Chapter 2
Ancient and Modern Concepts About the Asteraceae Taxonomy

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Abstract This chapter provides an update on the systematics of Asteraceae (formerly known as Compositae), which is the largest vascular plant family. This update includes the changes of concepts that have occurred from the old times of the elementary recognition of the Asteraceae as a natural group of angiosperms in the last decades of the eighteenth century up to the advanced plant systematics trends of the twenty-first century. This contribution is to provide non-scholars in neither botany nor plant systematics some knowledge about this complex mega-family, its infra-familial relationships and the nomenclatural crossroads.

Keywords Asteraceae · Plant systematics · New concepts · Cladistic studies · Infra-familial taxonomy

2.1 Introduction

Asteraceae Bercht. and J. Presl. nom. Cons. (1820) (=Compositae Giseke, = Synanthereae Cass.), is a phylogenetically advanced cosmopolitan plant family among the dicotyledons that is easily exomorphologically recognized by its typical racemose inflorescence: the flower or pseudanthial head (also named capitulum), formed by a variable (1[1] to numerous) number of sessile, sympetalous, synanthereous and epigynous flowers arising from a common receptacle – this can be either flat, convex or hollow – whole set is surrounded by phyllaries (an uni-pluriseriate bracteal involucre, frequently leaflike).

[1] In genera like *Corymbium*, *Echinops*, *Hecastocleis* and *Lagascea*.

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The Asteraceae family comprises more than 25,000 plant species distributed in about 1500–1700 genera, thus being the largest plant family among vascular plants. Members of this family are widespread along all continents, except Antarctica. These plants grow from the sea level up to high mountain environments, around 5000 m a. s. l., and also spread from tropical rainforests to arid desert places. The morphological exclusive (or quasi-exclusive) traits of Asteraceae are vast and should deserve a glossary in order to explain their meanings to the lay (for a description of the general morphology of the family, see Cabrera 1974, Freire 2009a, 2013).

About reproductive strategies, so important for a basic discipline as biology, it should be remembered that Asteraceae have proterandrous flowers, and cross-pollination is widespread, occurring through zoophilous pollination, mostly entomophilous (Hymenoptera, Lepidoptera, etc.). However, birds could also perform it in several cases and anemophilous taxa also occur. Several alternatives of sexual expression are shown by various members of this family: dioecy, monoecy, etc. However, selfing and even apomixis are sometimes present, following different evolutive tendencies within this large family. Seed dispersal is also very diversified in different infra-familial groups: cypsela hairiness, pappus consistency and disposition[2] and/or various trichomatous ornamentations (or even the complete flower head receptacle is involved, as in *Xanthium*), either helped or not by some animals, are involved on known strategies for the spatial dispersion of propagules.

On phytochemical grounds, the Compositae/Asteraceae are recognized for storing carbohydrate polymer polyfructosans such as inulin and for the occurrence of polyacetylenes and sesquiterpene lactones and – among other alkaloids – for the hepatotoxic pyrrolizidine compounds, as well as for the absence of iridoid compounds as remarkable characters.

As the wide range of sesquiterpene lactones from this family – more than 8000 compounds have been reported – have been extensively and deeply surveyed everywhere (e.g. Seaman 1982; Seaman and Funk 1983; Hristozov et al. 2007; Zidorn 2008; Scotti et al. 2012; Bruno et al. 2013; among many others), and as it is also considered in the present volume, their details and implications shall not be treated in this chapter.

A miscellaneous list of other types of metabolites like phenolics, diterpenes, amides, cyanogenic glycosides, etc., have also been extensively found in members of Asteraceae (Seaman et al. 1990; Francisco and Pimenta Pinotti 2000; Bohm and Stuessy 2001; Emerenciano et al. 2001; Rios 2012; Granica and Zidorn 2015).

2.2 Asteraceae in Old Times Plant Systematics: Its Influences

It is well known that ancient botanical classification systems relied on quite elementary comparative exomorphology traits, and therefore, their scope was obviously very limited, as compared to current standards in plant systematics (Crisci and

[2] The wind-moved propagules with a light hairy pappus like in thistles (*Cirsium, Carduus*).

López Armengol 1983; Stuessy 2002; Stuessy and Funk 2013). However, influences of such ancient taxonomic systems persist today, among other nomenclatural issues of plant taxonomy (a certain stability of scientific names is still desirable even in the fast-changing advanced biology of today). This situation is exemplified by large and diverse plant families such as the Asteraceae mega-family. Asteraceae's infra-familial-, tribal- and generic-level organization is still under study and is very controversial, a fact quite understandable for such a large and complex taxon. On the other hand, the reverberations entailed by the old infra-familial and generic classification systems – some of them known to be wrong according to current plant systematics concepts – may sometimes reinforce misconceptions held by other groups of scientists (e.g. those engaged on agronomic, phytochemical or ethnopharmacological research, among another group of "users" of basic plant systematics scientific data). Information about accurate field localization (even those out of modern GPS data) of a particular plant species can only be found in old-fashioned generic monographies and/or from aged floristic treatments for the Asteraceae and not in recent papers dealing with current systematic updates of these taxa. Some of such precise chorological information becomes relevant when endangered plant species are considered.

The exact provenance of a given plant species in wild environments becomes increasingly important, keeping in pace with the risk of extinction of such taxon. In such old floras and related papers, still valuable on chorological terms, a non-updated infra-familial systematics is often presented; or even worse, their specific delimitations ought to be reconsidered before a particular phytochemical analysis is performed, especially if any valid chemotaxonomical conclusion could eventually be proposed.

The idea of considering the Asteraceae as a distinctive, recognizable plant family began to achieve wide acceptation among botanists in the last decades of the eighteenth century. This recognition accompanied the widespread use of the old and more imperfect Linnaean classification system, under whose rules, the taxonomical category that we nowadays know as a "plant family", were still not considered. The correct nomenclature for such taxonomic category, i.e. "family" (Brown 1817), used to be variable in those times, and it was only in the second half of the nineteenth century when most researchers began to refer to a given plant family employing such taxonomical category (and therefore, abandoning older denominations such as "ordines naturales plantarum", "cohort", etc.).

As mentioned, a reasonable consensus about the scope and a clear definition of what we actually call the family Asteraceae (or Compositae) has already occurred since the last decade of the eighteenth century (Giseke 1792) and during the early years of the nineteenth century (Berchtold and Presl 1820; de Candolle 1836, 1838; Cassini 1816; Dumortier 1822). Most of the precursor researchers working on the systematics of Compositae agreed on the delimitation of the family; however, controversies and polemical issues about the infra-familial taxonomic arrangement often arouse. For example, de Cassini (1816) accepted 19 tribes within the Compositae, whilst de Candolle (1836, 1838) and Lessing (1832) recognized 8 tribes within the same family: Vernonieae, Eupatorieae, Astereae, Senecioneae, Cynareae, Mutisieae, Nassauvineae and Cichorieae. In those days, comparative studies based on rough exomorphology studies of plants were paramount, thus disregarding both ontogenical and/or evolutive presumptions whose importance began to be considered about a century later.

Later, in the second half of the nineteenth century, Bentham (1873) made important advances in the infra-familial taxonomy of Compositae. The author divided the family in two main groups: the subfamilies Liguloideae and Tubuloideae. Bentham assigned only one tribe – the Cichorioideae to the Liguloideae – proposing 12 tribes for the second subfamily: Anthemideae, Astereae, Arctotideae, Calenduleae, Cynareae (= Cardueae), Eupatorieae, Helenieae, Heliantheae, Inuleae, Mutisieae, Vernonieae and Senecioneae. In those times, Darwinism and evolution concepts had already appeared in biology, and the influences of such discoveries soon developed. The infra-familial arrangement proposed by Bentham enjoyed considerable importance during the last quarter of the nineteenth century due to Hoffmann's (1894) treatment of the Compositae for Engler and Prantl's *Die Natürlichen Pflanzenfamilien*, which was a respectful classification system for plants. Hoffmann (1894) recognized two subfamilies, Tubiflorae and Liguliflorae, thus completing the 13 tribes previously quoted. Meanwhile, the advances in optics, together with the application of sophisticated techniques, as well as the advances in genetics, cytology and embryology and even the serotaxonomic approaches of the early twentieth century, improved plant anatomical recording of data and plant systematics outputs.

Consequently, Hoffmann's (as an Englerian-based taxonomy, i.e. a long-lasting natural classification system) and Bentham's systems lasted up to the second half of the twentieth century – even exceeding the 1950s. This fact can be exemplified by the existence of many published reports on Asteraceae taxonomy and floristics, among which are those corresponding to Angel L. Cabrera (and to some of his co-workers and disciples such as Sáenz (1981) and Cabrera and Ragonese (1978)). Spanish-born Argentinean botanist A. L. Cabrera (1908–1999) was one of the most prominent South-American synantherologists of the twentieth century. His multiple contributions are reflected in the establishment of several generic keys and important monographic treatments (Cabrera 1962, 1965, 1971a, 1982), as well as his floristic approaches to the same family (Cabrera 1963, 1971b, 1974, 1978), and through his influences on many of his students. As South America is a very important subcontinent in terms of Asteraceae biohistory (Katinas et al. 2007), Cabrera's works have also served as the basis for floristic treatments carried out in some Argentina neighbouring countries (Cabrera and Klein 1973, 1975), Even during more recent years, and although acknowledging more recent approaches to Asteraceae infra-familial systematics carried out by other botanists, Cabrera and his co-workers have still followed Bentham's traditional tribal and generic arrangement for their floristic works on South-American specimens (Cabrera and Freire 1998; Cabrera 1999; Cabrera et al. 2009). The importance of such regional botanical studies, disregarding new or more advanced treatments for the family and/or subordinate taxa, has sometimes been overstressed by plant taxonomy misusers from other disciplines.

2.3 Towards a "Contemporary" Asteraceae Systematics

After World War II, novel mathematical approaches to biological classifications began to appear, some of them in the field of phenetics (Sneath and Sokal 1973), which enjoyed considerably influences during the 1960s and 1970s, and later (mainly around cladistics or phylogenetics), through the developments of the German entomologist Willi Hennig's ideas (Hennig 1966) and many other scientists (Estabrook 1972; Funk and Stuessy 1978; Wiley 1981; Stevens 1991, etc.), a trend which accentuated from the 1970s onwards. In parallel, new data began to be more seriously considered as more useful approaches to plant systematics, as a great amount of novel information on cytogenetics, phytochemistry, exomorphology, plant anatomy, embryology, palynology, plant physiology, molecular biology, ecology, phytogeography, among other disciplines, appeared together with more sensitive laboratory techniques and improved informatics tools, capable of analysing large data sets very quickly.

New insights on the taxonomy of Asteraceae were achieved by several researchers, especially from the 1970s onwards: King and Robinson (1970) have established new study criteria for the Asteraceae upon considering the so-called microcharacters. Few years later, they proposed a new arrangement for the tribe Eupatorieae (King and Robinson 1987) suggesting, for example, the convenience of splitting a big genus like *Eupatorium* into several other equivalent taxa. Another important innovation was the proposition of a new tribe, Liabeae (Robinson and Brettel, 1973; Carlquist 1976). These authors also suggested changes at the infra-familial level, considering two subfamilies, Cichorioideae and Asteroideae, each one comprising six tribes. Wagenitz (1976) was also concerned about Asteraceae systematics. Thus, a great deal of data summarizing the advances in the 1960s and 1970s was presented in the book edited by Heywood et al. (1977).

In parallel, new systematic concepts, techniques and treatments using cladistic approaches appeared and were applied for most plant families (Crisci and Stuessy 1980; Crisci 1982, etc.). Many of these scientists were also engaged on research in the Asteraceae (Crisci 1980; Funk 1985; Katinas 1996 just to quote very few). New studies on tribal systematics were then performed and published, thus introducing modifications to the elementary concepts developed by Cassini and Bentham.

The molecular studies performed by Jansen and Palmer (1987) have also led to major changes in the infra-familial systematics of Asteraceae. These authors proposed the Barnadesiinae (*Barnadesia*, *Chuquiraga* and *Dasyphyllum*) be included as a subtribe within the Mutisieae tribe, due to the presence of a DNA inversion in that group of plants that is absent in the rest of the family. Therefore, Barnadesiinae should constitute a basimorphic subfamily (Barnadesioideae) within the Asteraceae. Obviously, the approaches proposed by Cabrera on Mutisieae (Cabrera 1977) began to change very deeply. These modifications were based not only on molecular but also on micromorphological pollen data, among others, and very miscellaneous informations were responsible of such advances (Katinas 1994; Katinas et al. 2008, 2009; Roque and Funk 2013; Tellería et al. 2013; Funk et al. 2014; Hernández et al. 2015).

According to Robinson and Brettel (1973), the Liabeae tribe and its components have received more attention (Gutiérrez 2003, 2010; Gutiérrez and Luna 2013; Gutiérrez and Katinas 2015).

Bremer (1994) has proposed an infra-familial classification within the Asteraceae. According to cladistic studies using multiple kinds of data sets, his system (Bremer 1994) recognized 3 subfamilies with a total of 18 tribes for the Asteraceae: (1) subfamily Barnadesioideae (Barnadesieae tribe), (2) subfamily Cichorioideae (Mutisieae, Cardueae, Lactuceae, Arctoteae, Vernonieae and Liabeae) and (3) subfamily Asteroideae (Inuleae, Gnaphalieae, Plucheeae, Astereae, Anthemideae, Senecioneae, Helenieae, Heliantheae, Calenduleae and Eupatorieae).

However, further studies and molecular approaches (Panero and Funk 2002, 2008) increased to twelve the number of proposed subfamilies within Asteraceae: Barnadesioideae (about 9 genera), Mutisioideae (approximately 44 genera), Stifftioideae (10 genera), Wunderlichioideae (8 genera), Gochnatioideae (5 genera), Hecastocleidoideae (monogeneric subfamily), Carduoideae (more than 100 genera), Pertyoideae (6 genera), Gymnarrhenoideae (1 genus), Cichorioideae (more than 220 genera), Corymbioideae (few genera) and Asteroideae, which remains the largest subfamily, comprising more than 15,000 species which belong to important recognizable tribes, many of them with very large genera such as *Senecio* sensu *lato*, *Vernonia* sensu *lato*, *Artemisia* L., *Centaurea* L., *Eupatorium* sensu *lato*, *Verbesina* L., etc. An obvious tribal reorganization was then also suggested, considering 35 tribes.

Additionally, Jeffrey (2007) has proposed another subfamilial and tribal arrangement for the Asteraceae; however, he recognized only five subfamilies.

Slowly, some of these recent systematic proposals become more and more frequently incorporated on more “traditional” approaches to this mega-family, thus updating some treatments of the family for floristic contributions (Freire 2009a).

Generic and specific studies are also under deep changes due to the use of modern analytical techniques and advanced classification methodologies. A consequence of the evolution in the generic concepts in this family is, for example, within the large tribe Vernoniaeae (comprising more than 1000 species). Among other modifications, Robinson has proposed the creation of several new genera by splitting the large genus *Vernonia* Schreb (Robinson 1999). This is one of the groups within Asteraceae that shows a wide range of cytological characters (different karyotypes, basic chromosome numbers (Dematteis 1997; Angulo and Dematteis 2006, 2015). Among them, *Chrysolaena* H. Rob. (Robinson 1988) is one of the taxa segregated from *Vernonia* sl., such as *Lessingianthus* H. Rob. and *Cyrtocymura* H. Rob. (Dematteis 2009a, b). This group is quite complex, and even infraspecific interesting situations have been considered, regardless of the generic final delimitation within the tribe (Dematteis 2004; Freire 2008).

The large *Senecio* genus, sensu *lato*, which comprises around 1000 species, and also its important tribe within the subfamily Asteroideae, the Senecioneae, have also undergone various changes in the light of new systematic evidences (Pelser et al.

2007; Nordenstam et al. 2009; Devos et al. 2010, among many other authors). Furthermore, additional studies performed in several taxa have resulted in the reformulation of several genera and/or in the appearance of new generic concepts, as is the case of the new genus *Xenophyllum* Funk which was segregated from *Werneria* Kunth (Funk 1997).

Anderberg (1989) has splitted Inuleae into three equivalent taxa; as a consequence, such generic reorganization of former components of Inuleae sensu *lato* began to be treated as separate taxa (Anderberg 1991; Freire and Iharlegui 1997; Anderberg et al. 2005; Freire 2009b).

The tribe Astereae has been revisited (Nesom 1994), and also several genera belonging to it have been studied quite recently (Bonifacino 2009; Bonifacino and Funk 2012).

In order to be brief, no additional details in terms of tribal and/or generic novelties will be mentioned herein; however, the reader may consult the vast literature data published over the last 20 years.

New advanced attempts to understand the Asteraceae systematics are currently being made by the use of sophisticated softwares for crude data analyses (Hristozov et al. 2007; Ernst 2013; Mandel et al. 2015).

Nowadays, facing this enormous, quasi-planetary distributed plant family (Funk et al. 2009), the amount of available information useful for plant systematics is increasing exponentially, along with the development of new well-founded criteria. The development of such criteria can be achieved with the aid of novel study techniques and accompanied by a large availability of herbarium sheets and worldwide plant sample materials. All these processes are directly proportional to an increase in the number of botanists, among other researchers, who are engaged in the study of this family. Consequently, the output in the number and variety of publications is very large. Only a very small fraction of such literature data has been outlined in this chapter.

2.4 Conclusion

Perhaps more than in any other plant family, the enormous size and complexity of this vascular plant taxon accounts for the great deal of literature published so far on the subject. It also implies improvements at the infra-familial level as well as changes in the nomenclature. To sum up, the “endless synthesis” that refers to plant systematics research is what makes the infra-familial taxonomy of Asteraceae so complex, variable and fascinating to researchers from very different backgrounds, from old-gone times to our present.

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