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Plant anatomy: history and future directions

Plant anatomy - history and interfaces

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Abstract

Traditionally, plant anatomy, along with external morphology, cytology, and palynology, has been classified as a component of the field of Plant Morphology, as set out in the Table of Areas of Knowledge of the National Council for Scientific and Technological Development (CNPq). This subdivision is not adopted equally worldwide, and the terms denote varied interpretations even among teaching and research institutions in Brazil. However, since the mid-20th century, plant anatomy has been regarded as a separate branch of plant morphology, referring solely to studying the plant's internal structure, including plant histology and cytology. Whichever division it best fits into, plant anatomy is one of the oldest disciplines in botanical science. It remains a powerful source of information, with significant knowledge accumulated over centuries of research. In this text, we present a history of plant anatomy with emphasis on the scientists, their discoveries, and works from antiquity to modern times that contributed to the development and progress of this fundamental area of the *Scientia Amabilis*. Finally, we present the beginning and progress of plant anatomy in Brazil. A summary of the current state and perspectives for future research to promote further integration of the various aspects of plant anatomy are listed.

Key words: comparative plant anatomy, functional plant anatomy, systematic plant anatomy, wood anatomy.

Resumo

Tradicionalmente, a anatomia vegetal, juntamente com a morfologia externa, citologia e palinologia, tem sido classificada como um componente da área de Morfologia Vegetal, conforme Tabela de Áreas do Conhecimento do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). Essa subdivisão não é adotada igualmente em todo o mundo, e os termos denotam interpretações variadas mesmo entre instituições de ensino e pesquisa no Brasil. No entanto, desde meados do século 20, a anatomia vegetal tem sido considerada como um ramo separado da morfologia vegetal, referindo-se unicamente ao estudo da estrutura interna da planta, incluindo histologia e citologia. Independentemente da divisão em que melhor se enquadre, a anatomia vegetal é uma das disciplinas mais antigas da ciência botânica e continua sendo uma poderosa fonte de informação, com significativo conhecimento acumulado ao longo de séculos de pesquisas. Neste texto, apresentamos um histórico da anatomia vegetal com ênfase nos cientistas, suas descobertas e trabalhos desde a antiguidade até os tempos modernos que contribuíram para o desenvolvimento e progresso desta área fundamental da *Scientia Amabilis*. Ao final, nós relatamos o início e progresso da anatomia vegetal no Brasil. Uma síntese do estado atual e perspectivas para pesquisas futuras, a fim de promover uma maior integração dos vários aspectos da anatomia vegetal, são listadas.

Palavras-chave: anatomia vegetal comparativa, anatomia vegetal funcional, anatomia vegetal sistemática, anatomia da madeira.

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The History of Plant Anatomy

The beginning and development of plant anatomy have been registered and updated by different authors, with particular emphasis on the information provided by Scott (1889), Eames & McDaniels (1953), Baas (1982), Cutler *et al*. (2008) and Watt (2022), from whom we take examples and references. These authors served as a basis and inspiration for writing this text.

Our text uses plant anatomy as the general term for plant organ internal structure. Similar to other branches of biology, plant anatomy studies originated with the microscope's invention.

Circa 1590, Dutchmen Hans Janssen and his son Zacharias, who were eyeglasses manufacturers, invented a device capable of magnifying the image of small objects. This microscope comprised two glass lenses mounted on two ends of a tube and enabled approximately 30 times the magnification of images. Later, the Dutchman Antonie van Leeuwenhoek (1632–1723), a naturalist and microscope constructor, perfected the rudimentary microscope to allow magnification up to 300 times with reasonable image clarity. Leeuwenhoek was the first to use the microscope to examine biological material and documented the presence of perforated vessels in the xylem. From these discoveries, Robert Hooke (1635–1703), an English physicist, astronomer and paleontologist, improved the microscope with compound lenses capable of magnifying 30x to 40x. The instrument became known as a compound microscope due to using two lenses, the ocular and the objective. Hooke's book "Micrographia, or,Some Physiological Descriptions of Minute Bodies Made by Magnifying Glasses with Observations and Inquiries Thereupon", published in 1665, was notable for its meticulous descriptions and illustrations, as well as for its comprehensive account of natural objects, such as the structure of feathers, the sting of a bee, the radula or "tongue" of mollusks, and the famous illustration of cork, which was the first documentation of a plant cell. In this book, Hooke described cork as consisting of "little boxes or cells, distinct from one another", not realizing that he had discovered the smallest unit of tissue in living beings, the cell. Later, in 1838, the cell was demonstrated in plants by Mathias Jacob Schleiden (1804–1881), a German physician and botanist, and in 1839, in animal tissues, by Theodor Ambrose Hubert Schwann (1810–1882), a German physician, the pioneer of Cell Theory. Despite the importance of Hooke's work, the dissection and illustration of cork, and the proposal of the term *cell*, his book Micrographia cannot be considered the first publication in plant anatomy because it lacked a defined objective.

Throughout the 17th century, the compound microscope became popular and was widely used in biological research. During this period, detailed and more accurate descriptions of the internal structures of plants were made.

The origin of studies in plant anatomy can be attributed to Nehemiah Grew (1641–1712) and Marcello Malpighi (1628–1694), physicians who worked independently in England and Italy, respectively. They were pioneers in the microscopic examination of plant cells and tissues, establishing the foundation of our current understanding of plant anatomy. Grew was considered the pioneer of plant anatomy, and used the term *vesicles* to refer to cells. He recognized and accurately depicted the reproductive organs of plants and their parts and classified plant tissues into different "bodies" (woody parts, fibers, pith, parenchyma, and pulp). He also recognized vertical and horizontal tissue systems and described the secondary growth of bark and wood. The "Anatomy of Vegetables Begun" (1672) is one of his books. Grew, and especially Malpighi, focused on the functional aspects of anatomical structures, particularly those involved in conduction. The monograph "Anatome Plantarum" (1675), by Malpighi, is considered the first step toward the progress of plant biology, specifically plant morphology and anatomy. Written with precision, under the limitations imposed by the level of knowledge at the time, Malpighi treated the plant as a system and recognized the synergistic functioning of its organs. Based on his microscopic observations, he described and illustrated spiral vessels and stomata. By providing an analogy to insect tracheae or mammalian bronchi, he considered that spiral vessels were responsible for facilitating air transport. Malpighi has used many terms adopted in plant morphology and anatomy even today.

Simultaneously, significant advances happened in optics with the invention of achromatic lenses by Chester Moore Hall (1703–1771), a British lawyer and inventor who produced the first achromatic lenses in 1729 or 1733 (conflicting reports). He used the achromatic lens to construct the first achromatic telescope, a refractor telescope devoid of chromatic aberration (color distortion). The development of numerous designs of lenses and more advanced microscopes subsequently led to remarkable progress in anatomical discoveries.

Considering the historical relevance of the complexity of this information, we have compiled information on certain plant scientists from the 18th to the 20th centuries, their main discoveries, and works that leveraged knowledge about plant anatomy and played a pivotal role in establishing plant anatomy as a distinct field of study. In this scenario, we initially highlight the relevance of Robert Brown (1773–1858), a Scottish researcher considered the discoverer of the cell nucleus. Although many cytologists before him had already observed the nucleus, they had not understood the enormous importance of this structure in the life of cells. The immense merit credited to Brown was attributed to his precise recognition of the nucleus as a fundamental component of cells. The name he assigned to the structure expresses this conviction, as the word *nucleus* is derived from the Greek nux, which means seed.

Wilhelm Hofmeister (1824–1877), a German biologist and botanist, was the first to describe the alternation of generations in the life cycle of terrestrial plants in 1851 and considered this phenomenon a collective unifying principle of all plants. Hofmeister's contributions have also been cited in the early studies of plant embryology.

Johann Jacob Bernhardi (1774–1850), a German physician and naturalist, described annular thickenings in xylem vessels. He observed that the annular and spiral thickenings connect the primary wall and that the vessel elements do not undergo metamorphosis.

Johann Jakob Paul Moldenhawer (1766–1827), a German botanist, made numerous important discoveries in plant anatomy. He demonstrated that each cell had its own wall. He developed maceration techniques and coined the term *fibrovascular bundle* for the "cords composed of fibers, vessels, and parenchyma". In 1812, Moldenhawer published "Beyträge zur Anatomie der Pflanzen", providing detailed depictions based on the investigation of plant tissues.

Ludolph Treviranus (1779–1864), a German naturalist and pteridologist, discovered that vessels are formed by the disappearance of transverse walls between a series of cells. He observed the development of spiral thickenings in vessel elements.

Charles-François Brisseau de Mirbel (1776–1854), a French botanist, published "Traité d'Anatomie et de Physiologie Végétales" in 1802, laying the foundations of plant cytology.

Augustin Pyrame de Candolle (1778–1841), a Swiss botanist, published the work "Théorie Élémentaire de la Botanique" in 1813. In this book, he contended that the classification of plants should be exclusively based on anatomy rather than physiology. Thus, de Candolle established structural criteria to define and distinguish plant genera.

However, the effective development of plant anatomy dates to the mid-19th century. It originates from the publication of "Grundzüge der Anatomie und Physiologie der vegetabilischen Zelle" in 1851 by the German botanist Hugo von Mohl (1805–1872). The contributions of von Mohl were extensive; he improved the techniques for microscope preparation and the optical aspects of the instrument. Working with cytology, he coined the term *protoplasm* and demonstrated that this compartment is the source of intracellular movements. He identified the plasma membrane and was the first microscopist to describe the behavior of the protoplasm during cell division. His contributions to understanding the cell wall are remarkable: he advocated the currently acknowledged concept of cell wall growth by apposition. Von Mohl provided the first comprehensive understanding of the true nature of the nucleus and demonstrated the cellular origin of vessels and fibers. He also described the relationship between the primary and secondary layers of the cell wall and the characteristics of pits in cell walls. At the anatomical level, von Mohl's pioneering research on the structure of palms, cycads, and tree ferns formed a solid foundation for subsequent research. Later, he focused his research on the anatomy of stems of dicotyledons and gymnosperms. After observing the bark and cork, he described the formation and origin of different types of bark and lenticels.

In the 19th century, in 1837, Theodor Hartig (1805–1880), a German entomologist and botanist, discovered and named the *phloem sieve tube*.

Wilhelm von Nageli (1817–1891), a Swiss physician and botanist, discovered what later became known as the chromosome. Among his various contributions, he studied the ontogeny of apical meristems and showed the distinction between primary and secondary meristems; he described the development of vascular bundles from the procambium and used the terms *xylem* and *phloem* to classify the different parts of the vascular bundle. He also proposed that the thickening of the cell wall occurs through intussusception.

Carl Sanio (1832–1891), a German physician and botanist, conducted a comprehensive analysis of *Pinus* samples to elucidate the origin, structure, and functioning of the vascular cambium, the areolar pits, and the periderm development.

Johannes von Hanstein (1822–1880), a German botanist, gained recognition for his studies on the behavior of the shoot apex. He introduced the theory of histogens and coined the terms *dermatogen*, *periblem*, *plerome*, and *calyptrogen*.

Julius von Sachs (1832–1897), an eminent German draughtsman and botanist, established the fundamental principles of microchemical methods and the structure and arrangement of cells in apical meristems. He described chlorophyll and proposed that the pigment serves as the site of assimilatory activity in the green leaves of plants.

Eduard Strasburger (1844–1912), a German botanist of Polish origin, was one of the most prominent anatomists of the 19th century. He described the mitotic cycle in plant cells and showed that new cell nuclei can emerge from the division of previous nuclei. His monograph, "Studien Über Protoplasma", was published in 1876.

Simon Schwendener (1829–1919), a Swiss botanist and assistant to Carl Wilhelm von Nageli (1817–1891), was appointed as a botany professor at the University of Munich in 1860–1867. He also assumed the role of director of the Botanical Garden of Basel. In 1877, Wilhelm Hofmeister (1824–1877) was succeeded by Schwendener as a professor of botany at the University of Tübingen, and from 1878 until his retirement in 1910, Schwendener was a professor at the University of Berlin. He was recognized for his investigations into plant anatomy and physiology, focusing on the interrelationship between plant structure and function. He adopted a mechanistic approach in his botanical studies, believing that plant anatomy follows the mechanics' principles. He conducted extensive research on the mechanics of sap ascent, the pulvinus in a leaf, the positioning of leaves on the plant, the association between stomata and their guard cells, and the mechanism of anther opening. He mentored several students and assistants during his long career, including Gottlieb Haberlandt, Richard Kolkwitz, Emil Heinricher, Max Westermaier, Georg Volkens, and Otto Heinrich Warburg. Simon Schwendener's research stimulated the study of anatomy from a physiological perspective.

The expansion of studies involving the anatomy and physiology of plants co-occurred in different regions of the world. Gottlieb Haberlandt (1854–1945), an Austrian botanist, is recognized as one of the prominent pioneers of physiological anatomy and advocated for the integrated study of structure and function. In his publication "Physiologische Pflanzenanatomie" (1884), Haberlandt classified tissues based on their function, such as mechanical, absorptive, and photosynthetic, disregarding existing morphological classifications and arrangements. Despite his system lacking acceptance from other botanists, analyses of the relationships between structure, function, and environment are still frequently used by those who study plant adaptations to the environment. Research with this focus was compiled by Klaus Napp-Zinn (1927–1993) a German botanist, dedicated to the study of the physiological functions of leaves, and their anatomical basis. Like Napp-Zinn's "Blattanatomie der Gymnospermen", published in 1966, their compilations "Blattanatomie der Angionspermen" (1973/1974), contains a comprehensive history of development and the topographic anatomy of the leaves of Angiospermae including a bibliography and detailed index, will be indispensable for botanical study and research. Napp-Zinn (1973/1974) draws the conclusions from almost 6,000 studies published up to and including 1972, in which about 3,000 authors have contributed to the knowledge of the structures and of the anatomical aspects of the development of angiosperm leaves. The text is supplemented by 280 carefully selected, newly drawn illustrations (approx. 650 detail figures) and also 68 tables. Next, the work "Anatomie des Blattes II. Blattanatomie der Angiospermen. B. Experimentelle und ökologische Anatomie des Angiospermenblattes" (1984) Napp-Zinn deals with the influence of external factors, of genetic information and of the «internal conditions» resulting from these two (KLEBS) on the structure of angiosperm leaves. The first of two chapters and is devoted to the relationships between external factors and leaf structure. In the first chapter, plants in selected locations - ranging from humid tropical forests, through mangrove swamps and deserts right up to mountain pinnacles and laboratories - are used as the basis for discussing complex substances known as histones. The remaining chapters are devoted to analyzing the effective factors in detail: light (intensity, photoperiod, and wavelength), temperature, atmospheric factors, water, soil and heterotrophism. As far as possible, an attempt has been made in each chapter to start with what has been discovered in Nature and go on to planned experiments, and thus acquire an insight into the mutual interaction between anatomy and physiology. As well as the author's illustrations - excellent, as always - there are numerous tables with statistical information. The present edition gives a resume of about 3,000 publications, including studies on the leaf anatomy from Cerrado and Amazon-Caatinga plants published by Berta Lange de Morretes. It is an inexhaustible source of information, not only for plant anatomists, morphologists and system analysts, but also for physiologists interested in metabolism and development, ecologists, plant geographers and people specializing in environmental protection, and plant and animal nutrition.

The association between plant anatomy, physiology, and genetics comes from Johannes Schmidt (1841–1924), a Danish naturalist and botanist who was a student of Eugen Warming. Schmidt proposed the tunica-corpus theory, which pertains to the organization of the apical meristem of the stem based on planes of cell division.

Around 1890, the "Center for Studies in Plant Anatomy and Physiology" was established at the Timiryazev Institute, of the Russian Academy of Sciences in Saint Petersburg. The foundation of this Center was initiated by the Russian botanist Andrei Famintsyn (1835–1918), who is widely known in Russia and abroad for his pioneering work in various fields of plant physiology. He was the author of the first Russian course on plant physiology for universities and the first fundamental monograph, "Metabolism and Energy Conversion in Plants" (1883), which was republished 100 years later in the series Classics of Science. Dmitry Ivanovsky (1864–1920), one of his students, initiated his studies in plant virology and later pursued formal education in botany from 1896–1901, gaining recognition as an esteemed plant anatomist and physiologist. His investigations centered on photosynthesis, explicitly focusing on the structure of chloroplasts and the role of pigments in leaves.

Wood anatomy, a branch of plant anatomy that focuses on the study of the various types of cells that constitute wood (or secondary xylem), their functions, organization, and structural peculiarities, had its origins marked in the 16th century with the studies of Cordus and Andrea Caesalpino (see Baas 1982). However, during the 18th and 19th centuries, this branch of plant anatomy expanded in various parts of the world with the studies of Auguste Mathieu and Hermann Hodlinger, considered the true precursors of this branch of plant anatomy. Woody anatomy includes diverse approaches such as the descriptive anatomy of wood; comparative anatomy, structural variability, and wood identification; structure-function relationships, ultrastructure, and ecological anatomy of wood; fossil woods, archaeology, and paleontology; systematic and phylogenetic wood anatomy; and cambium differentiation and wood development, and microscopic methods. At the end of the 20th century and the beginning of this century, studies were directed toward the physical and mechanical properties of wood due to the need to identify the anatomy of wood for technological purposes. Since its establishment in 1970, the International Association of Wood Anatomists (IAWA) has played an essential role in promoting studies on wood and bark anatomy, with the International Association of Wood Anatomists (IAWA) Journal being an indispensable reference for those dedicated to this field.

Vernon Cheadle (1910–1995) was a renowned and prolific botanist from the University of California, Santa Barbara. His research focused on the structure and function of conducting cells. As a professor, he strongly influenced his students and generations of researchers studying phloem, including Katherine Esau and Franklin Ray Evert. His vast collections, which include approximately 15,000 plant specimens and 60,000 histological slides, are housed in the research and teaching center that bears his name, the "Cheadle Center for Biodiversity and Ecological Restoration".

A detailed account of "Systematic, phylogenetic, and ecological wood anatomy - history and perspectives" was published by Pieter Baas in 1982 in the "New Perspectives in Wood Anatomy" on the 50th Anniversary of the IAWA. In 1994, Mary Gregory published a bibliography of systematic wood anatomy of dicotyledons with a compilation of studies conducted in the late 20th century. At the same time, Philip Larson (1994) published "The Vascular Cambium: Development and Structure". Following this period, Sherwin Carlquist (2001) published "Comparative Wood Anatomy: Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood" a precious book written in the current language and richly illustrated.

Knowledge from studies on plant anatomy focusing on taxonomy was compiled by Hans Solereder in 1908 in their "Systematiche Anatomie der Dikotyledonen" book. Further, results of studies performed until the mid-20th century showing the relation between systematic anatomy and taxonomy were gathered by Metcalfe & Chalk (1950), published in two volumes entitled "Anatomy of the Dicotyledons; Leaves, Stem, and Wood in Relation to Taxonomy with Notes on Economic Uses". A few decades later, Metcalfe & Chalk (1979) published "Systematic Anatomy of Leaf and Stem, with a Brief History of the Subject". The second edition (1979) of this book was expanded to include not only the additional data concerning the histology of the vegetative organs that have been accumulated since 1950; this new edition also covered briefly the main taxonomic views concerning the interrelationships of families and other higher taxa that depend on other laboratory disciplines such as palynology, embryology, and chemotaxonomy, all of which are now accepted as forming parts of the general subject of taxonomy. Following these steps, we have the compilations of Davis (1966), "Systematic Embryology of the Angiosperms" and Dahlgren *et al.* (1985), "The Families of Monocotyledons: Structure, Evolution, and Taxonomy".

In fact, the effectiveness of anatomical data in taxonomy and determination of hierarchical relationships at the family level has an extensive history, as shown by Endress *et al*. (2000) in the volume 49 of Taxon, entitled "Systematic Plant Morphology and Anatomy-50 Years of Progress". In this publication, the authors emphasize the pioneering work of Ludwig Adolph Timotheus Radlkofer (1895), who used anatomical data, including wood anatomy, in taxonomic studies of Sapindaceae, including important compilations and compendiums widely used today.

The book "Plant Taxonomy: the Systematic Evaluation of Comparative Data", edited by Tod F. Stuessy (2009), deserves special recognition as it synthesizes various branches of botany, including anatomical, embryological, cytological, and reproductive data of plants. Moreover, the importance of anatomical data in taxonomic studies is stressed by Stuessy (2009) that presents a considerable number of references and illustrations, including monographs on the anatomy of specific taxonomic groups, for example, Gramineae, Palmae, Juncales, Comelinales-Zingiberales, Cyperaceae, Dioscoreales, Helobiae, and Iridaceae.

Studies in comparative anatomy and phylogeny of vascular plants were pioneered by Edward Charles Jeffrey (1866–1952), a Canadian botanist. Strongly influenced by Charles Darwin's hypothesis of the Origin of Species, Jeffrey used anatomy to establish the evolutionary history and sequence of vascular plants in geological time and their inter-relationships. Jeffrey developed microscopic techniques to obtain thin sections of refractory plant materials, such as wood and fossilized remains. Based on his research, he published "The Anatomy of Woody Plants" in 1917.

Adriance Sherwood Foster (1901–1973) was an American botanist who pioneered the study of shoot apical meristems, leaf morphogenesis, and leaf venation. Foster also proposed new criteria and terms for describing the growth zones of the apical meristem of gymnosperms, including the concepts of *initiation zone*, *mantle layer*, *zone of central mother cells*, *rib meristem*, *medulla*, *cambium cells zone* at the shoot apex, and *quiescent center* in the roots. His books, "Practical Plant Anatomy" (1960) and "Comparative Morphology of Vascular Plants" (1974), the latter co-authored by Ernest M. Gifford Jr., were widely adopted by anatomists. The relevance of "Comparative Morphology of Vascular Plants" extended beyond Foster's trajectory, as Gifford published the third edition of the work in 1989, posthumously keeping Foster as the second author; the book is used as a reference for studies of plant morphology (*sensu lato*) even in present times.

Agnes Arber (1869–1960) was a scholarly scientist from the United Kingdom who, besides being a bibliographer, historian, and philosopher of botanical science, studied the morphology and anatomy of monocotyledons. She commenced a series of studies on the floral structure of monocotyledons in the 1930s. Arber was also an excellent artist. She personally illustrated her articles, monographs, and books. She published several books, for example, "Herbals: Their Origin and Evolution" (published in 1912, reviewed in 1938), where Agnes Arber's Herbals stands as the major survey of the period 1470 to 1670 when botany evolved into a scientific discipline separate from herbalism. This development is reflected in contemporary herbals, "Water Plants: A Study of Aquatic Angiosperms" (1920), "Monocotyledons: A Morphological Study" (1925), "The Gramineae: A Study of Cereal, Bamboo, and Grass" (1934), "The Natural Philosophy of Plant Form" (1950), and "The Mind and the Eye" (1954). Her books became classics and are characterized by a wide range of perspectives, a philosophical vision, and a pronounced and meticulous attention to detail. According to William T. Stearn (cited by Schmid 2001), Arber was undoubtedly an exceptional morphologist and anatomist of the first half of the 20th century, whose influence on contemporary botany was profound albeit poorly documented.

Katherine Esau (1898–1997), an American botanist of Russian origin, was one of the most notable plant anatomists of the 20th century. She became internationally known for her pioneering work on the structure and development of phloem, viral diseases of plants, and her influential plant anatomy textbooks. The book "Plant Anatomy" (1965) became mandatory reading in American colleges and several other parts of the world. In the early 1960s, Esau introduced transmission electron microscopy. She ensured the study of the ultrastructural characteristics of cells, becoming a pioneer in using this tool for the anatomical study of plants. In "The Phloem" (1969), published as the fifth volume of the series "Handbuch zur Pflanzenanatomie", Esau reviewed the studies of the phloem since their beginnings, and she relied on data from her studies. Esau's contributions to our understanding of plant structure, spanning over seven decades, have propelled the field of plant anatomy as a science and set new standards of excellence for investigating anatomical problems in plant sciences.

In the 20th century, Ray Franklin Evert (1931–), an American educator and researcher, initiated research on vascular cambium and the seasonal development of secondary xylem and phloem in woody dicotyledons, advancing studies on bark anatomy. In 2006, Evert published the book "Esau's Plant Anatomy: Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development", where he makes a profound review of the world-renowned book "Plant Anatomy" (Esau 1965), broadly expanding the information contained in the Esau's book, including research with modern approaches. The number of references Evert includes makes this work an important reference for undergraduate and postgraduate students, professors, and researchers in plant anatomy.

We emphasize that the information presented here about the beginning and development of plant anatomy as a science is limited primarily to researchers and institutions in Europe, the United Kingdom, and North America. However, the beginning of the studies that led to the understanding of the internal organization of plants was wider than European and American scientists. Many relevant works, compendiums, and monographs on plant anatomy and cytology have also been published by renowned researchers in other world regions. However, these works are difficult to access since many of them were written in native languages and have not been translated into English. For those with time and interest in botanical history, especially in anatomy and the pioneers of research in the field, and who possess skills for bibliographic research, an online survey will reveal many other interesting data.

In the global context, Professor P. Jayaraman (1936–), a renowned Indian botanist, is considered the "father of plant anatomy in India." After retiring from Presidency College, Chennai, he founded the "Plant Anatomy Research Centre (PARC)". PARC brings together researchers, students, professors, scientists, and other interested individuals who visit its laboratory in search of plant identification, consultation, guidance, and anatomical description. Many also visit PARC to consult collections of slides, rare and valuable books, theses, dissertations, monographs, and difficult-to-access periodicals. The PARC team holds weekly research meetings to discuss advances in plant anatomy. In fact, PARC is a reference center for plant anatomists in India and has a reputable repository of hundreds of plant anatomy images focusing on medicinal plant species.

Plant Anatomy in Brazil: from the beginning to the impressive progress

The emergence of plant anatomy in Brazil as a field of knowledge and research has a close association with the establishment of the country's first research institutions, such as the Rio de Janeiro Botanical Garden, the National Museum of the Federal University of Rio de Janeiro, and the University of São Paulo. Here, we will only highlight the pioneers of plant anatomy in each of these institutions.

The Rio de Janeiro Botanical Garden (JBRJ), currently known as the Rio de Janeiro Botanical Garden Research Institute (JBRJ), was founded and began its activities in 1808. According to the publication available on the website of JBRJ (https://www.gov.br/jbrj/pt-br/assuntos/299), a section dedicated to the study of plant anatomy, particularly the structure of wood from timber species, was established at the Botanical Garden at the end of the 1920s under the leadership of Fernando Romano Milanez (1905–1987). Milanez was a phytopathologist who studied various aspects of plant anatomy, including wood anatomy, crystal cells in the xylem, ontogeny of laticifers, and resin ducts in the secondary xylem. He also developed and refined various microscopic techniques. In 1936, with the consolidation of research in wood anatomy, JBRJ organized the 1st International Meeting of Wood Anatomists. During this period, in addition to courses on wood anatomy, scientific publications produced in the plant anatomy sector of JBRJ have boosted Brazil's newly formed field of plant anatomy. In the Revista Florestal (volume 1, issue 2, pages 6–8, from 1929), we can find the first publication by Milanez *et al.* on the wood anatomy of Brazilian native species. From then on, numerous studies on the anatomy of wood, leaves, fruits, seeds, and latex were carried out at the Structural Botany Laboratory of JBRJ, and such studies were published, among other journals, in Archivos do Jardim Botânico, the country's first scientific journal exclusively dedicated to botany, and later in Rodriguésia (starting from 1930). Milanez mentored several graduate students in plant anatomy, with special mention of Cecília Gonçalves Costa (1928–), who significantly contributed to the field in the country. Cecília, a pharmacist from Maranhão state, Brazil, was incorporated into the Structural Botany Laboratory of JBRJ in 1962. Together with other researchers, she continued the studies of wood anatomy. She expanded her research to include other aspects of plant anatomy, such as bark anatomy, leaf anatomy, dendrochronology, and ecological anatomy of species from the Atlantic Forest and Cerrado. Milanez has mentored students from the Graduate Programs of the National School of Tropical Botany in the JBRJ, the University of Brasília, and the Federal University of Rio de Janeiro, thus forming several generations of anatomists who now work in different educational and research institutions in the country. The Electron Microscopy Laboratory was established at JBRJ in the 1950s; this project was planned and led by Raul Dodsworth Machado (1917–1996), who furthered research in structural botany. Raul Machado completed an internship at the Rockefeller Institute under the mentorship of Keith Porter (1912–1997). Porter is widely recognized as the father of cell biology. He pioneered cell studies using the high-voltage electron microscope, enabling him to study the concept of structural integration in the cellular cytoplasm. In this laboratory, Raul studied the endoplasmic reticulum of plant cells, obtaining micrographs that became classics and that enabled his appearance on journal covers and textbooks. Raul Machado has contributed to training many Brazilian researchers who use electron microscopy as their primary investigative tool.

The National Museum (MN), in turn, was founded in 1818. It is affiliated with the Federal University of Rio de Janeiro (UFRJ) and is considered one of the Brazil's oldest scientific institutions. Since its inception, the MN/UFRJ has been organized into sections, with the Botany Section essentially composed of renowned taxonomists, including Luiz Emygdio de Mello Filho (1913–2002), a physician, naturalist, and pharmacist. Between 1950 and 1990, although he did not work directly in the field, Luiz Emygdio mentored several students pursuing the master in plant anatomy course, including Léa de Jesus Neves (1938–), who played a significant role in the field of plant anatomy, especially in training generations of qualified anatomists to work in different research areas of this discipline.

Established in 1934, the University of São Paulo (USP) is one of the largest institutions in Latin America. According to USP website (www.ib.usp.br/botanica/info/historico.html), the Department of Botany started activities that same year. In the early 1940s, Berta Lange de Morretes (1917–2016), who had been recently graduated from the first class of the Natural History course at the Faculty of Philosophy, Sciences, and Letters of the University of São Paulo (FFCL-USP) and was one of the first professors at the Botany Department along with Mercedes Rachid-Edwards, introduced research on the anatomy of cerrado plants, focusing on leaf and underground system adaptations. In 1963, Walkyria Rossi Monteiro (1939–) and Nanuza Luiza de Menezes (1934–), former students of USP, were hired to join the plant anatomy team. Walkyria and Nanuza pioneered angiosperm embryology and floral vasculature in Brazil, respectively. With the implementation of the doctorate undergraduate program in botany, many individuals from different regions of Brazil interested in plant anatomy came to USP to obtain master's or doctoral degrees in botany. Many of these graduates are currently developing relevant work in research and training of higher-level personnel in plant anatomy at institutions across Brazil and abroad.

Among the pioneers of plant anatomy in Brazil, Professor Therezinha Paviani (1930–2014) also merits mention. She is one of the founders of the Department of Botany at the University of Brasília and its botany graduate program. Hired in 1969, she dedicated herself to studying the anatomy of cerrado plants and was one of the first to describe the xylopodium. Therezinha demonstrated a deep dedication to teaching and research on cerrado plants and inspired generations of students and professors.

Plant anatomy has rapidly transformed in the last 20 years, thanks to the development of sophisticated equipment, new technologies, and the integration of detailed anatomical studies with other areas of plant biology. For more details on the advances in botanical science over the last 20 years in Brazil, mainly in plant anatomy, we suggest reading the text written by Ana Giulietti-Harley and Vera Lucia Scatena, chapter 6 of the book "Sociedade Botânica do Brasil: História, Desenvolvimento e Contribuição para a Ciência do Brasil em seus 70 Anos de Existência", published on the 70th anniversary of the Botanical Society of Brazil (SBB). Giulietti-Harley & Scatena (2021) emphasize that the growth of plant anatomy as a research field is accompanied by the expansion and distribution of graduate programs in botany in different regions of the country, by the creation of several scientific societies, including the SBB (founded in 1950) and the importance of National Botany Congresses in the professional development of students, updating the knowledge of botanists, and disseminating research in plant anatomy. The authors emphasize the importance of the AnatoEncontros (https://www.youtube.com/c/), created on YouTube during the critical period of the Covid-19 pandemic; the channel continues active until now, bringing together anatomist researchers from several institutions in Brazil. Lectures deal with various themes of plant anatomy and are delivered through live streams, allowing real-time interaction between the public and the speaker at the end of the meetings. The lectures are available to the entire community, promoting the dissemination, updating, and popularization of plant anatomy as a scientific discipline with its fundamentals, principles, and methods.

Our literature dedicated to teaching plant anatomy was, until recently, impoverished. The Anatomists Core of the SBB has assumed a leading role in discussing and directing critical issues in the field. One such issue was the need for collaboration among anatomists to publish a basic book on plant anatomy featuring examples from the Brazilian flora. The "Anatomia Vegetal" book (2022), currently in its fourth edition, is a result of these efforts and has become a bestseller. This book, edited by Beatriz Appezzato-da-Glória and Sandra Maria Carmello-Guerreiro, is richly illustrated, especially with species of Brazilian flora, and brings together texts by national authors of recognized competence. The informative content is addressed in disciplines of undergraduate and graduate courses in Biological Sciences and related areas.

Other important factors in the development of research and teaching in botanical science in Brazil should be highlighted: the creation, in 1951, of the National Council for Scientific and Technological Development of Brazil (CNPq) at the federal level; the creation of Research Support Foundations at the states, with emphasis on the Research Support Foundation in the state of São Paulo (created in 1960); the creation of University Publishers, which made possible to publish new titles at reduced prices. Since then, we have observed an increase in the number of researchers and professors in plant anatomy who receive a CNPq Research Productivity grant, demonstrating high quality and high productivity in the area. The number of research projects sponsored by these funding institutions and scientific articles published in international journals of high circulation and impact with an effective editorial policy has also significantly increased.

Current state and perspectives

Plant anatomy is a scientific discipline that involves the detailed study of particular organs or structures from various perspectives. The appreciation of plant anatomy as a field of knowledge remains essential for understanding many aspects of plant biology, ranging from molecular to ecological issues. From the basic science to its numerous interfaces, detailed knowledge of plant anatomy has applications in physiology, ecology, taxonomy, and evolutionary biology. Anatomical data proves highly valuable in solving taxonomic and phylogenetic challenges, as it often facilitates the recognition of homologies between morphological characteristics, which can assist in interpreting evolutionary pathways.

The publication "Systematic Plant Morphology and Anatomy-50 Years of Progress" by Endress *et al*. (2000) emphasizes the importance of new techniques and sophisticated optical equipment, new methods, and concepts in systematics (cladistics, evolutionary paleobotany, molecular systematics, and molecular developmental genetics), and the integration of anatomical and microstructural data with molecular data for the construction of increasingly robust phylogeny of angiosperms. In plant anatomy, the integration of ecological and anatomical systematics, composing "ecophyletic" anatomy, leads to a better understanding of the driving forces behind the evolutionary diversification of wood and the anatomical attributes of leaves. However, the authors emphasize that the interlinking of ecological (extrinsic) and organizational (intrinsic) constraints at the origin of form remains a major challenge for future studies.

In their book entitled "Plant Anatomy: An Applied Approach", Cutler *et al*. (2008) express concern that the teaching of plant anatomy as a field of knowledge is increasingly marginalized and its content reduced in the college biology courses. One potential solution to address this issue is to promote awareness of anatomical studies' broader significance and value, beginning from their role as a basic science (that allows the discovery, diagnosis, and detailed description of new structures) to their use as support for all areas of plant biology. It is necessary to overcome the instrumental and inadequate view of plant anatomy as a tool.

In addition to the notable progress in research on various aspects of structural biology, including plant anatomy, it is crucial to acknowledge the increased emphasis on molecular biology and its impact on the future of structural biology, as emphasized by Sokoloff *et al*. (2021) in the article "Plant Anatomy: At the Heart of Modern Botany".

Peter Nick (2022), in his article "The Return of the Functional Morphologists", draws attention to the complementarity of microscope and the micropipette: these tools are not mutually exclusive but complementary. Although describing a tissue, a structure, or a cell is not an end for research to be fruitful, the "where" must remain integrated with the "why" to explain a process. Form and function are two sides of the same coin, distinct from one other, but composing a unity. Therefore, they should always be understood together: it is impossible to unravel the association between form and function by studying only the structure or vice versa.

Future research must extend beyond the complete description of anatomical details and aim to integrate anatomy with other subareas of botany. It is essential to adopt an evolutionary approach when analyzing the expression and function of genes, which should be complemented with a thorough examination of structural data generated by qualified anatomists, particularly those hailing from Brazil.

In the last decade, Brazilian authors have largely contributed to studies published in quality international journals focused on botany. These journals regularly and frequently feature numerous Brazilian plant anatomists who have contributed to the field of structural botany in the country, which can be verified by simply consulting the Lattes Platform of the CNPq. Examination of citations of the articles published by our researchers in databases such as the Web of Science (Clarivate) and Scopus (Elsevier) reveals that the international community recognizes the research conducted in plant anatomy in our country. Frequently, Brazilian anatomists have been publishing in collaboration with researchers from renowned international institutions. Thus, from the first steps in the 1920s, plant anatomy grew in Brazil and earned the respect of the scientific community around the world. Brazilian researchers who work with plant anatomy have their names recorded in the history of institutions, publishers, and journals that are a reference for quality in the area of botany. And we are only starting!

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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