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Systematics, Ecology, and Chromosomal Evolution of *Melampodium* (Asteraceae)

Analysis of Species from Latin America and the Southwestern United States

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Melampodium divaricatum, an attractive species widely distributed throughout Latin America.

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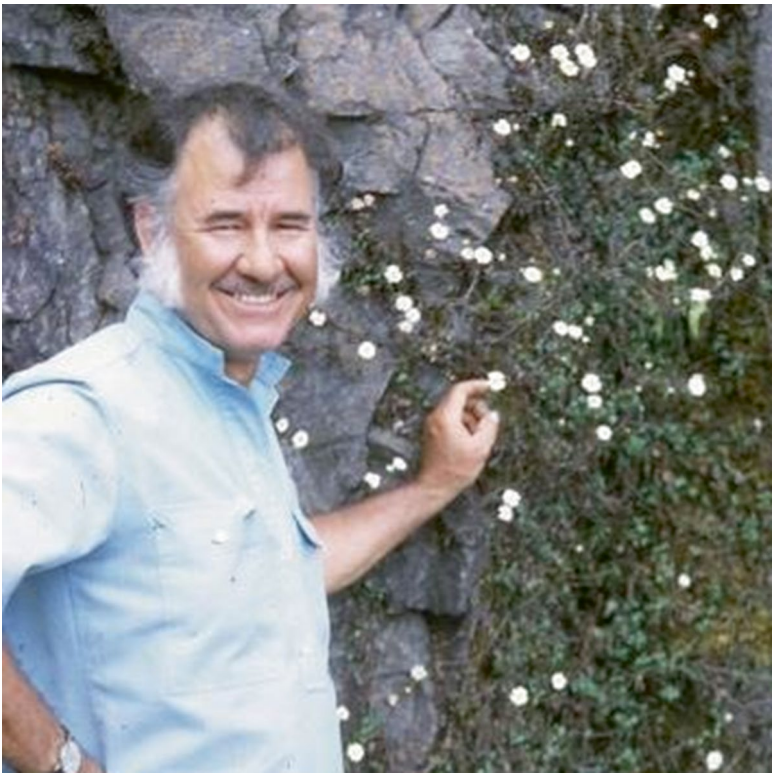
ISBN 978-3-031-81994-0 ISBN 978-3-031-81995-7 (eBook)
https://doi.org/10.1007/978-3-031-81995-7

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

We dedicate this book to the memory of Billie Lee Turner (1925–2020), former Professor at the University of Texas, Austin, who was responsible for opening the door to Melampodium *for the senior author, which eventually made this book possible. He was an outstanding plant systematist and a stimulating and supportive mentor.*



Preface

How and why we have dedicated time and resources to understanding *Melampodium* deserves some explanation. Of all the plants on Earth, why this particular genus? The story begins in 1965 with the start of a Ph.D. study by T. Stuessy, conducted at the University of Texas under the supervision of Prof. Billie Lee Turner. During Stuessy's first week in Austin, Turner led him to the hallway of the fourth floor of the Biological Sciences Building and the many cases of Asteraceae (Compositae), each containing genera housed in folders, with species organized alphabetically. There was quite a bit of *Melampodium*; in fact, the entire right row of shelves contained numerous species of this genus. Turner said: "Now, *Melampodium* is an interesting genus, lots of taxonomic problems, needs careful work. And there is chromosomal variation, too, which should be significant in the systematics and evolution of the group. How would you like to do your thesis on this genus? The group is largely Mexican in distribution, and I know you wanted to do research with plants from that region." Being terribly naïve about research at this point, Stuessy simply said: "OK. I'll do it."

The selection of *Melampodium* for systematic research was not done after months of careful literature searching, evaluating alternative genera, and discussing bold biological questions. No hypotheses were formulated; it was just very simple. From 1965 to 1968, Stuessy immersed himself in the world of *Melampodium*, finally publishing articles on chromosome studies (1970a) and phylogeny (1971), followed by a comprehensive revision of the genus (1972). Further work extended to related genera (Stuessy, 1969, 1970b), the subtribe (Stuessy, 1973a), and eventually the entire tribe (Stuessy, 1977, 1980).

After graduation from Texas, Stuessy joined the faculty at Ohio State University, Columbus, eventually moving on to examine other Mexican genera of Asteraceae (e.g., *Baltimora*, Stuessy, 1973b; *Lagascea*, Stuessy, 1978; *Isocarpha*, Keil and Stuessy, 1981; *Otopappus*, Hartman & Stuessy, 1983). Some collaborative work on *Melampodium* was published with phytochemists, especially Prof. Klaus Fischer and colleagues of the Department of Chemistry of Louisiana State University (sesquiterpene lactones; Seaman et al., 1980) and Prof. Bruce A. Bohm of the Department of Botany at the University of British Columbia (flavonoids; Bohm & Stuessy, 1991,

2001). Some small grants enabled more populational sampling within the white-rayed complex, which many years later was published (Stuessy et al., 2004).

Into the 1970s and 1980s, quantitative methods for assessing relationships became popular, and this led to a cladistic study of *Melampodium* (Stuessy, 1979), based on data accumulated during the revision of the genus. This placed the understanding of phylogeny of the group on a firmer basis. The cladistic investigation was complemented by numerical taxonomic studies (phenetics) in collaboration with Prof. Jorge V. Crisci from the Universidad Nacional de La Plata, Argentina (Stuessy & Crisci, 1984). These quantitative studies demonstrated the robustness of some of the infrageneric units (sections) within the taxonomy of the genus, and they highlighted a few others that were only weakly supported.

Work on *Melampodium* slowed down considerably as Stuessy moved in 1997 to the Department of Botany and Biodiversity Research of the University of Vienna, Austria, where he became involved with research projects of island biology (especially in the Juan Fernández Archipelago, Chile, and Ullung Island, Korea) and speciation and biogeography in the genus *Hypochaeris* of South America and the Mediterranean region. The research environment in Vienna was rich with colleagues pursuing many different botanical avenues from floristics, monography, morphology, DNA, and cytogenetics. The institute had a long tradition in cytology and cytogenetics, and this continues to the present day.

During a departmental seminar in Vienna, it was decided to read the new book, a chapter per week, by Donald Levin (2002): *The Role of Chromosomal Change in Plant Evolution*. As there were more weeks than chapters, additional presentations were solicited, and Stuessy talked about the wide chromosomal variation in *Melampodium*. This generated some interest, and after the presentation, Hanna Weiss-Schneeweiss, a postdoc in the department, said: "This range of chromosome numbers is quite impressive in *Melampodium*, and it might make sense to look at this again with modern molecular approaches, especially involving DNA." After more discussion, it became obvious that modern investigations could indeed reveal evolutionary relationships more precisely, plus indicating pathways (and perhaps also mechanisms) of chromosomal change within the genus.

Thanks to the generosity of the Austrian Science Fund (FWF), including a Hertha Firnberg fellowship to Hanna Weiss-Schneeweiss, substantial three-year funding was obtained that allowed progress on *Melampodium* to be made. This provided money for collecting trips to Mexico and adjacent regions, as well as laboratory studies, including molecular analyses. A good basis for the project was that Stuessy knew the species of *Melampodium*, having collected them back in the 1960s, which meant that it should be possible to collect material (seeds, leaves for DNA work, buds for cytological studies, and herbarium vouchers) without too much difficulty. Two graduate students, Cordula Blöch and Carolin Rebernig, joined the group and each completed their Ph.D. theses within the project. This FWF project was followed by another three-year effort, this time with emphasis on the origin of polyploid species and the biogeography of selected species complexes. A third Ph.D. student, Jamie MacCann, joined the team in this second grant phase to add expertise in phylogenetic analyses. The principals for this work were: Tod Stuessy,

coordinator of field studies with our collaborator, José L. Villaseñor, of the National Herbarium (MEXU), Universidad Nacional Autónoma de México (UNAM); Hanna Weiss-Schneeweiss, cytogeneticist; and Gerald M. Schneeweiss as phylogenetic and biogeographic expert. This team produced a series of interesting papers (e.g., Blöch et al., 2009; Rebernig et al., 2010a, b, 2012; Weiss-Schneeweiss et al., 2012; McCann et al., 2016, 2018, 2020).

Despite the many publications on *Melampodium* over the past 50 years, never has this information been synthesized into a whole so that the genus might serve as an instructive case study of plant systematics and chromosomal evolution. It is this interest that has led to the preparation of the present book. It begins by introducing the morphology and habitat preferences of the genus. Species occur all over Mexico, and there are very few regions of the country where one cannot find at least one species. This is not a genus that stays nestled in secluded nearly inaccessible valleys, requiring backpacking for two days to find populations. *Melampodium* does quite well with disturbance and can often survive along fence rows, old agricultural fields, and even around buildings. One of the species, *M. divaricatum* (see Frontispiece), has been successfully transported inadvertently to many other countries, and its vitality and adaptability have led to its being introduced to cultivation in the United States and Europe. Because of the existence of people in Mexico for so many centuries, it makes one wonder what the human impact might have been on the original distributional patterns of species within the genus.

Melampodium, therefore, represents a very good case study of a plant genus in which chromosomal change has played an important role in its evolution, with 13 different chromosome numbers ($n = 9, 10, 11, 12, 14, 18, 20, 23, 24, 27, 28, 30, 33$), one of the longest series among genera of Asteraceae (Watanabe, 2008; Semple & Watanabe, 2009). Furthermore, numerical and structural chromosomal changes have accompanied a radiation of species over the varied Latin American landscape, especially in Mexico, allowing colonization of lowland tropical forests, pine-oak associations, thorn-scrub vegetation, savannas, mesquite-grassland, and arid deserts. The background of morphological and ecological diversity within the genus has been combined with detailed DNA studies of phylogeny and phylogeography, plus cytogenetic analyses.

There is much more that future studies of *Melampodium* can teach us about plant adaptation and speciation. It is a group well-positioned for greenhouse studies to reveal more clearly the isolating mechanisms and genetic affinities of taxa. *Melampodium* has a simple monoecious breeding system, with male (disc) flowers in the center of the flowering head and female (ray) flowers toward the exterior. Removal of the disc during development renders the head functionally female, and the reverse when the developing ray flowers are removed. These simple manipulations, plus adaptability to greenhouse culture and ease of seed germination, greatly facilitate making crosses within and among species of the genus. Some preliminary crossing studies have been accomplished (see Chap. 8), but much more can be done.

So, in large measure, this book is a progress report on understanding evolution within *Melampodium*. Our goal has been to bring together the scattered literature on the genus, plus adding new interpretations, to establish a research platform from

which further investigations can yield deeper insights. In the meantime, we hope that the reader finds the genus as instructive and fascinating as we have found it over these many years.

Columbus, OH, USA — Tod F. Stuessy
Vienna, Austria — Hanna Weiss-Schneeweiss
Gerald M. Schneeweiss
Ciudad de México, México — José L. Villaseñor

Acknowledgments

All authors are indebted to many institutions and persons who have helped bring a book into print. This work is no exception. Appreciation must go to the institutions that have provided salaries, offices, herbaria, and laboratories for the conduct of the research and writing of this book: Department of Botany, University of Texas, Austin; Department of Botany, The Ohio State University; Department (now Division) of Systematic and Evolutionary Botany, University of Vienna, Austria; and Department of Botany of the Universidad Nacional Autónoma de México (UNAM). Permissions for leaves of absence from campus for field work were provided for T. Stuessy by the University of Texas, The Ohio State University, and the University of Vienna; and for J. L. Villaseñor, from UNAM. Without this administrative support for research on *Melampodium*, it simply would not have been completed.

Research does not get done without financial resources. We have been fortunate to have received several grants that have made our work possible. The principal source of the initial funding came from the U.S. National Science Foundation, which supported Stuessy for two years during doctoral work on *Melampodium* at Texas (through a traineeship grant to Prof. Frank Blair, No. GB-6914). One field excursion to Mexico was partially supported by an NSF grant to Prof. Howard Arnott (No. GB-1458), and supplemental aid came from Sigma Xi. During postdoctoral studies on Melampodiinae at Harvard University in 1971–1972, Stuessy received support from the Maria Moors Cabot Foundation. At Ohio State, he also received a small institutional grant that allowed more field work (and subsequent cytological studies) on the white-rayed complex of the genus. Major funding materialized in Vienna with two three-year FWF (Austrian Science Fund) grants, the first to Stuessy and H. Weiss-Schneeweiss (FWF Grant No. P18201), and the second to H. Weiss-Schneeweiss, G. M. Schneeweiss, and Stuessy (FWF Grant No. P25131). A small grant was provided from the Commission for Interdisciplinary Ecological Studies (KIÖS) of the Austrian Academy of Sciences (No. P2007-12 to TFS). Additional support was also provided by FWF to H. Weiss-Schneeweiss with a postdoctoral Hertha-Firnberg Fellowship (T-218). Very important is to mention the very strong support from the University of Vienna for the purchase of major

laboratory equipment for molecular phylogenetic investigations on *Melampodium* and other projects.

The research grants in Vienna made possible Ph.D. investigations by Cordula Blöch, Jamie McCann, and Carolin Rebernig. They accompanied Stuessy and Villaseñor on field trips to Mexico and the southwestern United States, and they carried out most of the laboratory work on bioinformatics and molecular phylogenetics.

Many other persons over the years also contributed to the success of the research effort, and most are so indicated as co-authors on papers. These include: Katharina E. Bardy, Michael H. Barfuss, Bruce A. Bohm, Jere N. Brunken, Jorge V. Crisci, Nicolas (Klaus) H. Fischer, Sabine Jakob, Tae-Soo Jang, David J. Keil, Jiři Macas, Nicholas J. Matzke, Petr Novák, Renate Obermayer, Arun Pandey, Peter Schönswetter, Fred C. Seaman, Scott D. Sundberg, and Barbara Turner. Without contributions from these excellent colleagues and researchers, our work with *Melampodium* would not have been accomplished.

Other persons and institutions have contributed important help in different capacities. A special thanks goes to Enrique Ortiz of the Department of Botany, UNAM, for assistance with field work, databasing of collected specimens, production of distribution maps, and excellent photographs of species of *Melampodium*, many of which appear in this book. Distributional data come from Stuessy (1972), herbarium records at UNAM, and GBIF. Patrick Alexander, Donovan Bailey, Jorge Calónico, Ismael Calzada, Gabriel Flores, Sylvia Kelso, Michael Lenko, Chris Meacham, Monique Reed, Joaquin Sánchez, John Schoenhofen, Richard Spellenberg, and Hugh Wilson also helped with aspects of facilitating field collections. Technical support in Vienna was also provided by Verena Klejna and Gudrun Kohl. Tom Wendt of the Herbarium at the University of Texas (TEX) kindly permitted us to investigate DNA from collections of the recently described *Melampodium moctezumum* (Turner, 2007) and *M. elottianum* (Turner, 2016). Permits for field collections in Mexico were generously provided for Villaseñor et al. from SEMARNAT and in Costa Rica by CONAGEBIO. We also thank Prof. Hennig Adsersen for providing material of *Lecocarpus* for analysis.

Many of the illustrations in this book have come from our own photographs, figures, and maps. Use of some images has been allowed under: Creative Commons (Figs. 2.4A, 2.9A, 4.11A [Hugh Iltis], 4.11B); Wikimedia Commons (Figs. 2.9B, 4.12A–C); and STM publishers agreement (Figs. 2.2, 2.6, 2.7, 4.9, 4.13, and 8.2; Table 8.2). Several individuals have kindly given permission to reproduce additional images: Paul Fontaine (Fig. 2.4B,C); Reed F. Noss (Fig. 1.1); A. Michael Powell (dedication photo); Ingo Schubert (Fig. 1.3); Richard Spellenberg (Fig. 3.2); and Jun Wen (Fig. 1.2). Marek Brys from WorldAtlas.com kindly allowed use of a map of Mexico (Fig. 4.8).

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Media] (Fig. 7.9); *International Journal of Plant Sciences* [University of Chicago Press] (Figs. 5.7, 5.8, 5.9, and 7.2); *Journal of Systematics and Evolution* [John Wiley] (Fig. 1.2); *Madroño* [California Botanical Society] (Figs. 8.6, 8.7, 8.8, and 10.6; Table 8.3); *Molecular Ecology* [John Wiley] (Figs. 9.7, 9.8, and 9.9); *Molecular Phylogenetics and Evolution* [Elsevier] (Figs. 6.4, 6.5, 6.6, 9.10, 9.11, and 9.12); *PLoS One* [Public Library of Science] (Fig. 7.3); *Rhodora* [New England Botanical Society] (Figs. 3.3, 3.4, and 3.5); *Systematic Biology* [Oxford University Press] (Figs. 7.7 and 7.8); *Taxon* [John Wiley] (Figs. 3.1, 6.1, 6.2, 6.7, 6.8, 6.9, 6.10, and 10.7); *Wildflower* [Lady Bird Johnson Wildflower Center] (Fig. 2.1A).

Books do not just appear out of nowhere—they must be produced. For this we enthusiastically thank our editor at Springer Nature, Kenneth Teng, who has been consistently supportive of this book project and made many helpful suggestions for its improvement. We also thank our production editors, Kalai Shahethya, and Mahalakshmi Saravanan, for shepherding our rough files into quality final presentations.

Contents

Chapter 1
Biodiversity and Chromosomal Evolution

The world we call home, our Earth, is a paradise. This blue, white, and green marble hurtling through black space is sheathed by a mantle of oxygen and other gasses that allows millions of life forms to exist**.** They abound on land, in the sea, and in the air, some being as large as the California big trees, or whales that inhabit the ocean, but others being minute, such as the bacteria and viruses, which are far beyond detection with human eyesight. Somewhere in between are humans, members of our species, that survive by utilizing the energy resources from the sun that have been captured by green plants in the manufacture of carbohydrates. From these building blocks, other organic compounds developed and eventually led to the formation of life forms of increasing complexity that now serve as foods for all animals, including ourselves.

The total of life forms on the planet is its biodiversity. The total number of species is still unknown, but estimates range upward of 8.7 million (Mora et al., 2011) or even more, of which only about 2.1 million have been described formally so far (IUCN, 2022). For proper management of biotic resources for our survival, and for that of other species on the planet, inventorying of these life forms must have a very high priority (Stuessy, 2020a). It is difficult to manage anything effectively when so much data are lacking. The challenge is made even greater because the highest levels of biodiversity reside in countries that are still developing and do not have large amounts of excess money for research activities.

Biodiversity involves species, because these represent basic units of diversity that we can observe and understand most easily, but it also involves their functions and interactions that contribute to the formation of ecosystems. In a broader context, biodiversity can be envisaged as consisting of structural, functional, and compositional dimensions (Fig. 1.1), and these involve different hierarchical levels, such as genes, populations, communities, and landscapes. The compositional aspect is the usual concept of biodiversity, ranging from genetic diversity, through populations, species, and finally ecosystems. But these levels also form more general structures over the landscape, involving genes, populations, habitats, and landscapes.

T. F. Stuessy et al., *Systematics, Ecology, and Chromosomal Evolution of* Melampodium *(Asteraceae)*, https://doi.org/10.1007/978-3-031-81995-7_1

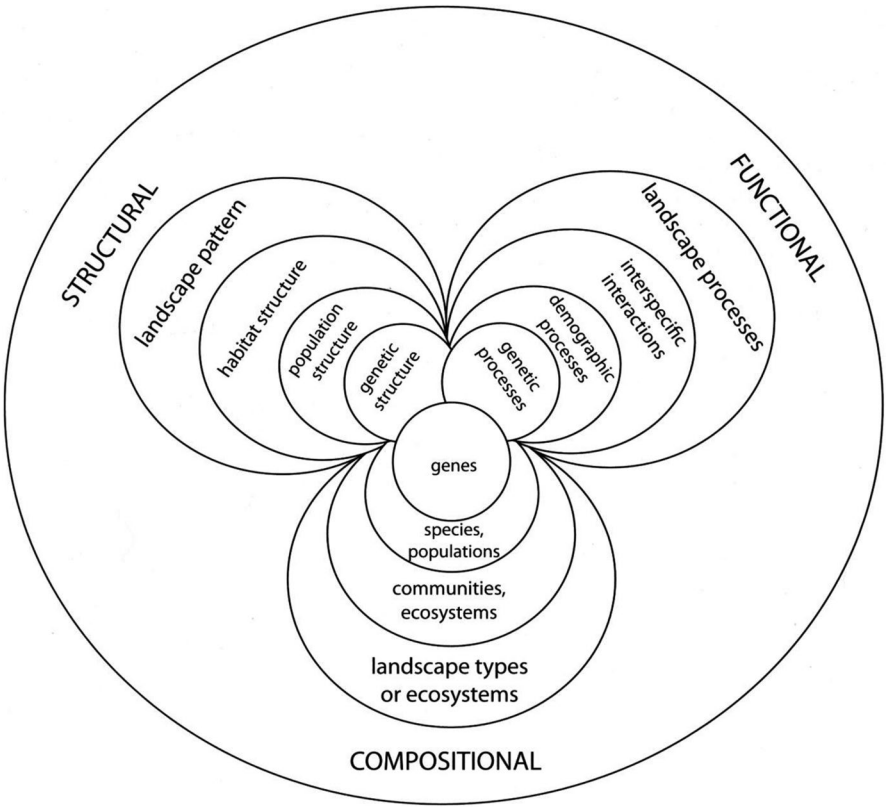

Fig. 1.1 Aspects of biodiversity (structural, compositional, functional) at different levels of organization. (Modified from Noss, 1990: 357)

Furthermore, within these structures are functional aspects that begin with genetic processes and then extend up the hierarchy to include demographic processes, interspecific interactions, and even landscape processes.

The Importance of Biodiversity

It takes little imagination to appreciate how vital biodiversity, in all its dimensions, is for human success on this planet. The basic values of biodiversity deal with goods, information, services, and psychological benefits. As for goods, the amount of harvesting of timber for wood resources worldwide is immense. We remind ourselves that the rooms in which we live are constructed from water-conducting tissues of trees, their secondary xylem. These same tissues are used as fuel in many countries, providing warmth during cold seasons and for cooking year-round. Plants also are used for foods, not only harvested directly from the forests, but also grown

in massive factory farms on gigantic scales in the production of wheat, corn (maize), rice, soybean, and numerous others. In addition to foods, plants are extremely important for their fibers that get woven into clothing, plus cords and ropes of a wide variety. Plants also provide medicinals to help alleviate human suffering (Bernardini et al., 2018), with as much as 25% of present pharmaceuticals having been originally derived from natural plant populations (Miller, 1996).

Biodiversity also provides information regarding our natural world. Curiosity is one reason people seek to learn about other species that share our planet, but it is also a desire to manage the environment and increase our chances of survival. The more we can control our environment, the more stable will be our existence, and presumably the happier we will be both now and for future generations. In dealing with microbes, many of which are pathogenic, we need information about their lifestyles, their metabolism, and their reproduction to be able to restrict their harmful effects on us and all other species in the ecosystem.

The services offered by biodiversity come in diverse forms. We are familiar with recreational activities associated with turf grasses in golf courses, football stadiums, and parks, plus the richer organismal diversity presented in zoos and botanical gardens. But even more important is how the individual species interact to create working ecosystems that give us rain, nitrogen fixation, pollination, and carbon cycles. Many studies have been done that suggest that high levels of biodiversity provide greater stability for ecosystem functions (e.g., Tilman et al., 2006; Naeem et al., 2012; Reich et al., 2012; Wang & Loreau, 2016). The yearly economic value of these services is unbelievably high, having been estimated by Costanza et al. (1997) to be somewhere between 16 and 54 trillion dollars (US).

Finally, no one can deny the importance of biodiversity, especially plant diversity, for human well-being. Beautiful flowers are used to celebrate nearly all stages of human life from birth, birthdays, marriage, having children, illness, and finally death. Humans also need contact with animals, as easily witnessed by a large number of domesticated pets, especially dogs and cats, but extending to all other manner of organisms, such as tropical fish, birds, lizards, hamsters, guinea pigs, etc. Humans need this contact with other life forms, and getting out into Nature for an afternoon hike on a path through the woods is extremely therapeutic for shedding stresses at work and home, appropriately referred to as "forest bathing" (Li, 2010; Lee et al., 2011; Farkic et al., 2021). Our species evolved in Nature, and we still have a need to return to these roots, to relax back into our original environment.

But despite the acknowledged value of biodiversity, many challenges exist for its present and future maintenance. The news is full of reports of declining sizes of populations of large animals, such as pandas, tigers, and elephants, suggesting that in future decades these magnificent creatures will only survive in zoos or small reserves, if they survive at all. But the problem goes much deeper, such as the loss of predatory fish in the oceans (Pauly & Maclean, 2003), or the global decline in pollinators (Potts et al., 2010). Regarding plants, it has been estimated that 21–47% of all plant species are now threatened (Pitman & Jørgensen, 2002; RBG Kew, 2016).

The fundamental cause of the loss of biodiversity is the ever-increasing human "footprint" (Kareiva et al., 2007). As of November 15, 2022, the human population

reached eight billion persons for the first time in history. With more people come more roads, shipping lanes, and cultivation of land for more food. Human-associated travel has also resulted in the introduction of invasive species of plants and animals (sometimes referred to as the Homogenocene; Samways, 1999) that compete with native species for ever-dwindling resources (Perrings et al., 2005; Powell et al., 2011). Forests have been cut for wood resources and to provide more land for domesticated plant cultivation. The rate of global tropical forest removal has also continued at a high level of approximately six to eight million hectares each year (Achard et al., 2002; Mitchard, 2018). This not only impacts the loss of biodiversity directly, but it also contributes to the broader problem of global warming, which in turn has a greater negative impact on flowering and fruiting time of plants (e.g., Büntgen et al., 2022), which can have consequences for migrating birds that use fruits during their long-distance travels (Both et al., 2006). As temperatures increase, drought can ensue, which will negatively impact amphibians in their aquatic habitats.

Patterns of Biodiversity

Despite centuries of natural history collecting and study, we still have no clear idea of the exact numbers of species that populate our planet. The good news is that the systematic biology community has come together in a rare demonstration of unity around the priority of a global organismal inventory (Anonymous., 1994; Daly et al., 2012). This means getting out into poorly explored regions of the world and making observations and collections. Today, sampling can be of whole organisms or portions of them for DNA laboratory analysis. DNA inventorying, in fact, is essential for learning about microbes, such as in the deep ocean, or fungi, in the soil, for which little morphological information has been accumulated. Sweeping and analyzing the air has even revealed unknown organisms (Johnson et al., 2022). Although much interest toward a global inventory has been provided, successful implementation requires efforts back to the political level, which scientists are often averse to address (Stuessy, 2020b).

Once a general idea of biodiversity for a group is available, usually after decades or even centuries of adequate collecting and study, a more comprehensive investigation is needed to bring all information together and provide a more insightful synthesis. The main publication from these efforts is the biological monograph (Stuessy & Lack, 2011). The general term, monograph, can mean any type of scholarly publication, usually of a large and comprehensive nature. The biological monograph, along with less comprehensive similar publications, the synopsis and revision (Stuessy, 1993), provides the baseline understanding of biological groups. This is the best possible interpretation of the biodiversity of a selected group of organisms at a particular point in time (Borsch et al., 2015; Grace et al., 2021). Floras also contribute to revealing patterns of biodiversity, but their focus is on showing what

species inhabit particular areas of the Earth (often political regions, such as countries, states, or provinces) and not on evolutionary relationships.

The biological monograph brings together all available knowledge about a taxonomic group, often a genus, and it weaves this information together with the goals of providing a classification and constructing a phylogeny. These two goals are interwoven, as most classificatory efforts deal directly or indirectly with time-related aspects of evolution of the group. The results are two patterns of biodiversity, the classification and the phylogeny. Without this foundation, it is virtually impossible to infer the processes that produce diversity. Evolution cannot be examined precisely unless we are investigating closely related populations or species, and the clearest presentation of these patterns is in the monograph.

Plant monographs began in the eighteenth century (Stuessy, 2025) and became more common in the nineteenth century and into the first half of the twentieth century. Doctoral training for graduate students used to focus on selected genera (such as *Melampodium*; see Preface), as working out relationships was viewed as good experience for the young plant systematist. It still is a valuable training ground, but with the proliferation of new DNA data, plus the numerous computer programs developed to analyze these data, many young doctoral candidates opt for more analytical projects, especially those involving bioinformatics. This relates to the changing dimensions of plant systematics. Decades ago, an important talent for success was a strong visual memory, which allowed plant images to be stored and intuitively compared with each other, hence facilitating the production of a classification. This ability is still important, but so now is analytical and mathematical ability, favoring students with a strong quantitative background. Furthermore, new Artificial Intelligence (AI) tools are now available to assist with making visual comparisons (Wäldchen et al., 2018; Yigit et al., 2019; Picek et al., 2022).

The most fundamental part of the monograph is the clarification of the limits of species. Many aspects of biodiversity deal with the specific level (especially with governmental regulations), and this level of the taxonomic hierarchy is also fundamental for understanding recognition of genera, families, and higher-level taxa. To investigate species requires adopting a species concept that is workable for the group in question, and this will vary depending on the organisms. The resolution of species limits requires using different lines of evidence (Fig. 1.2), but morphology is always fundamental. The phenotype is what the organism uses for adaptation and interactions with the changing environment, and it is also the level that humans normally use in dealing with species. To these baseline data are added distributions and ecology, to provide the spatial dimension. Some species inhabit very particular habitats, and this is most important to document, especially for conservation purposes. In addition to morphology, distributions, and ecology, other data are brought to bear on understanding the limits of species, such as anatomy, embryology, phytochemistry, DNA sequences, cytology, and cytogenetics. Also important in the monograph is to have the nomenclature resolved, so that consistent and stable names will be available for all species. Biodiversity in a group without an accompanying stable nomenclature is virtually useless for human communication. Armed with consistent species concepts and names, identification keys can be produced that

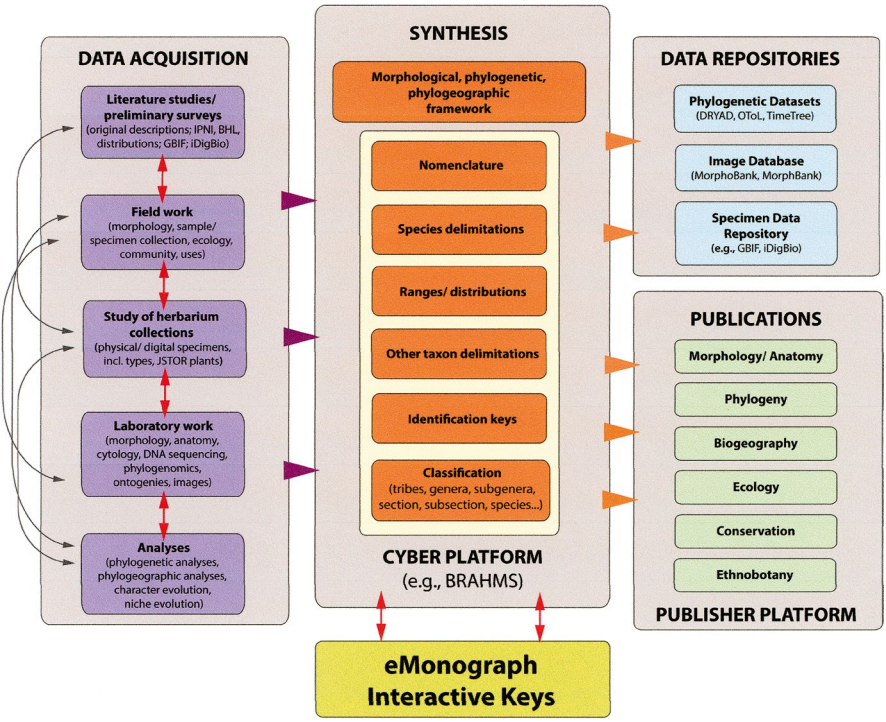

Fig. 1.2 Tasks and workflow in modern botanical monography. (From Wen et al., 2015)

allow other persons to identify specimens in their local areas and for museum workers to identify specimens from faraway regions.

Because of the significance of monographs for understanding biodiversity, and with the realization of the many pressures that biodiversity now faces, concerns have arisen on how monographs might continue to be completed and disseminated more widely. A recent conference was held to address this, and other issues, regarding botanical monographs (Marhold & Stuessy, 2013). A paradox was indicated, wherein young investigators are turning more to DNA analysis and away from monography, which means that fewer new hypotheses of relationships will be developed in the future. The use of Internet resources is one obvious way that more information can be disseminated to the general public at very little cost. Interaction with citizen science groups, such as iNaturalist, should also be encouraged. An Internet monograph can have many photographs of features of the organisms, their habitats, and data on all sorts of other comparative information, including phylogenetic trees. Certain aspects of the monographs can also be designed for the general reader, an encapsulation of relationships and nomenclature, leaving details in other folders for the professional systematist. Collaboration of workers from different subfields on the same genus should also be encouraged, but this involves a