BIOLOGICA NYSSANA
10 (2) December 2019: 77-85
DOI: 10.5281/zenodo.3600177
13th Symposium on the Flora of Southeastern Serbia and Neighboring Regions

Micromorphology and anatomy in systematics of Asteraceae. An old-fashioned approach?

Review Article

Peđa Janaćković
University of Belgrade, Faculty of Biology, Department of Morphology and Systematics of Plants, Studentski trg 16, Belgrade, Serbia
pjanackovic@bio.bg.ac.rs (corresponding author)

Alfonso Susanna
Botanic Institute of Barcelona (IBB, CSIC-ICUB), Pg. del Migdia s. n., 08038 Barcelona, Spain
asusanna@ibb.csic.es

Petar D. Marin
University of Belgrade, Faculty of Biology, Department of Morphology and Systematics of Plants, Studentski trg 16, Belgrade, Serbia
pdmarin@bio.bg.ac.rs

Received: October 27, 2019
Revised: November 28, 2019
Accepted: December 17, 2019

Abstract:
The comparative study of plant morphology, intertwined with anatomy, has always been the basis for plant systematics, which strives to explain diversity, evolution and phylogeny of plants. In the molecular era, some authors diminish importance of morphology and especially anatomy in systematic and phylogenetic studies of plants. However, are molecular data exclusively a primary and self-sufficient approach in taxonomic research of plants? This review paper addresses this issue through specific examples. Studies of some Asteraceae taxa showed that morphological, micromorphological and anatomical data are extremely important in systematics. New opportunities for systematic morphology, micromorphology and anatomy in case of Asteraceae taxonomy, but certainly also in other plant groups, that were not present in the premolecular era, are opening regarding synergistic multidisciplinary taxonomic, evolutionary and phylogenetic studies that combine molecular with morphological, anatomical and other analyses (e.g. chemophenetics - describes a given taxon phenetically using specialized metabolites as phytochemical characters), keeping in the throne these "old fashioned" approaches.

Key words:
morphology, taxonomy, characters, synergy

Apstract:
Mikromorfologija i anatomija u sistematici familije Asteraceae. Staromodan pristup?
Uporedna studija morfologije isprepletene sa anatomijom, uvek je bila osnova za sistematiku biljaka koja teži da objasni raznolikost, evoluciju i filogeniju biljaka. U molekularnom dobu, u sistematskim i filogenetskim studijama biljaka, neki autori umanjuju značaj morfologije, a posebno anatomije biljaka. Međutim, da li su molekularne metode i podaci isključivo primaran i samodovoljan pristup u taksonomskom istraživanju biljaka? Ovaj pregledni rad, kroz određene primere, daje odgovor na ovo pitanje. Istraživanja određenih taksona iz familije Asteraceae pokazala su da su morfološki, mikromorfološki i anatomski podaci izuzetno važni u sistematici. Novi pristupi u sistematskoj morfologiji, mikromorfologiji i anatomiji u slučaju taksonomije Asteraceae, ali sigurno i u slučaju taksonomije drugih grupa biljaka, koji nisu bili mogući u premolekularnom dobu, otvaraju se sada kao sinergija multidisciplinarnih taksonomskih, evolucionih i filogenetskih studija koje kombinuju molekularne sa morfološkim, anatomskim i drugim analizama i pristupima (npr. hemofenetika koja opisuje dati takson fenetički, upotrebom specijalizovanih metabolita kao fitohemijskih karaktera), držeći na prestolu ove „staromodne" pristupe.

Ključne reči:
morfologija, taksonomija, karakteri, sinergija

Introduction

The comparative study of plant structure has always been the backbone of plant systematics, which strives to elucidate plant diversity, phylogeny and evolution (Endress et al., 2000). Plant taxonomic studies traditionally use morphological and karyological (Stebbins, 1953), as well as micromorphological characters (Hayat et al., 2009; Bak & Ozcan, 2018). Micromorphological characters are of decisive importance in unring taxonomic and phylogenetic relationships of various plant groups and have been successfully used in plant systematic studies for decades (Endress et al., 2000). For more than a century, comparative anatomy is used as a tool in the plant systematics. Anatomical characters are very important in perceiving systematic and phylogenetic relationships of particular plant groups. Indeed, anatomical features can provide useful characters which could help in identification of problematic plant taxa, as well as establishing their taxonomic relationships (Metcalfe & Chalk, 1957; Scatena et al., 2005; Makbul et al., 2011; Sosa et al., 2014; Karanović et al., 2015, Gavrilović et al., 2019a, b; Janaćković et al., 2019).

On the other hand, the data provided by the phytochemists are extremely difficult to interpret in a cladistic context. Even so, integration of phytochemical and macro-molecular characters can be of prominent benefit, and can help, for example, in the delineation of clades so far only supported by DNA sequence data (Enke et al., 2012). In order to overcome the confusion in the interpretation of phytochemical characters (specialized metabolites that actually describe the given taxon phenetically) as phylogenetic characters and "under the umbrella" of the term chemotaxonomy (which is mistakenly identified with chemosystematics), the new term chemophenetics has been proposed by Zidorn, (2019). Nevertheless, chemophenetic studies contribute to the phenetic description of taxa, similarly to anatomical, morphological and karyologycal approaches, which have already been recognized as of major importance for establishing "natural" systems and which continue to be of the highest importance for the description of organisms classified with the help of modern molecular methods (Zidorn, 2019).

Asteraceae (Compositae), habitually known as the daisy or sunflower family, represent one of three mega-diverse families which jointly count more than 25% of all extant angiosperm species (Mandel et al., 2019). Asteraceae, counting 25000–35000 species, comprise 10% of all flowering plant species. Members of the sunflower family occur on every continent including Antarctica (Smith & Richardson, 2011) and inhabit nearly every type of habitat on Earth with the largest concentration of species in deserts, prairies, steppes, montane regions, and areas with Mediterranean-like climates (Mandel et al., 2019). According to newer fossil data and recent molecular clock dating, Asteraceae likely originated during the Late Cretaceous: ~83 MYA (Mandel et al., 2019). According to Mandel et al. (2019) the family consists of 13 subfamilies and 47 tribes. Asteraceae also includes species of wide economic interest, e.g. vegetables, sources of oil, medicinal plants, insecticides and many horticultural and garden ornamentals. However, some species of Asteraceae constitute a big problem for agriculture as noxious weeds. As a one of the largest, natural (with a combination of several specialized morphological characteristics e.g., capitula, highly reduced and modified flowers, syngenesious anthers, inferior ovaries and very unique in the plant kingdom fruit - cypsela) and economically most important families of flowering plants Asteraceae has been researched for centuries.

Characters related to form, whether gross morphology, micromorphology, anatomy, embryology, palinology and so forth, regarded as morphologycal data, have larger impact on the cladistics and classification of the Asteraceae than other characters e.g. chemical and molecular data (Schönberger, 2002; Stuessy, 2009). Molecular data are significant but also insufficient, that is why, in some cases, better phylogenetic reconstructions of the Asteraceae are obtained taking into account also a morphological data (Pornpongrungrueng et al., 2007; Gruenstaeudl et al., 2009; Wang et al., 2013). More recent, modern-day studies of Asteraceae taxa have shown that morphological, micromorphological and anatomical data are still extremely important in systematics of Asteraceae family (Makbul et al., 2011; Wang et al., 2013; Sosa et al., 2014; Karanović et al., 2015; Bombo et al., 2016; Ginko et al., 2016; Batista and De Souza, 2017; Gavrilović et al., 2017; Gavrilović et al., 2018a, b; Gavrilović et al., 2019a, b; Janaćković et al., 2019).

Brief history and modern-day micromorphology and anatomy in systematics of Asteraceae

Micromorphology

A different sets of characters has been used to demarcate the Asteraceae. Certainly, one of the pioneer work regarding micromorpholgical approaches to Asteraceae classification was done by Cassini (1821). These summarize many of the microscopic traits on which Cassini based his tribes. Of these, pronate versus recurved mature style branches, stigmatic surfaces, truncate to enlarged style appendages, bases of the anther thecae with or without tails, shape of the anther collar and form of the corolla are most important. The stigmatic surfaces of many tribes (Mutisieae, Lactuceae, Vernonieae, Arctotideae, Eremothamneae, Cardueae) are consistently continuous over the inner surface of the style branch. In other tribes (Eupatorieae, Anthemideae, Astereae, most Inuleae, most Heliantheae, most Senecioneae) the stigmatic surface is divided into two lines.

The nature of endothecial tissue of the stamens, which could be polarized or radial, showed to be good character in taxonomy within Senecioneae (Dormer, 1962). In subtribes Senecioninae and Othonninae, the endothecium is radial in all genera except *Dauresia, Graphistylis*, and perhaps *Synotis*. In

Tussilagininae s.str. a polarized endothecium is the rule, but the radial type has been recorded in several genera (*Tephroseris, Nemosenecio, Psacaliopsis, Psacalium, Arnoglossum*); in *Sinosenecio* both types and an intermediate pattern seem to occur (Jeffrey & Chen, 1984). Moreover, the anthers of Cichorieae members vary considerably in length, but this variation probably occurs repeatedly within many genera and is therefore only of taxonomic relevance at the species level (Kilian et al., 2009). In Arctotideae morphological and micromorphological characters confirmed close relationships between the *Gorteria* clade and *Berkheya* clade (Karis et al., 2009).

Microcharacters of involucral bracts are considered very helpful for delimitation in certain taxonomic groups of Asteraceae (e.g., for subtribes of Cardueae, with spiny pectinate-fimbriate appendages in Cardopatiinae; usually spiny, innermost exappendiculate or with rudimentary appendages in Carduinae; inner often conspicuous and coloured in Carlininae; scarious, fimbriate, pectinate, spiny or unarmed appendage in Centaureinae; and in many rows in Echinopsinae (Robinson, 2009; Susanna & Garcia-Jacas, 2009).

Certain floral microcharacters (anther size, shape of the anther apical appendage, configuration of stigmatic areas on the inner surface of the style branch, and configuration of the endothecial thickenings and of the filament collar) of 36 taxa of *Sinosenecio* showed that these floral characters are highly consistent with evidence from molecular systematics and cytology and provide the most important diagnostic characters in the tribe Senecioneae, as in the family at large and strongly suggest a polyphyletic nature of this genus, as well as the need of a taxonomic change at generic level (Liu & Yang, 2011).

Still nowadays, micromorphological investigations of Asteraceae could provide some novel characters (Erbar & Leins, 2015; Gavrilović et al. 2017, 2019b). Investigating style morphology of 395 species of 258 genera (covering all, in that time, 44 tribes of the Asteraceae), Erbar & Leins (2015) found a new microstructural feature, namely, often conspicuous cuticular patterns on the stylar hairs (involved in secondary pollen presentation) and stylar appendages. They determined five different patterns of cuticular striation and when they put these patterns onto a generalized phylogenetic tree (based on molecular data), they concluded that there is considerable homoplasy in these features. Nevertheless, cuticular patterns are still useful in characterizing some clades within the family. Gavrilović et al. (2017) investigating involucral bract micromorphology found, for the first time, a large number of densely packed crystals on the involucral bract surface. Also, the presence of nonglandular, curly trichomes and biseriate glandular trichomes on the bract surface, as well as the sylvite crystals on the petal surface of *X. cylindraceum*, clearly differentiates this species from *X. annuum* (Gavrilović et al., 2017). Comparative micromorphological analyses were conducted on five members of the Xerantheminae, both perennial (*Amphoricarpos exsul* and *Shangwua masarica*) and annual (*Chardinia orientalis*, *Siebera pungens* and *Xeranthemum inapertum*), showing that micromorphological traits link together perennial species, some link annual ones, some are species-specific, and some are common to all taxa (Gavrilović et al., 2019b).

We could conclude that morphology and micromorphology of florets (e.g., style base, anther appendages, trichomes on corollas), and inflorescence (involucral bracts characters, e.g., crystals and glandular and nonglandular trichomes on their wall) were used as major distinguishing features for subtribal and generic delimitation, even though these characters can sometimes be significant at the species level.

Anatomy

At the beginning of the twentieth century Col (1899-1901), in light of anatomy, reviewed in considerable detail distribution of laticiferous versus resiniferous tissue throughout the Asteraceae. Taxa with latex in canals or sacs occur in several tribes of the subfamily Cichorioideae and consistently in the Lactuceae, but very rarely in the Asteroideae, where resin sacs and resin canals are common. Carlquist (1966) investigated the basic plan of the wood anatomy of Asteraceae (focusing on four tribes, Anthemideae, Ambrosieae, Calenduleae, and Arctotideae), which provided useful tribal characters and minor intertribal variation. Even though Carlquist (1966) stated that Asteraceae members share a basically specialized wood plan and that wood anatomy is not likely to reward one with tribal or subtribal characters, certain characters are of systematic value within Anthemideae, Ambrosieae, Calenduleae, and Arctotideae (e.g., carbonized resins in intercellular spaces, secretory canals in rays, patterns of crystal occurrence are characters which may be of specific or generic value).

Metcalfe & Chalk (1957) noted some particular anatomical traits, which showed to have taxonomic importance within the family, e.g., presence of secretory and laticiferous canals, types of nonglandular and glandular trichomes, occurrence of medullar and cortical vascular bundles and presence of anomalous secondary thickening. Also, anatomical characteristics observable in Asteraceae are: (a) presence of various types of glandular and non-glandular trichomes; (b) papillae on the abaxial leaf epidermis; (c) anomocytic, anisocytic and rarely heliocytic stomata types; (d) presence of hydathodes; (e) presence of hypodermis; (f) homogeneous or heterogeneous mesophyll and (g) vascular bundles with a parenchymatic sheath composed of large cells (Metcalfe & Chalk, 1979).

Anatomy of several members of the tribe Senecioneae showed that they possess resin ducts in stems, leaves and roots, sometimes also in floral parts, and even in cotyledons. The resin production is noted as stickiness and exudates on vegetative parts. This occurs in the tussilaginoid as well as in senecioid group (Nordenstam et al., 2009).

Ginko et al. (2016) investigated suitability of anatomical characters of root and rhizome of 59 species belonging to 34 genera and 12 subtribes from tribes Cardueae and Cichorieae for taxonomic classification and phylogenetic reconstruction. In this case, anatomy is demonstrated as valuable to discriminate tribes and many species but not so for subtribes and genera. However, most anatomical traits seems to be homoplastic, which limits their application as phylogenetically informative characters.

Bombo et al. (2016) stated that anatomical features can help in resolving taxonomical problems within the genus *Aldama* La Llave, especially among Brazilian members, which are difficult to identify taxonomically. On the basis of their findings, the authors concluded that anatomy is able to provide data which assist with the taxonomic problems within the four analysed species.

The systematic value of leaf epidermal characters in Asteraceae has been proven by numerous studies, as leaf surface is under strong genetic control (Adedeji & Jewoola, 2008; Karanović et al., 2015). Some leaf blade characters (e.g., epidermal anticlinal cell walls, epicuticular wax and trichome type) have shown to be diagnostic to separate *Aster* L., *Galatella* Cass. and *Tripolium* Nees (Karanović et al., 2015). A comparative study of the leaf epidermis in 12 species of Asteraceae showed that the type and shape of trichomes, nature of cuticular striations and stomatal type are taxonomically important for the delimitation of species (Adedeji & Jewoola, 2008).

Qualitative anatomical characters (e.g., shape of the young stem and peduncle cross-sections, type of glandular trichomes and occurrence of cortical vascular bundles) were shown to be useful in delimitating *X. annuum* from *X. cylindraceum* (Gavrilović et al., 2019a). Moreover, some of the anatomical characters found in *Xeranthemum* (secondary growth in roots and dorsiventral leaves) suggested that adaptation from mesophytic to xeric habitats (Gavrilović et al., 2019a) are important for phylogenetic relationships within Xerantheminae.

Anatomical data can also contribute in resolving complex taxonomy of certain genera, e.g. *Artemisia*. In anatomical investigation of five *Artemisia* species, Janaćković et al. (2019) showed that some characters link together *A. absinthium* and *A. arborescens* from the same section; some other connect species belonging to different sections (*A. campestris* and *A. arborescens*; *A. absinthium* and *A. judaica*; *A. judaica* and *A. herba-alba*), while some could be considered as species-specific.

We could summarize that certain anatomical characters, such us distribution of laticiferous versus resiniferous tissue is useful on subfamily an tribal level, while patterns of crystal occurrence might be significant at species or genus level. Occurrence of cortical vascular bundles seems to be important on species level. Root and rhizome anatomical traits have proven to be useful on tribal and species, but not on the genus level. Leaf anatomical epidermal character are diagnostic and can be used for delimiting species. Also, qualitative anatomical characters may have role in understanding and solving phylogenetic relationships, which are reflected in the systematics of given taxa.

Micromorphology and anatomy of cypsela

The cypsela is a special form of dry indehiscent fruit in which the seed coat (testa) and fruit wall (pericarp) are tightly attached to one another and is exclusive characteristic of the family Asteraceae (Roth, 1977). As an exclusive fruit of the family cypsela and its features have been attracted by Tournefort (1694), Vaillant (1719), Cassini (1819), Lessing (1832), Bentham (1873), Hoffman (1894), Cronquist (1955), Robinson (1977), Bremer (1994), Nordenstam (1994), Rao & Datt (1996), Robinson (1999), Nordenstam et al. (2006), Lack (2007) and Mukherje & Nordenstam (2004, 2010). Cypsela morphology (macro- and micromorphology) and anatomy have been widely used in illuminating taxonomic relationships in Asteraceae and still represents a source of valid taxonomic characters (Lavialle, 1912; Stebbins, 1953; Wagenitz, 1976; Dittrich 1977; Barthlott, 1984; Singh & Pandey, 1984; Dittrich, 1985; Bruhl & Quinn, 1990; Glynis, 1993; Geng et al., 1994; Blanca & Díaz de la Guardia, 1997; Petit, 1997; Häffner, 2000; Zhu et al., 2006; Garg & Sharma, 2007; Pandey & Kumari, 2007; Zarembo and Boyko, 2008; Abid & Qaiser, 2009; Abid & Ali, 2010; Inceer et al., 2012; Ozcan & Akinci, 2019). This is why micromorphology and anatomy of cypsela are separated herein. Bremer (1987) stated the importance of cypselae characters at lower taxonomic levels but not at the tribal level. In Asteraceae, the anatomy and micromorphology of cypselas are taxonomically significant at both genus and species levels (Abid & Qaiser, 2009, Kulkarni, 2013, Hussein & Eldemerdash, 2016; Karanović et al., 2016; Gavrilović et al., 2019b).

Cypselae size and shape, number of ribs, presence of prickles, ornamentation of the intercostal gaps, tapering (sharp or gradual) of the body/beak junction, shape of the beak, degree of swelling at its apex and pubescence of the annulus are diagnostic in *Tragopogon* L. (Blanca & Díaz de la Guardia, 1997). Micromorphological characters of the cypselae (shape, surface, colour, size), pappus (stucture, shape, number, colour, size) and carpopodium (shape, position, diameter) in the tribes Senecioneae and Anthemidae are useful for assessing the relationship and delimitation at both generic and specific levels (Abid & Qaiser, 2009; Abid & Ali, 2010).

As a result of morphological and anatomical investigations of the cypselae in East Asian species of *Rhaponticum* Vaill., *Klasea* Cass., *Serratula* L. and *Synurus* Iljin in the tribe Cardueae s.l., Zarembo & Boyko (2008) clarified the following diagnostic traits at the species level: topography of epidermal cells of the pericarp, presence of phlobaphenes, occurrence, topography and localization of calcium oxalate crystals, and occurrence and location of secretory ducts in the mesocarp.

Karanović et al. (2016) showed that, besides receptacle characters, organisation of sclerenchymatous tissue in a fruit is a feature that tend to be diagnostic for genera *Inula, Pulicaria, Dittrichia* and *Limbarda*. Also, some fruit features have been demonstrated to be especially useful in distinguishing certain similar species (e.g., *Inula britannica* from *I. oculus-christi*). Moreover, authors stated that *I. helenium* should be separated from the *Inula* genus, as its authenticity is evident base on cypsela characters.

Silva et al. (2017) showed that features of the cypselae of the subtribe Disynaphiinae such as the carpopodium, floral disc, pappus, outer mesocarp, sclerenchyma, phytomelanin layer, ribs and trichomes are valuable at both generic and specific levels. Moreover, authors revealed the presence of a multiplicative pericarp only in a few *Symphyopappus* spp., rare trait in Asteraceae, which probably evolved independently in the family. Cypsela structure also supports the exclusion of *Disynaphia praeficta* from the subtribe, since this species possesses several different characters comparing with other representatives of Disynaphiinae.

Characters of cypselae are shown to be very informative at generic level within Xerantheminae (Gavrilović et al., 2019). For instance, *Shangwua* is distinguished from other genera in having glabrous cypsela, while *Chardinia* only possesses papillose cypsela surface. Moreover, cypsela features of Xerantheminae taxa are significant for phylogeny of the subtribe (some characters share all members, while some characters separates annual from perennial genera).

Ozcan & Akinci (2019) evaluated feasibility of cypsela characters as taxonomic markers investigating 21 taxa representing 12 genera of the tribe Cardueae. They observed considerable variability in surface sculptures of pappus and cypselae, as well as in pericarp and testa structures. Authors concluded that micromorphological and anatomical cypsela characters are distinct between the genera and are also useful for delimiting species.

Conclusion and future prospects

The breakthrough of molecular tools in plant systematics and its contribution to phylogenetic frameworks was and it is still a tremendous stimulus for comparative morphology and anatomy.

One should have in mind that the structure and biology of a majority of Asteraceae members are far from sufficiently investigated, thus combining morpho-anatomical, phytochemical, and molecular studies are necessary to explore them.

Although this overview represents only a glimpse of a role of micromorphological and anatomical approaches to Asteraceae systematics, it gives an valuable insight and perspective of this topic. Thus, the accumulated knowledge and permanent investigation of Asteraceae taxa using micromorphological and anatomical methods will put light on branching topologies of phylogenetic trees which molecular data established.

New opportunities for systematic morphology, micromorphology and anatomy in case of Asteraceae taxonomy, but certainly also in other plant groups, which were not present in the premolecular era, are now opening regarding synergistic multidisciplinary taxonomic, evolutionary and phylogenetic studies which combine molecular with morphological, anatomical and other approaches (e.g. chemophenetics), keeping in the throne these "old fashioned" approaches.

Acknowledgements. We acknowledge the financial support provided by the Serbian Ministry of Education, Science and Technological Development, project No. 173029.

References

Abid, R., Ali, N. 2010: Cypsela morphology and its taxonomic significance for the tribe Senecioneae (Asteraceae) from Pakistan. *Pakistan Journal of Botany*, 42: 117–133.

Abid, R. D., Qaiser, M. 2009: Taxonomic significance of the cypsela morphology in the tribe Anthemideae (Asteraceae) from Pakistan and Kashmir. *Pakistan Journal of Botany*, 41: 555–579.

Adedeji, O., Jewoola, O. A. 2008: Importance of leaf epidermal characters in the Asteraceae family. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 36:7–16

Bak, F. E., Ozcan, M. 2018: Pollen morphology of endemic NE Anatolian *Cirsium* taxa (Asteraceae). *Pakistan Journal of Botany*, 50 (3): 1181–1185.

Barthlott, W. 1984: Microstructural features of seed surfaces. In: Heywood, V. H., Moore, D. M. (eds.), *Current concepts in plant taxonomy*. Academic Press, Cambridge, pp. 95–105.

Batista, M. F., De Souza, L. A. 2017:. Flower structure in ten Asteraceae species: considerations about the importance of morpho-anatomical features at species and tribal level. *Brazilian Journal of Botany*, 40(1): 265–279.

Bentham, G. 1873: Notes on the classification, history, and geographical distribution of Compositae. *Botanical journal of the Linnean Society*, 13(70-72): 335–577.

Blanca, C. C., Guardia, C. D. 1997: Fruit morphology in *Tragopogon* L. (Compositae: Lactuceae) from the Iberian Peninsula. *Botanical journal of the Linnean Society*, 125: 319–329.

Bombo, A. B., Filartiga, A. L., Appezzato-da-Glória, B. 2016: Solving taxonomic problems within the *Aldama* genus based on anatomical characters. *Australian Journal of Botany*, 64(6): 501–512.

Bremer, K. 1987: Tribal interrelationships of the Asteraceae. Cladistics 3: 210–253.

Bremer, K. 1994: Asteraceae. Cladistics and Classification. Timber Press, Portland.

Bruhl, J. J., Quinn, C. J. 1990:. Cypsela anatomy in the 'Cotuleae' (Asteraceae–Anthemideae). *Botanical Journal of the Linnean Society*, 102(1): 37–59.

Carlquist, S. 1966: Wood anatomy of Anthemideae, Ambrosieae, Calenduleae and Articotideae (Compositae). *Aliso*, 6:1–23

Cassini, A. H. G. 1819: Suite du sixième mémoire sur la famille des Synanthérées, contenant les caractères des tribus. *Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts*, 88: 196–198.

Cassini, H. 1821. Hélianthées [with discussion of tribes]. In: Cuvier, F. (ed.), *Dictionnaire des Sciences Naturelles*, ed. 2, vol. 20. Le Normant, Paris. pp. 354–385

Col, A. 1889-1901:. Quelques recherches sur l'appareil sécréteur des Composées. *Journal de Botanique (Morot)*, 17: 252–318, 18: 110–133, 153–175. Columbia University Press, New York.

Cronquist, A. 1955:. Phylogeny and taxonomy of the Compositae. *American Midland Naturalist*, 478–511.

Dittrich, M. 1977. Cynareae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds.), *The Biology and Chemistry of the Compositae 2*. Academic Press, London, New York, San Francisco, pp. 999–1015.

Dittrich, M. 1985. Morphologische und anatomische Untersuchungen an Blüten und Früchten der Gattung *Carlina* (Compositae). *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie*, 107: 591–609.

Dormer, K. J. 1962: The fibrous layer in the anthers of Compositae. *The New Phytologist*, 61(2): 150–153.

Endress, P. K., Baas, P., Gregory, M. 2000: Systematic plant morphology and anatomy - 50 years of progress. *Taxon*, 49(3): 401–434.

Enke, N., Gemeinholzer, B., Zidorn, C. 2012: Molecular and phytochemical systematics of the subtribe Hypochaeridinae (Asteraceae, Cichorieae). *Organisms Diversity & Evolution*, 12(1): 1–16.

Erbar, C., Leins, P. 2015: Cuticular patterns on stylar hairs in Asteraceae: a new micromorphological feature. *International Journal of Plant Sciences*, 176(3): 269–284.

Garg, S. K., Sharma, K. C. 2007: Taxonomical significance of the micromorphological and scanning electron microscopic surface patterns of cypselas in some members of the tribe Heliantheae (Asteraceae). *Feddes Repertorium*, 118: 165–191.

Gavrilović, M., Erić, S., Marin, P. D., Garcia-Jacas, N., Susanna, A., Janaćković, P. 2017: Scanning electron microscopy coupled with energy dispersive spectrometric analysis reveals for the first time weddellite and sylvite crystals on the surface of involucral bracts and petals of two *Xeranthemum* L. (Compositae) species. *Microscopy and Microanalysis*, 23(3): 679–686.

Gavrilović, M., Tešević, V., Đorđević, I. S., Rajčević, N., Bakhia, A., Jacas, N. G., Susanna, A., Janaćković, P. T. 2018a: Leaf micromorphology, antioxidative activity and a new record of 3-deoxyamphoricarpolide of relict and limestone endemic *Amphoricarpos elegans* Albov (Compositae) from Georgia. *Archives of Biological Sciences*, 70(4): 613–620.

Gavrilović, M., de Oliveira, A. F. M., Barbosa, M. O., Garcia-Jacas, N., Susanna, A., Marin, P. D., Janaćković, P. 2018b: Micromorphology and fatty acid composition of the cypselae of *Xeranthemum cylindraceum* Sm.(Asteraceae, Cardueae). *Botanica Serbica*, 42 (2): 241–250.

Gavrilović, M., Rančić, D., Škundrić, T., Dajić-Stevanović, Z., Marin, P., Garcia-Jacas, N., Susanna, A., Janaćković, P. 2019a: Anatomical characteristics of *Xeranthemum* L. (Compositae) species: taxonomical insights and evolution of life form. *Pakistan Journal of Botany*, 51: 1007–1019.

Gavrilović, M., Jacas, N. G., Susanna, A., Marin, P. D., Janaćković, P. 2019b: How does micromorphology reflect taxonomy within the *Xeranthemum* group (Cardueae-Asteraceae)?. *Flora*, 252, 51–61.

Geng, S. L., An, Z. X., Tian, Y. W. 1994: The studies of fruit anatomy and systematic classification of tribe Senecioneae in Xinjiang. *Journal of Agriculture & Life Sciences*, 17: 9–17.

Ginko, E., Dobeš, C., Saukel, J. 2016: Suitability of root and rhizome anatomy for taxonomic classification and reconstruction of phylogenetic relationships in the tribes Cardueae and Cichorieae (Asteraceae). *Scientia Pharmaceutica*, 84: 585–602.

Glynis, V. C. 1993. The anatomy of the cypselae of species of *Cineraria* L (Asteraceae–Senecioneae) and its taxonomic signif-icance. *Botanical journal of the Linnean Society*, 112: 319–334.

Gruenstaeudl, M., Urtubey, E., Jansen, R. K., Samuel, R., Barfuss, M. H., Stuessy, T. F. 2009: Phylogeny of Barnadesioideae (Asteraceae) inferred from DNA sequence data and morphology. *Molecular Phylogenetics and Evolution*, 51(3): 572–587.

Häffner, E. 2000: On the phylogeny of the subtribe Carduinae (tribe Cardueae, Compositae). *Englera*, 21: 1–208.

Hayat, M. Q., Ashraf, M., Khan, M. A., Yasmin, G., Shaheen, N., Jabeen, S. 2009: Diversity of foliar trichomes and their systematic implications in the genus *Artemisia* (Asteraceae). *International Journal of Agriculture and Biology*, 11: 542–546.

Hoffmann O. 1890-1894: Compositae. In: Engler, A., Prantle, K. (eds.), *Dienatürlichen Pflanzenfamilien*, Engelmann, Leipzig 4(5): 87–387.

Hussein, H. A., Eldemerdash, M. M. 2016: Comparative morphology and surface microsculpture of cypsela in some taxa of the Asteraceae and their taxonomic significance. *Egyptian Journal of Botany*, 56: 409–422.

Inceer, H., Bal, M., Ceter, T., Pinar, N.M. 2012: Fruit structure of 12 Turkish endemic *Tripleurospermum* Sch. Bip. (Asteraceae) taxa and its taxonomic implications. *Plant Systematics and Evolution*, 298: 845–855.

Janaćković, P., Gavrilović, M., Rančić, D., Dajić-Stevanović, Z., Giweli, A. A., Marin, P. D. 2019: Comparative anatomical investigation of five *Artemisia* L. (Anthemideae, Asteraceae) species in view of taxonomy. *Brazilian Journal of Botany*, 42(1): 135–147.

Jeffrey, C., Chen, Y. L. 1984: Taxonomic studies on the tribe Senecioneae (Compositae) of Eastern Asia. *Kew Bulletin*, 39: 205–446.

Karanović, D., Luković, J., Zorić, L., Anačkov, G., Boža, P. 2015: Taxonomic status of *Aster*, *Galatella* and *Tripolium* (Asteraceae) in view of anatomical and micro-morphological evidence. *Nordic Journal of Botany*, 33: 484–497.

Karanović, D., Zorić, L., Zlatković, B., Boža, P., Luković, J. 2016: Carpological and receptacular morpho-anatomical characters of *Inula*, *Dittrichia*, *Limbarda* and *Pulicaria* species (Compositae, Inuleae): Taxonomic implications. *Flora*, 219, 48–61.

Karis, P.O., Funk, V., McKenzie, R.J., Barker, N.P., Chan, R. 2009: Arctotideae. In: Funk, V. A., Susanna, A., Stuessy, T.F., Bayer, R.J. (eds.), *Systematics, Evolution and Biogeography of Compositae*. IAPT, Vienna, pp. 385–411.

Kilian, N., Gemeinholzer, B., Walter Lack, H. 2009: Cichorieae In: Funk, V. A., Susanna, A., Stuessy, T.F., Bayer, R.J. (eds.), *Systematics, Evolution and Biogeography of Compositae*. IAPT, Vienna, pp. 343–383.

Kulkarni, S. V. 2013: SEM studies of achenes in some taxa of Asteraceae. *International Journal of Environmental Rehabilitation and Conservation*, 4: 87–97.

Lack, H.W. 2007: Cichorieae. In: Kadereit, J.W., Jeffrey, C. (eds.), *The Families and Genera of Vascular Plants, Vol. 8, Flowering Plants, Eudicots. Asterales*. Springer, Berlin. pp. 180–199.

Lavialle, P. 1912: Recherches sur le développement de l'ovaire en fruit chez les Composées. Masson.

Lessing, C. F. 1832: Synopsis generum Compositarum. Duncker & Humblot, Berlin.

Liu, Y., Yang, Q. E. 2011: Floral micromorphology and its systematic implications in the genus *Sinosenecio* (Senecioneae-Asteraceae). *Plant Systematics and Evolution*, 291(3-4): 243–256.

Makbul, S., Güler, N. S., Durmuş, N., Güven, S. 2011: Changes in anatomical and physiological parameters of soybean under drought stress. *Turkish Journal of Botany*, 35(4): 369–377.

Mandel, J. R., Dikow, R. B., Siniscalchi, C. M., Thapa, R., Watson, L. E., Funk, V. A. 2019: A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *Proceedings of the National Academy of Sciences*, 116 (28) 14083–14088.

Metcalfe, C. R., Chalk, L. 1957: Anatomy of the Dicotyledons. Clarendon Press, Oxford.

Metcalfe, C. R., Chalk, L. 1979: Anatomy of dicotyledons: systematic anatomy of the leaf and stem, with a brief history of the subject, vol 1. Claredon Press, Oxford.

Mukherjee, S. K., Nordenstam, B. 2010: Distribution of calcium oxalate crystals in the cypselar walls in some members of the Compositae and their taxonomic significance. *Compositae Newsletter*, 48: 63–88.

Mukherjee, S. K., Nordenstam, B. 2004: Diversity of carpopodial structure in the Asteraceae and its taxonomic significance. *Compositae Newsletter*, 41: 29–50.

Nordenstam, B. 1994: Tribe Calenduleae. Asteraceae. Cladistics and Classification. Timber Press, Portland, 365-376.

Nordenstam, B. 2007: Tribe Calenduleae Cass. (1819). In: Kadereit, J. W., Jeffrey, C. (eds), *The families and genera of vascular plants*, *Vol. 8*. Springer, Berlin, Heidelberg, pp. 241–245.

Nordenstam, B., Pelser, P.B., Kadereit, J.W., Watson, L.E. 2009: Senecioneae. In: Funk, V. A., Susanna, A., Stuessy, T.F., Bayer, R.J. (eds.), *Systematics, Evolution and Biogeography of Compositae*. IAPT, Vienna, pp. 503–525.

Ozcan, M., Akinci, N. 2019: Micromorpho-anatomical fruit characteristics and pappus features of representative Cardueae (Asteraceae) taxa: their systematic significance. *Flora*, 256: 16–35.

Pandey, A. K., Kumari, A. 2007: Anatomical patterns of pericarp in Asteraceae. In: Chauhan, S. V. S., Rana, A., Chauhan, S. (eds), *Plant Reproductive Biology and Biotechnology*. Aavishkar Publisher, Jaipur, pp. 64–77.

Petit, D. P. 1997: Generic interrelationships of the Cardueae (Compositae): a cladistic analysis of morphological data. *Plant Systematics and Evolution*, 207: 173–203.

Pornpongrungrueng, P., Borchsenius, F., Englund, M., Anderberg, A. A., Gustafsson, M. H. 2007: Phylogenetic relationships in *Blumea* (Asteraceae: Inuleae) as evidenced by molecular and morphological data. *Plant Systematics and Evolution*, 269(3–4): 223–243.

Rao, R. R., Dutt, B. 1996: Diversity and phytogeography of Indian Compositae. In: Hind, D. J. N., Beentje, H. J. (eds.), *Compositae: Systematics. Proceedings of the International Compositae Conference 1*, Royal Botanic Garden, Kew. pp. 445–461.

Robinson, H. 1977: An analysis of the characters and relationships of the tribes Eupatorieae and Vernonieae (Asteraceae). *Systematic Botany*, 2(3): 199–208.

Robinson, H. 2009: An introduction to micro-characters of Compositae. In: Funk, V. A., Susanna, A., Stuessy, T.F., Bayer, R.J. (eds.), *Systematics, Evolution and Biogeography of Compositae*. IAPT, Vienna, pp. 89–100.

Robinson, H. 1999: Two new subtribes Stokesiinae and Pacourininae, of the Vernonieae (Asteraceae). *Proceedings of the Biological Society of Washington*, 112: 216–219.

Roth, I. 1977: Fruits of Angiosperms. Gebrüder Borntraeger, Berlin.

Scatena, V. L., Giulietti, A. M., Borba, E. L., Van den Berg, C. 2005: Anatomy of Brazilian Eriocaulaceae: correlation with taxonomy and habitat using multivariate analyses. *Plant Systematics and Evolution*, 253: 1–22.

Schönberger, I. 2002: Biosystematics and taxonomy of the *Ozothamnus leptophyllus* (Compositae) complex in New Zealand. Doctorate. University of Canterbury.

Silva, T. D., Marzinek, J., Hattori, E. K., Nakajima, J. N., De-Paula, O. C. 2017: Comparative cypsela morphology in Disynaphiinae and implications for their systematics and evolution (Eupatorieae: Asteraceae). *Botanical Journal of the Linnean Society*, 186(1): 89–107.

Singh, R. P., Pandey, A. K. 1984: Development and structure of seeds and fruits in Compositae - Cynareae. *Phytomorphology*, 34: 1–10.

Smith, R. I. L., Richardson, M. 2011: Fuegian plants in Antarctica: natural or anthropogenically assisted immigrants? *Biological Invasions*, 13(1): 1–5.

Sosa, M. M., Via do Pico, G. M., Dematteis, M. 2014: Comparative anatomy of leaves and stems in some species of the South American genus *Chrysolaena* (Vernonieae, Asteraceae) and taxonomic implications. *Nordic Journal of Botany*, 32: 611–619.

Stebbins, G. L. 1953: A new classification of the tribe Cichorieae, family Compositae. *Madroño*, 12(3): 65–81.

Stuessy, T. F. 2009: Plant taxonomy: The systematic evaluation of comparative data.–2nd ed. Columbia University Press, New York, Chichester, West Sussex.

Susanna, A., Garcia-Jacas, N. 2009: Cardueae (Carduoideae), In: Funk, V. A., Susanna, A., Stuessy, T.F., Bayer, R.J. (eds.), *Systematics, Evolution and Biogeography of Compositae*. IAPT, Vienna, pp. 293–313.

Tournefort, J.P. 1694: Élemens de Botanique. 3 vols. Imprimeric Royale, Paris.

Vaillant, S. 1719: Establishment de nouveau caracteres de triosfamillesou classes de plantes a fleur composes: scavoir, des Cynarocephales, des Corymbiferes, et des Cichoracees. Histoire de l' Academie Royale des Sciences avec les Memoires de Mathematique&des Physique (Paris 4) 1718: 143–191.

Wang, Y. J., von Raab-Straube, E., Susanna, A., Liu, J. Q. 2013: *Shangwua* (Compositae), a new genus from the Qinghai-Tibetan Plateau and Himalayas. *Taxon*, 62(5): 984–996.

Wang, Z. H., Peng, H., Kilian, N. 2013: Molecular phylogeny of the *Lactuca* alliance (Cichorieae subtribe Lactucinae, Asteraceae) with focus on their Chinese centre of diversity detects potential events of reticulation and chloroplast capture. *PLoS One*, 8(12): p.e82692.

Zarembo, E.V., Boyko, E.V. 2008: Carpology of some east Asian Cardueae (Asteraceae). *Anales del Jardín Botánico de Madrid*, 65: 129–134.

Zhu, S.X., Qin, H.N., Shih, C. 2006: Achene wall anatomy and surface sculpturing of *Lactuca* L. and related genera (Compositae: Lactuceae) with notes on their systematic significance. *Journal of Integrative Plant Biology*, 48: 390–399.

Zidorn, C. 2019: Plant chemophenetics – a new term for plant chemosystematics/plant chemotaxonomy in the macro-molecular era. *Phytochemistry*, 163: 147–148.