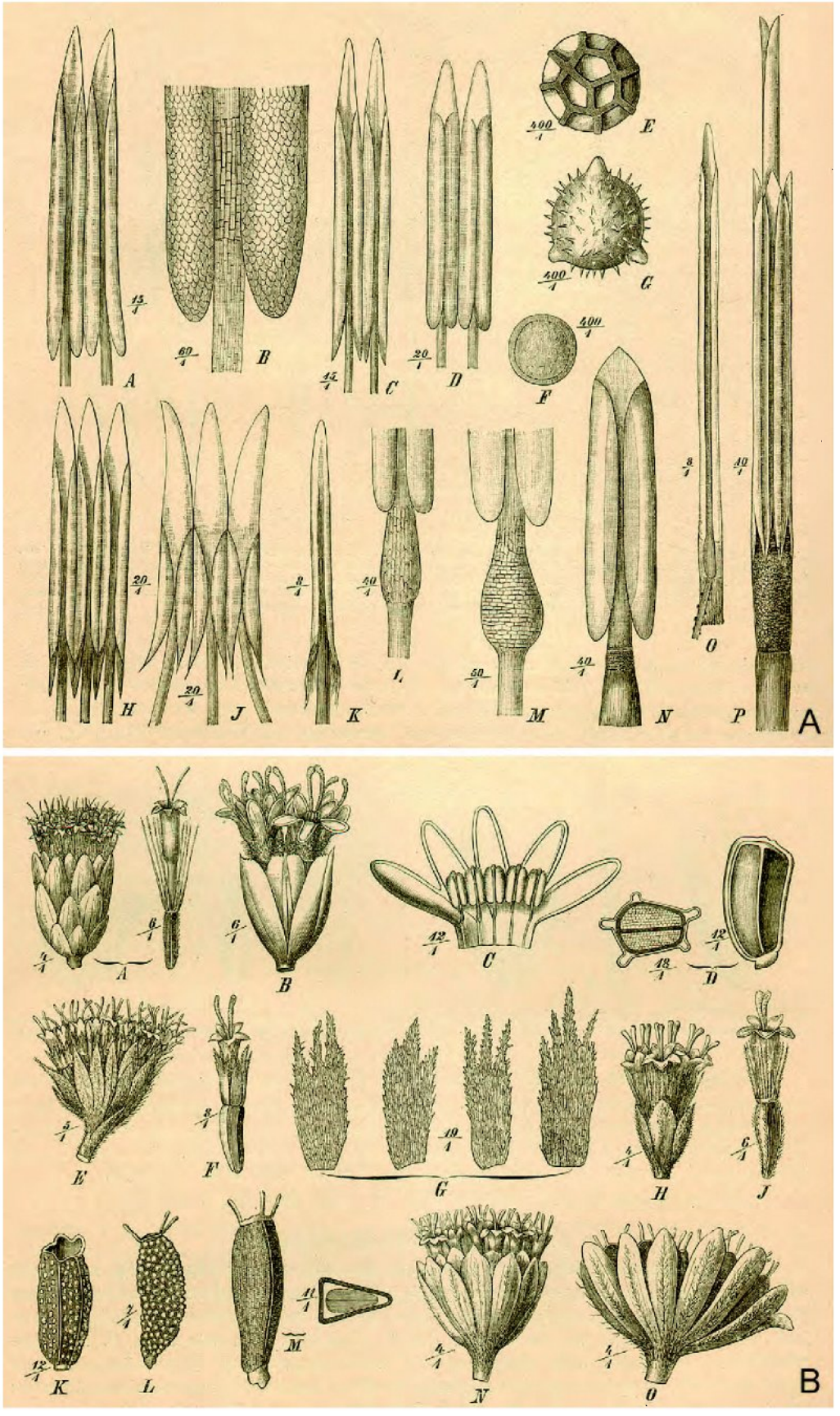


Fig. 1.15. Illustrations from Hoffmann's treatment of the Compositae for Engler and Prantl's *Die natürlichen Pflanzenfamilien*. These two figures, out of the 108 figures accompanying the text, show Hoffmann's detailed understanding of morphology in Compositae. **A** anther and pollen morphology; **B** plate depicting several Eupatorieae genera with a high degree of detail on pappus and achene structure. [From *Die natürlichen Pflanzenfamilien* 4(5); A, figure 65, page 104; B, figure 77, page 132; courtesy of MVFA herbarium; for original figure legends, see Appendix C.]

Casson in Hennepin, Illinois, and had a single child who lived only a few years. Robinson pursued graduate work at Strassburg University where he studied with Hermann Graf zu Solms-Laubach. His disseration was on plant anatomy and he graduated in 1889. Robinson returned to Cambridge, Massachusetts in 1890 where he became an assistant to Sereno Watson, then Curator of the Gray Herbarium at Harvard. He retained enthusiasm for Germanic culture and for some years conducted a course in scientific German. In 1892, Robinson was appointed successor to Sereno Watson upon the latter's death. In 1899, Robinson became the first incumbent of the Asa Gray Professorship of Systematic Botany established through a gift from Mrs. Gray.

During more than thirty years at the Gray Herbarium, Robinson improved the facility, greatly increased its budget, served as editor of the journal *Rhodora*, brought into final form the extensive manuscripts covering many families of plants in Gray's *Synoptical Flora of North America* (Gray 1878–1897), published extensively on Mexican collections of Pringle and Palmer, and completed the seventh edition of *Gray's Manual* (Robinson and Fernald 1908). Robinson encouraged collecting efforts in South America and his collaboration with South American botanists lead to his election as honorary academician of the Museo de La Plata (Argentina). In North America, Robinson was president of the Botanical Society of America (1900), vice-president of the American Association for the Advancement of Science (1905) and a member of the National Academy of Sciences.

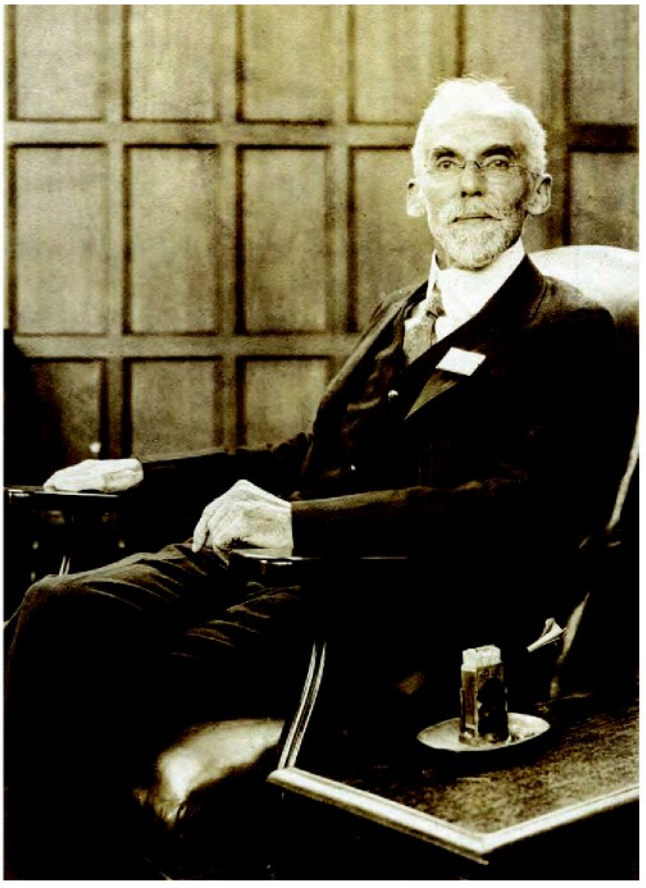


Fig. 1.16. Benjamin Lincoln Robinson (1864–1935). Photograph taken in 1926 at 4th International Botanical Congress, Ithaca, New York. [Courtesy of Hunt Institute.]

Robinson visited Europe a number of times to study type material. During International Botanical meetings, Robinson served as a member of the Commision internationale de Nomenclature botanique in 1905, as President of the International Botanical Congress at Brussels in 1910, and as a member of the Commission de Nomenclature général in 1926. Robinson was a corresponding member of the Deutsche Botanische Gesellschaft, of the Botanischer Verein der Provinz Brandenburg, a member of the Société de botanique de Genève, a foreign member of the Linnean Society of London, and a member of many other organizations.

Much of his research was devoted to the study of the Compositae tribe Eupatorieae. This included his treatments of *Eupatorium* and *Ophryosporus* in "Trees and shrubs of Mexico" (Standley 1926), and many other treatments cited in the latter work by S.F. Blake, including with Jesse Greenman on *Verbesina*. Robinson produced a series of studies on *Eupatorium*, *Mikania*, *Stevia*, and other genera for various countries in South America (see King and Robinson 1987). Benjamin L. Robinson was well aware of the artificiality of the system of classification within which he worked, for instance, in 1913 he included in the genus *Alomia* Kunth an element that he himself acknowledged was an epappose representative of *Trichogonia* DC. He (1926) comments in his description of the Mexican *Eupatoriun rivulorum*: "This species in habit, habitat, foliage, and in some details of pubescence recalls *Fleischmannia arguta* (Kunth) B.L. Rob. The species if referred to *Fleischmannia* would by its indefinite (though not very numerous) pappus bristles, break down the slight distinction between that genus and *Eupatorium*. If, on the other hand it is referred to *Eupatorium* (from which on technical grounds it cannot be readily separated) its close similarity to *Fleischmannia* must render the further separation of that genus rather artificial. Neither disposition is entirely satisfactory." In discovering that his *Eupatorium dejectum* was the same as *Helogyne tacaquirensis* Hieron., Robinson (1930) questioned the distinction of the latter genus. The genera that Robinson questioned have proven to be distinct, but only after severe redelimitation of *Eupatorium*, an operation that Robinson never undertook. Robinson understood that when using an artificial system, it had to be used rigorously even in defiance of obvious relationships. The fact that Robinson found the Bentham

system highly artificial at the generic level was not a surprise. By all indications, Bentham himself was fully aware of the artificiality of his system at various levels.

Robinson did very little fieldwork, apparently never visiting tropical America on whose flora he worked extensively. He did produce a number of students, including Sidney F. Blake, Merritt L. Fernald, Jesse M. Greenman, Lyman B. Smith, and at some stage Julian A. Steyermark.

Benjamin Lincoln Robinson died at Jaffrey, New Hampshire, July 27, 1935, after many years of suffering from pulmonary difficulties that ultimately developed into fibrosis. The biographic notes on B.L. Robinson presented here were adapted from Fernald (1935).

JAMES SMALL (1889–1955)

James Small was born in 1889 in Brechin, Forfarshire (United Kingdom). Beginning early in life, he was interested in plants and in 1913 he obtained his degree in pharmaceutical chemistry. Soon after graduating, he began teaching at the University of Durham, an activity that was interrupted by his participation in WWI. However, as a result of battle wounds, he left the army and was able to return to academic activities.

In 1917, Small married Helen Patisson with whom he had two sons and one daughter. Small taught in several universities across the United Kingdom, although he was also Chair of Botany at Queen's University in Belfast, Ireland, from 1920 until a few months before his death. He is mostly remembered for his *Textbook on Botany for Medical and Pharmaceutical Students* (Small 1921), his research on pH in plants (Small 1929, 1946), and his prolific production of papers on quantitative evolution. Small also conducted several ecological studies which eventually resulted in detailed floristic knowledge of several areas in the northern part of Ireland.

It was after his participation in the war that Small began his research on Compositae, research which would eventually lead to the publication of his doctoral monograph: "The origin and development of the Compositae" (Small 1917). In this contribution, Small presented a general introduction to the family with a detailed analysis of morphological characters as well as comments on the phylogenetic relationships and origins

Fig. 1.17. Photograph taken at a meeting of the British Association for the Advancement of Science held at Belfast in 1952. Seated, from left to right: N. Ferguson, J. Walton, J. Small, H. Thomas, J. Ramsbottom, G.N. Coates (seated on floor). [Courtesy of J.S. (Pat) Heslop-Harrison.]

of the family. He considered Senecioneae to be the basal group from which the rest of the family radiated. This view, although now proven incorrect, was a novelty at that time, particularly when other systematists had been considering Heliantheae as the most primitive element in the family. In his monograph, Small not only presented an updated morphological synopsis for the family but also, interestingly enough, the historical background associated with the study of each organ used in the classification of Compositae.

According to some accounts, Small was also notorious for being a rather charismatic individual who would delight audiences with provocative statements and a good sense of humor. He is also remembered for several inventions and improvisations, among which were a plant press and a leaf clasp, to aid in his daily work. He was an excellent photographer and member of three photographic societies, one of which was the Royal Photographic Society. Ironically, for someone so interested in photography, the only photograph we could find of him was from a group photo of the British Association, taken in Belfast in 1951 (Fig. 1.17).

Slightly over a year after retiring from the chair of Botany, James Small died on November 28, 1955. The biographic notes on Small presented here were adapted from Heslop-Harrison (1954, 1956).

SIDNEY FAY BLAKE (1892–1959)

Sidney Fay Blake (Fig. 1.18) was born on August 31, 1892 in Massachusetts. Natural History intrigued him early in his life: first ornithology and later, during his high school years, his passion for botany began.

Blake completed both undergraduate and graduate studies at Harvard University, having obtained his doctorate degree in 1917 with the taxonomic revision of *Viguiera* under the tutelage of B.L. Robinson. Blake was an avid collector and a keen observer of his natural surroundings; these activities led him to gain a deep understanding of the eastern North American Flora with special emphasis on Compositae, which constitute most of his more than 35,000 collections.

Barely in his early twenties, Blake was already sorting plant collections at the Smithsonian in 1913, and soon after that he was traveling through Europe visiting herbaria, a trip that was interrupted by the outbreak of WWI. Among other things, this trip to Europe resulted in Blake's returning with a massive collection of photographs of type specimens which have benefited countless botanists. Blake was soon offered two positions: one at the Smithsonian and the other at the US Department of Agriculture. Although he much preferred the position at the Smithsonian, family responsibilities forced him to accept the more "satisfactory" pay at USDA (Funk 2005). Over the years at USDA, he was heavily involved in administrative duties, a responsibility that he disliked intensely. Thus, we have in Blake yet another Compositae student that ended up doing most of his research in his spare time, a reality that did not deter him from publishing some 300 papers throughout his career.

When we look at Blake's published record, it is possible to glimpse a slight prevalence of Heliantheae taxa among his publications in Compositae; however, he worked with several other groups in the family, noticeably Astereae. His major contributions were his revisions of *Encelia* and *Viguiera*, and his treatment of the family for the "Flora of Utah and Nevada" (Tidestrom 1925), and the *Flowering Plants and Ferns of Arizona* (Kearney and Peebles 1942). However, the most important legacy of Blake's is in the hundreds of papers describing new species and reviewing small groups of Compositae both across North and South America. Blake is cited as the principal contributor of treatments to Compositae

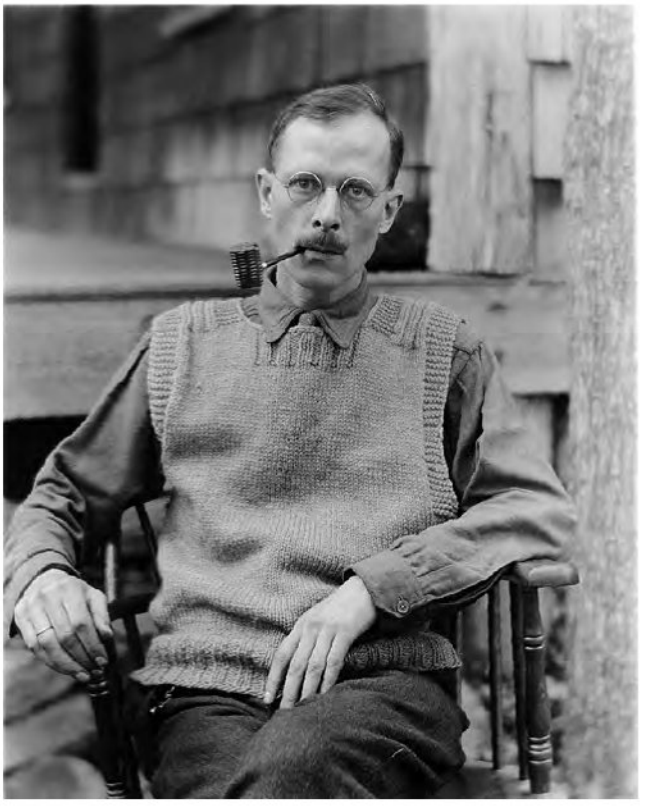


Fig. 1.18. Sidney Fay Blake (1892–1959). Photograph taken in Plummers Island (Maryland, US) at the cabin that serves as Washington Biologists' Field Club headquarters, to which Blake was elected as member in 1924 and of which he was president from 1931 to 1934. [Courtesy of Washington Biologists' Field Club.]

in Standley's (1926) "Trees and shrubs of Mexico", where he also contributed Meliaceae, Polygalaceae and Violaceae.

Thus, although Blake's contributions to botany dealt mainly with Compositae, he also published papers on other taxonomic groups, notably in Polygalaceae, a fact that clearly showed his broad botanical interest and expertise, even extending to botanical nomenclature. He also compiled a series of books on floras, the two best-known being *Guide to Popular Floras of the United States and Alaska* (Blake 1954), and *A Geographical Guide to the Floras of the World* (Blake and Atwood 1942 and 1961). This later one, produced in co-authorship with Alice C. Atwood, consisted of two volumes, the second of which was published posthumously in 1961.

Regarding phylogenetic insights, Blake (1935) cited the relationship of *Chionopappus* Benth. to *Liabum*, and as cited in Sandwith (1956) noted that *Philoglossa* DC. and *Cacosmia* Kunth were also related to *Liabum*, thus fully recognizing the entire group now placed in tribe Liabeae, which had previously been scattered among four different tribes.

Fond of poetry, Blake would recite long poems to endure long trips. In addition, he was a writer who left an unpublished notebook full of poems; he contributed to the Baker Street Journal with articles about Sherlock Holmes as well. He was a gentleman who led a quiet existence and was always held in high esteem by colleagues. Blake married a distant cousin, Doris Holmes, with whom he had one daughter.

After several years of heart trouble, possibly aggravated by too much work, Sidney F. Blake died in his USDA office of heart failure on December 31, 1959. Although his plants and some of his papers are housed at the US National Herbarium, Smithsonian Institution, his library and archives eventually ended up at the University of Texas where there is an S.F. Blake Chair that was previously held by Dr. Billie L. Turner, one of the editors of the Heywood et al. 1977 volume, and a well known synantherologist. When Turner retired, the Chair passed to Dr. Robert Jansen who was responsible for the first molecular work on Compositae (Jansen and Palmer 1987a).

Blake is commemorated by the generic name *Blakeanthus* R.M. King & H. Rob. (Compositae). The biographic notes on Blake presented here were adapted from Holmes (1960) and Funk (2005).

HERMANN MERXMÜLLER (1920–1988)

Herman Merxmüller (Fig. 1.19) was born in Munich on August 30, 1920. Merxmüller's interest in botany began very early in life. Ever since he was a school student, he collected avidly throughout Munich's surroundings and the Bavarian mountains. At the age of 17, he became a member of the Bavarian Botanical Society, where his comprehensive knowledge of the local flora immediately became evident, and this won him the respect of the botanical community. Merxmüller had to wait for WWII to end in order to proceed with his tertiary studies, which he started in 1946 at the University of Munich and finished in 1951 with a doctoral dissertation on plant distribution in the Alps.

Shortly after graduating, Merxmüller took a position as scientific assistant at the Botanische Staatssammlung, under the direction of Karl Suessenguth. It was Suessenguth who directed Merxmüller's attention to his own project of a Flora of South-West Africa. This was the starting point of a long relationship between Merxmüller and the flora of Africa.

Merxmüller's interest in complex groups led him to study European *Hieracium*, and eventually he fell under the spell of the whole Compositae family. His first contribution towards the understanding of southern African Compositae was his "Compositenstudien I" (Merxmüller 1950). This was followed by a long series of papers on Compositae, which ended with his "Compositenstudien XI" (Merxmüller 1980). Although Merxmüller centered his research on Southern Africa, he also collected extensively both in Europe and in South America.

The premature death of Suessenguth triggered important changes for Merxmüller. He first took on the position of his former director, adopting full responsibility for the South-West Africa floristic project. In a span of six years, which ended in 1972, he succeeded in publishing *Prodromus einer Flora von Südwestafrika* (Merxmüller 1966–1972). His participation in this project, accompanied by his several explorations throughout the region, led him to quickly gain notable expertise in the flora of the area. The specimens collected during these floristic endeavors fostered research on multiple fronts and initiated collaborations with many colleagues.

In 1958, Merxmüller was appointed to the Chair of Systematic Botany and founded the Institut für Systematische Botanik at Munich University. He became its first director, promoting research and re-establishing the links between German botany and the rest of the international community after the isolation that resulted from the war. In addition to his positions at the Institut and the Botanische Staatssammlung, beginning in 1969 he also assumed the position of Director of the Botanic Garden. Although not fond of bureaucracy, Merxmüller saw these executive positions as an ideal way to promote systematic research.

Merxmüller also dedicated a considerable time to the teaching of a yearly course on Systematic Botany during several years at the Institut. In 1980, he began to suffer

Fig. 1.19. Hermann Merxmüller (1920–1988). **A** Merxmüller (second from the right) and several colleagues in Namibia, near Brandberg in 1960, in one of his several explorations to the continent; **B** official photograph for the Institute, taken in 1980; **C** in his last class of Systematic Botany held in his institute's lecture hall in October 1985. [Photographs courtesy of Jürke Grau.]

from several health problems that forced him to resign from his positions and commitments, having presented his last lecture on systematics in October 1985 (Fig. 1.19C). Hermann Merxmüller died on February 8, 1988.

The biographic notes on Merxmüller presented here were adapted from Grau (1988) and Grau and Lippert (1988).

JOSÉ CUATRECASAS ARUMÍ (1903–1996)

José Cuatrecasas Arumí (Fig. 1.20), "Don José" as he would eventually be called, was born in Camprodon, Catalonia, Spain, on March 19, 1903. Cuatrecasas' father, a pharmacist and a judge, was responsible for teaching Cuatrecasas and the rest of his eight brothers and his one sister to read and write. It was at a young age that José Cuatrecasas developed a great interest in botany, while helping his father to gather plants for the family business. Following in his father's footsteps, he entered the Pharmacy School in Barcelona in 1918 and graduated as a Pharmacist in 1923.

A student of the renowned Pio Font Quer, Cuatrecasas obtained his doctorate at Universidad de Madrid in 1928. His dissertation was on the flora and vegetation of Macizo de Mágina (Cuatrecasas 1929), a remarkable contribution that shows the quality of Cuatrecasas' work from the very beginning. Cuatrecasas divided his time among several jobs: teaching Botany at the Universidad de Madrid, Curator of Tropical Botany at the Real Jardín Botánico de Madrid, and even director of the Jardín for two years.

In 1932, with the celebrations for the 200th anniversary of the birth of Celestino Mutis, the Spanish government sent a delegation of scientists to Colombia, including José Cuatrecasas. Cuatrecasas visited Nevado de Tolima; this first visit to Colombia and the Cordillera Central resulted in Cuatrecasas' passion for the northern Andes that would define his main botanical interests for the rest of his life.

After the end of the Spanish Civil War, and with the establishment of the *generalísimo*, it was not wise for members of the educated elite to remain in the country. At the time of the overthrow of the government Cuatrecasas was participating in the celebrations of the 400th anniversary of Santa Fé de Bogotá as an official delegate from that government. According to his journals from his 1938–39 trip to Colombia, he had friends move his family from Spain to Paris from whence they traveled to Colombia.

Cuatrecasas lived in Colombia from 1939 until 1947. In addition to the extensive field work and research he carried out during his time in the land of Mutis, he also taught at the Instituto de Ciencias Naturales de la Universidad de Colombia in Bogotá and the Escuela de Agricultura Tropical in Cali. In 1947, he moved to the United States to work at the Field Museum of Natural History in Chicago as curator of Colombian Botany. In 1955, he made his last move to Washington, D.C., where he became a Research Associate in the US National Herbarium, Department of Botany, in the National Museum of Natural History, Smithsonian Institution.

An enthusiastic collector, Cuatrecasas had passion for field botany, with a lifetime total of 40,000 collection numbers. He organized countless expeditions, and the vast majority of his copious collections are from the northern Andes, where he was captivated by the spell of the Colombian and Venezuelan páramos. In addition to his plant collecting, Cuatrecasas was a dedicated photographer taking over 20,000 images in many forms, including glass negatives, negatives, and slides. Many of his photos are of places, plants and peoples that no longer exist.

Cuatrecasas' achievements in Botany are monumental, and although he worked in several taxonomic groups such as Humiriaceae (Cuatrecasas 1961), Brunelliaceae (Cuatrecasas 1970, 1985), Malpighiaceae (Cuatrecasas 1958), and Sterculiaceae (Cuatrecasas 1964), the epicenter of his botanical enterprises resided in Compositae. The name Cuatrecasas is associated with more than 2300 records in IPNI, over 1280 of which are in Compositae, In fact, he described over 450 taxa, 348 in Compositae and over 150 taxa were named after him (not including some with the epithets of *pepi* and *tetroici*). There is hardly any large group in the family that Cuatrecasas failed to work on to some extent. However, his major interests were in Astereae (Cuatreacasas 1967, 1969), Senecioneae (Cuatrecasas 1950, 1951, 1978), and most notably in Heliantheae: Espeletiinae (Cuatrecasas, in press). Cuatrecasas had a fascination, shared by those lucky enough to have ever visited the páramos, for the "frailejones", common name given to the Espeletiinae pachycaul inhabitants in the grassy northern Andean highlands. He successfully devoted himself to seeing and studying every single species of this group in the field, noting the very interesting patterns in the distribution among the many species in this highly attractive group of Compositae. His magnum opus on Espeletiinae (a species level treatment for most of the subtribe), nearly completed at the time of his death, is now in process of being published. This large monograph has 350 illustrations and 1100 manuscript pages (Cuatrecasas, in press)

Always a visionary, and trying to boost botany wherever he was located, Cuatrecasas envisioned the idea of producing a flora for Colombia, arguably one of the most diverse countries in the New World, especially for Compositae. In 1957, Cuatrecasas' idea materialized in the creation of "Prima Flora Colombiana", of which he was the author of the first three contributions: Burseraceae

(Cuatrecasas 1957), Malpighiaceae (Cuatrecasas 1958), and Compositae: Astereae (Cuatrecasas 1969).

Another remarkable feat of Cuatrecasas was the origination of the idea of *Flora Neotropica*. He not only thought of it and helped start it, but also served as Scientific Director and President of the Organization Flora Neotropica from 1967 until 1977. It is in works like this undertaking, still in progress, that Don José's interest for advancing knowledge of Neotropical plants is strikingly evident.

José Cuatrecasas died in Washington, D.C., on May 23, 1996, ten days after his last day at work. Cuatrecasas was a true gentleman and a scholar. We find in him the 'kindred soul' of his southern South American counterpart and countryman, Ángel L. Cabrera. The two of

Fig. 1.20. José Cuatrecasas Arumí (1903–1996) on the day of his seventieth birthday in Páramo de las Moras (Cordillera Central, Colombia) holding a leaf of a "frailejón" (*Espeletia hartwegiana* Sch.Bip. ex Cuatrec.), plants for which he had a lifelong fascination. [Photograph from the Cuatrecasas Archives, courtesy of Smithsonian Institution.]

them were, for many years, the beacons of knowledge concerning Compositae of South America.

In the Compositae, Cuatrecasas is commemorated by the generic names *Cuatrecasanthus* H. Rob. and *Cuatrecasasiella* H. Rob. The biographic notes on Cuatrecasas presented here were adapted from Funk (1970, 2005, 2006), García (1997), López-Figueiras (1970), Merino (2003), Robinson (1970), and Robinson et al. (1996).

ÁNGEL LULIO CABRERA (1908–1999)

Ángel Lulio Cabrera (Fig. 1.21) was born in Madrid, Spain, on October 19, 1908. In 1925, he moved to Argentina, where his father, an eminent zoologist, was offered a professorship at the Museo de La Plata.

After joining his father on one of his first field trips to Patagonia, it became evident to Cabrera that his future was not zoology, and instead, he inclined towards botany. He focused on Compositae because he had difficulties when trying to key out specimens of this family from the La Plata area. These difficulties indicated that the taxonomy was in need of revision, and Cabrera was the individual who eventually would bring order to Compositae of southern South America.

Cabrera was a student of Lorenzo Parodi, one of the pillars of Argentine botany, and it was from the hand of Parodi that he started his career in systematics. Cabrera obtained his doctorate in 1931, and by then he had already published seven contributions on Compositae. Immediately after graduating, he started teaching at Universidad de La Plata, an activity that he would continue for most of his life, and that provided one of his most distinctive features: he always had a handful of young students under his tutelage.

Cabrera knew, like very few others, the flora of southern South America. However, he would hardly dare to express any opinion beyond the realm of his specialty, the systematics of Compositae and the phytogeography of South America. In 1945, he founded the Sociedad Argentina de Botánica, an academic society that would play a major role in fostering botany in Argentina and the rest of South America. He was also the editor of the society's journal, *Boletín de la Sociedad Argentina de Botánica*, from its beginning until 1977. Cabrera's vast academic contributions are characterized by a simple, economic, and notably informative style that brings to his publications a level of perfection that is still used as a guide for others.

Cabrera was a field botanist; he knew his daisies not only dry and mounted, but more importantly, alive in the field. On the countless field trips he undertook during his lifetime, he would often lead parties of five or even more botanists to remote areas of Argentina and neighboring countries. Showing remarkable organizational skills, Cabrera's field trips worked like well-oiled machines; orders were never given, but all participants freely took on their responsibilities. In the words of Roberto Kiesling, one of his most prominent students, and fellow during countless trips, "both in the field and in the lab, Cabrera shows no haste, but neither does he linger." These well-coordinated trips produced collections that were not only numerous, but also exemplary in quality. Visits to Europe to examine type specimens added an important aspect to Cabrera's work. The hard work during the day was compensated with enjoyable evenings at dinnertime, when Cabrera would delight his fellow botanists with countless anecdotes; nothing daunted his spirit, except for any manifested lack of enthusiasm for botany.

Ángel Lulio Cabrera died in La Plata, Argentina on July 8, 1999. He was a remarkable scholar and a passionate collector with a charismatic personality that, to this day, is remembered by every botanist who had ever met him. Cabrera's contributions to synantherology, encompassing the systematics of several groups (most notably basal Mutisieae s.l.), floristic treatments, and phytogeography, showed the diversity of Compositae in Southern South America. Among his most important contributions, there are many taxonomic revisions of genera in Mutisieae s.l. and Astereae, and most importantly his treatment of Compositae for all Argentinean regional floras up to his time such as *Flora de la Provincia de Buenos Aires* (Cabrera 1963), *Flora Patagónica* (Cabrera 1971), *Flora Ilustrada de Entre Ríos* (Cabrera 1974), and *Flora de la Provincia de Jujuy* (Cabrera 1978). Cabrera also participated in the treatment of the family in the Floras of Santa Catharina, Brazil (Cabrera and Klein 1973, 1989) and Paraguay (Cabrera 1996, 1998), and produced in co-authorship with Willink the masterpice *Biogeografía de América Latina* (Cabrera and Willink 1973). A search in IPNI reveals more than 800 records with his name, the vast majority of which are associated with taxa in Compositae, over a hundred of them representing new taxa he described, and over eighty taxa have been dedicated to him.

Cabrera not only generated an impressive published record, but a long list of notable students that still keep the spirit of this remarkable scientist alive. One of Cabrera's aspirations in his youth was to become a diplomat in order to travel to exotic places. Looking back on his academic career and successful life, it is evident that he achieved his goal, having become an ambassador for South American Compositae across the world. The biographic notes on Cabrera presented here were adapted from Crisci (1998, 2000), Katinas et al. (2007), Kiesling and Wrigh (1980), Kiesling (1999), and Múlgura De Romero and Price (1999).

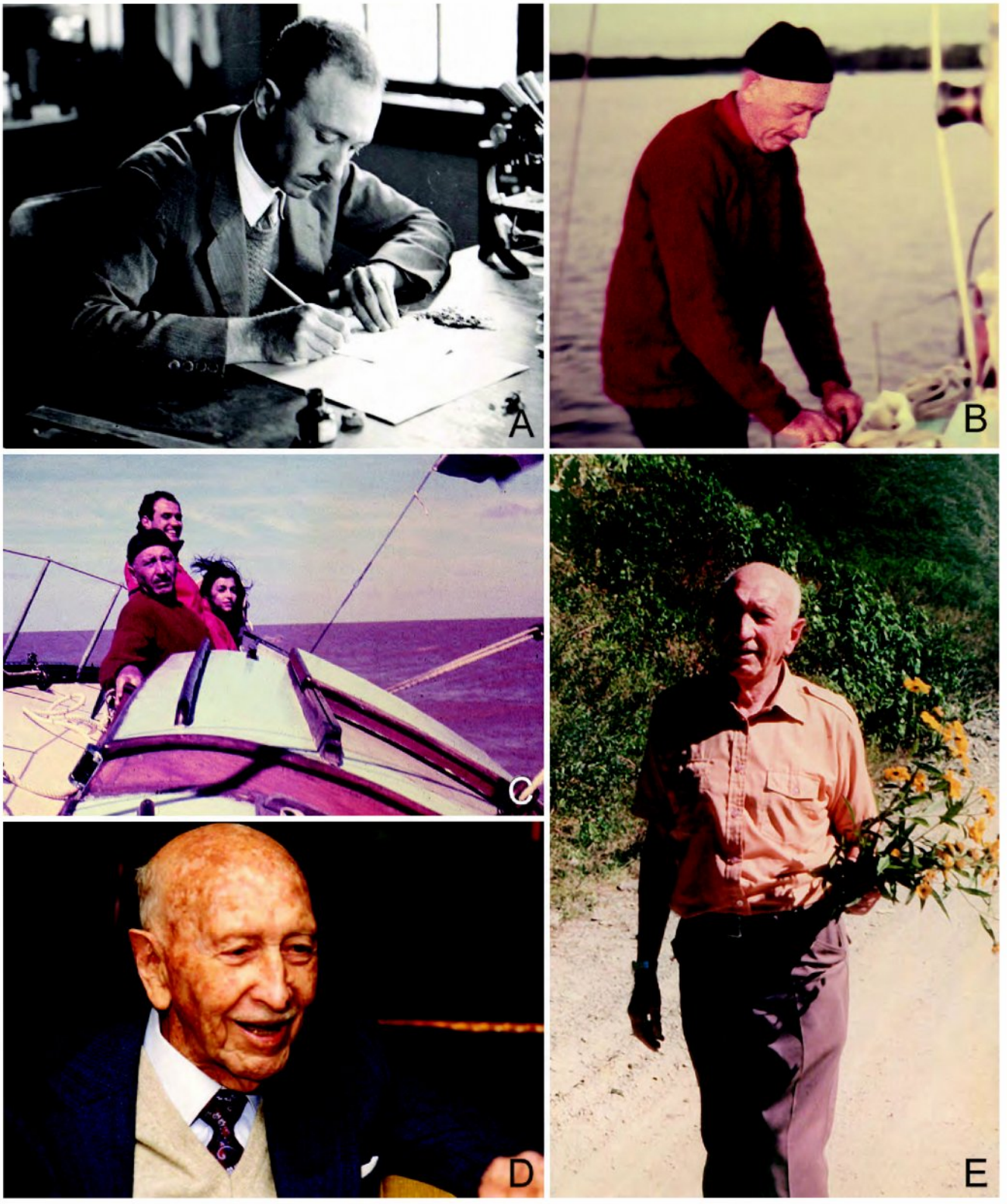


Fig. 1.21. Ángel Lulio Cabrera (1908–1999). **A** Cabrera in 1941 working at his desk in Museo de La Plata (Argentina); **B, C** Cabrera performing his roll as "the captain" of his own boat, which he used to conduct frequent botanical trips along Río de La Plata (C, together with one of his daughters and his son-in-law); **D** Cabrera aged 87 in 1995; **E** collecting comps in Jujuy, Argentina, in 1980. [A, D, photographs courtesy of J. Crisci and L. Katinas; B, C, E, photographs courtesy of R. Kiesling.]

ARTHUR CRONQUIST (1919–1992)

Arthur Cronquist (Fig. 1.22), known to his colleagues as "Art", was born on March 19, 1919 in San José, California. Much of his early years were spent in rural areas of the west coast, a situation that contributed to his affinity for outdoor activities and which left a clear imprint in someone destined to become a remarkable field botanist. As a student, Cronquist went through several summer jobs that demanded a great deal of field work; this experience eventually provided him with invaluable knowledge that he would use in the myriad of research projects undertaken during his lifetime. Cronquist's higher education was conducted in several universities, finally obtaining his doctoral degree in 1944 at the University of Minnesota.

Arthur Cronquist's life-long association with the New York Botanical Garden started in 1943, when he was invited to work as technical assistant. His areas of research encompassed a wide range of interests, from systematic and floristic projects to classification systems of the whole group of flowering plants. Cronquist believed that, given the resources available to him at the New York Botanical Garden, his time would be more productive if dedicated to the completion of floristic treatments. As a result he became the leading author for Compositae in many regional floras across North America, and contributed with several other families to other floristic projects both in the US and abroad. He is particularly remembered by his participation in the *New Britton and Brown Illustrated Flora* (Cronquist 1952; Gleason and Cronquist 1991), *Vascular Plants of the Pacific Northwest* (Hitchcock et al. 1955–1969), and the *Intermountain Flora* (Cronquist 1994; Cronquist et al. 1972, 1977, 1984; Holmgren et al. 2005).

During the year he spent in Belgium (1951–1952) he developed strong ties with European botanists and became increasingly interested in classification systems, and as a result he started publishing many papers on the subject, beginning in the late 1950s with his outline of the classification of dicotyledons (Cronquist 1957). Later on *The Evolution and Classification of Flowering Plants* would appear (Cronquist 1968), followed by *An Integrated System of Classification of Flowering Plants* (Cronquist 1981). He finally reached the climax of his career in this subject, with the second edition of *The Evolution and Classification of Flowering Plants* (Cronquist 1988). These books represent his most important productions in the realm of classification systems, and established his reputation as a botanist who worked beyond the borders of North America. Cronquist developed strong ties with his Armenian colleague, Armen Takhtajan, and in order to be able to have access to the wealth of Russian literature and better communicate with the Russian botanical community, he set himself to learn Russian, eventually becoming fluent in this language.

Cronquist's system of classification was adopted in many places and used as the system for large floristic undertakings such as the *Flora of North America* and *Flora of Australia* projects. Cronquist's understanding of the different groups of flowering plants was legendary, and he had first-hand experience with at least some element of every single family recognized in his system. Additionally, Cronquist produced a botany textbook that was widely used for over twenty years and that went through two editions.

His research on Compositae dealt with several revisionary treatments and theoretical papers, but he was largely involved with floristic treatments in North America, an activity in which he excelled. His practical knowledge of Compositae was unparalleled, proof of which can be seen in the clarity of the keys he constructed for his floras. With regards to his ideas on the internal organization of the Compositae, and more or less in the same line of thought as Bessey and Hutchinson, Cronquist viewed Heliantheae as the ancestral group in the family and set up a series of characteristics of the primitive members of the family (Cronquist 1955). Once he made up his mind he rarely changed it, but once Carlquist was able to provide him with enough data that he decided the basal members of the family were probably woody, not herbaceous (Cronquist 1977). Although many of his views

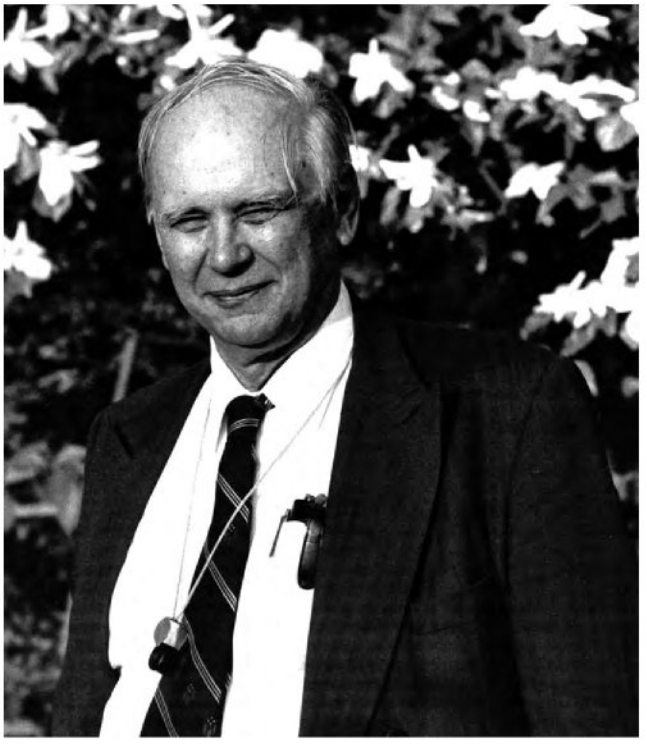


Fig. 1.22. Arthur Cronquist (1919–1992). [Photograph from *Taxon*-IAPT Archives.]

on the origin and evolution of the Compositae were not corroborated by DNA sequence data, he has left a lasting legacy in his major floristic undertakings across North America, and Cronquist will always be remembered as one of the influential figures of Compositae systematics of the 20th century.

Cronquist's towering figure, rising over two meters in height, and his profound tone of voice resulted in a "commanding" presence, which, added to his exceptional good sense of humor and his love of telling tall tales, often made him a highly agreeable individual. Arthur Cronquist died on March 22, 1992 while studying specimens of *Mentzelia* in the herbarium at Brigham Young University in Provo, Utah (US). The biographic notes on Cronquist presented here were largely adapted from Barkley (1992, 1993).

THE LATE 20th AND EARLY 21st CENTURY

As one might imagine, it was difficult to decide where to stop and who to include in this chapter. After much discussion, we decided to stop with the first meeting on the classification and evolution of the Compositae, held at Reading (UK) in 1975. This meeting sets a natural limit on synantherologists to be included in this study because it was attended by many of the scientists of that time who studied this important family, and the resulting published work, edited by Heywood, Harborne, and Turner (1977), was the standard reference for the family for many years. After over thirty years, most of those at the 1975 meeting are no longer actively working on the family, but some still are and of those, seven attended the meeting in Barcelona and eight (V.H. Heywood, C. Jeffrey, H.W. Lack, T. Mabry, B. Nordenstam, H. Robinson, J.J. Skvarla, and T.F. Stuessy) are authors on one or more chapters in this volume.

During the 20th century, in parallel with the increasing development of science as a whole, the number of researchers dedicated to the daisy family grew steadily with a significant advance in the knowledge of the family and understanding of the phylogenetic relationships at the tribal and generic level. As a simple marker of the advance in the knowledge of the family, the number of recognized genera since the treatment of Hoffmann at the end of the 19th century has doubled and it is now over 1700. The 20th century also witnessed the arrival of several techniques that increased our understanding of the family. Research methods involving counts of chromosome numbers, determining pollen structure, and understanding plant chemistry all contributed new information, and the classification of Compositae benefited from these new sets of data.

However, it is thanks to the wealth of DNA sequences accumulated during the last two decades that the relationships inside the family are now much better understood. Beginning with the seminal papers of Robert Jansen and his collaborators (Jansen and Palmer 1987a, b, 1988; Jansen et al. 1990, 1991) and increasing in number every year, the path of evolution in the family is becoming increasingly clear.

Before we finish it is critical that we acknowledge and honor all of the Compositae community, the myriad of contributors of taxonomic revisions of small groups, and the authors of regional and local floras who not infrequently are the first to draw attention to undescribed taxa and the first ones to record unknown information. They are too numerous to be mentioned here, but it is in large part due to their efforts that the savants mentioned here were able to draw their conclusions and push forward our understanding of Compositae.

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Chapter 2

The recent history of Compositae systematics: from daisies to deep achenes, sister groups and metatrees

Vernon H. Heywood

INTRODUCTION

The early history of Composite taxonomy and systematics has been covered in the introductory chapter up to the Proceedings of the 1975 symposium at the University of Reading, UK, entitled "An overture to the Compositae" (Heywood et al. 1977) and in the present contribution (Chapter 1), so I shall focus on advances in the subsequent twenty-five to thirty years during which we have witnessed a radical transformation of approaches to taxonomy and systematics and our understanding of phylogenetic relationships. Added to that have been drastic changes in the environmental, social and economic circumstances in which we practice our science.

THE SITUATION IN 1975

Life was exciting for taxonomists in the 1970s when the first Compositae symposium was held at Reading. The classification of the flowering plants was in a period of transition. Technical advances such as electron microscopy and analytical chemical techniques led to the production of new data from micromorphology, palynology and the chemistry of secondary compounds, and at the species and population level, the future direction of biosystematics and genecology was being debated—"Biosystematics at the crossroads" was the title of a symposium at the Seattle Botanical Congress in 1969, reflecting doubts about the validity of the biological species concept on both theoretical and practical grounds.

At that time, phenetic taxonomy/classification, with its emphasis on quantification of characters and character states, was part of an attempt to make the procedures of classification more explicit and reproducible, and numerical phenetics (numerical or Adansonian taxonomy) was being increasingly used to handle large datasets being produced, within the limitations of the then existing computing technology and instrumentation. Sokal and Sneath's *Principles of Numerical Taxonomy* (1963) was a highly influential text in this field and was updated as Sneath and Sokal's *Numerical Taxonomy: The Principles and Practice of Numerical Classification* (1973). Davis and Heywood's *Principles of Angiosperm Taxonomy*, which was also published in 1963, was not only the first textbook to provide a detailed analysis of the principles, issues and concepts of plant taxonomy but was essentially phenetic in its philosophy.

The phenetic approach was distinguished from the rather vague concept of evolutionary systematics sensu Mayr and from the emerging cladistic approach that was beginning to be espoused. Subsequently, during the 1960s and 1970s there was an almost endless debate regarding the relevant merits of phenetic and phylogenetic taxonomy in journals such as *Systematic Zoology*. Today