Hallmark Features of Stem Anatomy in the Family Lamiaceae

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HALLMARK FEATURES OF STEM ANATOMY IN THE FAMILY LAMIACEAE

By

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Submitted in Partial Fulfillment of the Requirements for Graduation with Honors from the South Carolina Honors College

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Thesis Summary

This project was a study of the stem structures of a group of plants in the Lamiaceae, or mint family. Well-known members of the Lamiaceae include sage, rosemary, basil, and several common weeds. Lamiaceae is a very large family, and species within it can be found all over the world. Species within Lamiaceae usually have a square-shaped stem. Beyond that basic shape, however, different species may have very different stem structures. It was thought that if stem structures proved unique enough, then a plant could be identified by stem structure alone. It was also thought that plants more closely related to each other would have more similar stem structures than less closely related plants, and that these similarities might help clarify relationships between species in Lamiaceae.

19 different species were chosen for this study, including two different types of basil, for a total of 20 examined plants. Very thin slices of the stems were cut using a tool called the hydromicrotome. Invented by the late John Herr, the hydromicrotome allows one to make very thin slices of plant tissue, about the thickness of a single sheet of foil. This project serves to showcase the use of the hydromicrotome itself, as well as the plants it was used to cut. Slices of the plant stems were stained, so that stem structures would be more visible, and photographed under a microscope at varying magnifications. A short description of the important features of each stem was written.

Four easily visible traits were compared between all 20 specimens, to see if any of them correlated to relationships between species. No trends were observed. However, each plant did have a unique structure, which might allow one to classify a plant as a specific species based on its stem. Stem structure can change with environment, though, so more research on how stem structure can differ within a species is necessary for such a classification system to work.
Abstract

Lamiaceae is a cosmopolitan family, containing around 236 genera and 7,534 species. The family has been the object of considerable taxonomic controversy and ultimate revision, especially concerning subfamilial and tribal limits. A broad-based anatomical approach has been undertaken to assess comparative anatomy of the stem as a reasonable systematic technique. The stems of several members of the family were compared. Cross-sections were made using the recently invented hydromicrotome, fixed, and examined at magnifications of 40x, 100x, and 400x. The common anatomical features of each sectioned species were determined, and used to establish a basic guide to the hallmark stem features of Lamiaceae. Such data provides a basis for future investigation, and will aid in the classification of newly described species and the reevaluation of those already established. Several anatomical features in particular were compared to see if any phylogenetic pattern arose. No trends were observed, but similarities and differences within genera were noted.

Background

Lamiaceae, or the mint family, is a cosmopolitan family containing, in some classifications, over 7,000 different species.\[^7\] This family is split into seven subfamilies, some of which contain a number of tribes and subtribes. Lamiaceae is also a historically convoluted family, in which interfamily relationships are often complex and unclear. Some modern researchers claim that the subfamily divisions of Lamiaceae are artificial taxa.\[^8\] Modern methods of phylogenetic analysis are beginning to be employed to clarify these convoluted relationships.\[^3\] In the 1990’s, work in DNA sequencing led to the reclassification of a number of species from the closely related Verbenaceae as members of the Lamiaceae.\[^2\] Such an incident shows how phylogenetics will prove useful to clarifying the intrafamily relationships of
Lamiaceae in the coming years. However, to date many species within the Lamiaceae have never undergone DNA analysis. Until DNA analysis can be more widely applied to the Lamiaceae, comparative anatomy may be used to aid in the classification and clarification of the family.

Anatomical features have frequently been used to identify relationships between species in the Lamiaceae, namely reproductive structures. Krestovskaja (1992) uses the shape of the corolla, the pubescence of the calyx, and the comparative size of stamens as diagnostic features.\textsuperscript{[10]} Hedge (1992) claimed that two of the best organs through which to study interspecies variation are the stamens and the nutlets.\textsuperscript{[8]} Vegetative anatomy, however, may be just as distinctly variable between species. New technology, such as the late John Herr’s hydromicrotome, may make it significantly easier to sample, examine, and preserve specimens of vegetative anatomy.

Stems of species within the Lamiaceae are known to have a common shape and structure, hereafter referred to as the classic Lamiaceae stem (Fig. 1). The classic Lamiaceae stem is square in shape, with four corners which may be rounded or sharp, and four faces between them. Just inwards of the epidermis within each corner is a region of angular or rarely lamellar collenchyma cells. Inwards of the angular collenchyma in the corners and the epidermis along the faces is a cortex of parenchyma cells. The parenchyma cells may be compact, or they may be separated by air spaces, in which case they are termed aerenchyma. Inwards of the cortex is vascular tissue. In the corners, the vascular tissue is composed of prominent, distinctive corner vascular bundles. The outermost vascular tissues in the bundle are small lignified phloem fibers, arranged in rows or clumps that span the whole outside of the vascular bundle. Inwards of the phloem fibers is a region of active phloem composed of sieve cells and companion cells follow immediately by a fascicular and interfascicular cambial zone. Directly within the active phloem is lignified xylem.
composed of tracheary elements such as tracheids and vessel elements, xylem parenchyma, and xylem fibers. The xylem, particularly the vessel elements, tend to be the largest and most distinctive aspects of the corner vascular bundle, and make up the bulk of its shape and size. The innermost portion of the corner vascular bundle is composed of unlignified tracheary elements and peripheral pith cells. In the faces of the square shape, the vascular tissue is composed of a vascular cambial zone that connects the large corner vascular bundles to each other. There may be smaller vascular bundles embedded within the vascular cambial zone, with roughly the same structure as the corner vascular bundle. Finally, inwards of the vascular tissue is the pith, which may be hollow or solid.

Lamiaceae are well-known to be a significantly variable family. Species may exhibit many unique variations of the classic Lamiaceae stem structure, such as in the shape of their corner vascular bundles or the presence and size of epidermal trichomes. Some stems may even deviate from this classic blueprint, forming structures entirely unique to their species. If these differences are characteristic to a species, and if patterns may be found in these differences, then stem structure could be used to study subfamily relations, to identify members of Lamiaceae at multiple taxonomic levels, and to help restructure some of the complex and artificial taxa within the family.

Materials and Methods

19 species were chosen for this study. These species were *Teucrium canadense* L. (subfam. Ajugoideae), *Lamium galeobdolon* (L.) Crantz (subfam. Lamioideae tribe Lamieae), *Leonotis nepetifolia* (L.) R. Br. (subfam. Lamioideae tribe Leucadeae), *Physostegia virginiana* (L.) Benth. (subfam. Lamioideae tribe Synandreae), *Stachys caroliniana* J. B. Nelson & D. A. Rayner (subfam. Lamioideae tribe Stachydeae), *Stachys floridana* Shuttlew. ex Benth. (subfam. Lamiaceae)
Garner


In the case of *O. basilicum*, two different cultivars—sweet basil and purple ruffles basil—were examined separately to help account for intraspecies variation. While small, this sample group contains four out of the seven subfamilies within Lamiaceae, and spans multiple tribes and subtribes. Though many of these species have been widely naturalized and cultivated, their native origins cover a wide geographic spectrum. *V. agnus-castus* was included in particular because it was one of the species reclassified as Lamiaceae from Verbenaceae following DNA analysis, and thus it was thought to have particularly unique stem anatomy. *Stachys, Salvia*, and *Scutellaria* are three of the largest genera within Lamiaceae; for this reason multiple species from each genus are examined. Voucher specimens of all species are on deposit in the A. C. Moore Herbarium, University of South Carolina (*T. canadense* USCH 116300; *L. galeobdolon* USCH 108050; *L. nepetifolia* USCH 108885; *P. virginiana* USCH 46126; *S. caroliniana* USCH
Samples of these 19 species were collected from local cultivated gardens. When possible, the third internode below the lowest point of inflorescence was isolated for sampling. If the third internode was too immature to section properly, then the fourth or fifth internode was used instead. In the case of incomplete samples, in which the third internode may not have been present, an estimate of the internode closest to the third was used. In the case of *R. officinalis*, which exhibited a particularly small internode space, sections were made without regard to internode.

Stem sections approximately 22 \( \mu \)m thick were cut with a hydromicrotome, an instrument created by the late John Herr. The hydromicrotome is structured so that the only portion of the specimen not secured by the metal base is the portion being removed as a section. This prevents the blade from causing depression of and subsequent damage to the specimen.\(^9\) Sections were then fixed in Carnoy’s #1 Fixative (100% ethanol and glacial acetic acid, 3:1) for at least one hour or up to 24 hours. Sections were then transferred to and stored in 70% ethanol.

Specimens selected for observation underwent a gradual hydration process, soaking first in 50% ethanol, then 35% ethanol, then water. Sections remained in each fluid for at least five minutes to ensure stable osmotic pressure and to prevent cell rupture or damage. The sections were then stained with a 0.05% aqueous solution of Toluidine Blue O for between two and five
minutes, depending on the size of the section in question. Sections were mounted on glass slides with water and covered with 0 thickness cover glass. Slide preparations were observed with the 4x, 10x, and 40x objectives of a Wild M-20 microscope, and photographs were taken using an AmScope Digital camera. In specimens with heavily or unusually lignified tissues, the samples were de-stained after initial examination and photography with a 20% solution of calcium chloride. This left stain only in the lignified tissues of the sample, and allowed lignified features to be examined and photographed with greater clarity. After being photographed, sections were transferred directly back to 70% ethanol for long-term storage.

Observations

*Teucrium canadense*

*Teucrium canadense*, also known as American germander, is an herbaceous perennial that grows in woody-based clumps and forms rhizomes. It has narrowly ovate, toothed leaves with reticulated veins. Its flowers lack an upper lip, but exhibit four stamens that project outward. It grows native in moist woods and marshes throughout North America.\[28\]

The stem of *T. canadense* overall adheres to the classic Lamiaceae shape. It has straight edges (Fig. 2), and rounded corners that bulge outwards slightly (Fig. 3). The epidermis of the stem is mainly glabrous, with an occasional non-glandular trichome. Inwards of the epidermis in the corners is a small region of lamellar collenchyma (LC) cells (Fig. 4). Directly within the lamellar collenchyma is a very thin region of packed parenchyma (Par.), with very few small air spaces between the cells. Inwards of the parenchyma is the corner vascular bundle. The corner vascular bundle in *T. canadense* is comprised of rows of lignified xylem vessel elements (VE), directly within a section of
very small lignified phloem tissue. The corner vascular is unevenly u-shaped, an effect caused by the number of xylem vessel elements per row decreasing markedly near the center of the bundle. Inwards of the vascular bundle is a section of pith parenchyma, and the innermost portion of the pith is hollow. Cellular debris lines the edge of the pith cavity, suggesting that the pith was once solid, and became hollow as the plant matured as a result of apoptosis.

Within the epidermis along the faces of the stem is a very thin region of lamellar collenchyma (Fig. 5). Inwards the lamellar collenchyma is a thin region of parenchyma, with very few air spaces. Inwards of the parenchyma is a vascular cambium (VE) containing smaller vascular bundles, up to three per face. Inwards of the vascular cambium is a thin section of pith parenchyma, and within this is the pith cavity.

*Lamium galeobdolon*

*Lamium galeobdolon*, also known as yellow archangel, is an herbaceous perennial plant. It has green ovate-cordate leaves with patches of silver, and small yellow flowers that grow in whorls. *Lamium galeobdolon* is native to Europe and western Asia, but it has been naturalized in several other parts of the world. It tends to grow in shady, moist environments.[11]

*L. galeobdolon* conforms closely to the classic Lamiaceae stem. Its edges are straight and its corners, while rounded, do not bulge. The epidermis is mainly glabrous, with a few trichomes, which may be extremely long. Within the epidermis in the corners is a very small section of angular collenchyma (AC) (Fig. 6). This section takes up only the outermost portion of the corner. Inwards the angular collenchyma is a region of parenchyma cells, which are closely packed with very few air spaces. Directly within the
parenchyma region is the corner vascular bundle. \textit{L. galeobdolon} has a very small, roughly oval-shaped vascular bundle, with vessel elements arranged in rows (Fig. 7). Inwards of the vascular bundle is the pith, comprised of packed parenchyma. The pith of \textit{L. galeobdolon} is solid.

Inward of the epidermis along the face of the stem is a region of packed parenchyma cells (Fig. 8). Inwards of the parenchyma is the vascular cambium connecting the corner vascular bundles. There are no smaller vascular bundles embedded along the faces, but there are denser, possibly more lignified portions that suggest areas of increased vascular activity. Inwards the vascular cambium is the solid pith.

\textit{Leonotis nepetifolia}

\textit{Leonotis nepetifolia} is an African weed, common to the roadsides and fields of central Kenya. It has upright stems ending in terminal inflorescences, each bearing globular clusters of flowers. \textit{L. nepetifolia} has now been naturalized to the tropics and subtropics of both hemispheres.\textsuperscript{[6]}

\textit{L. nepetifolia} roughly follows the classic Lamiaceae stem, though its shape is not that of a perfect square. Its corners bulge outwards (Fig. 9), and its faces curve inwards (Fig. 10). The epidermis is covered in a number of short multicellular trichomes, mainly glabrous but a few non-glabrous. Directly inwards the epidermis in both the corners and the faces is a thin region of angular collenchyma cells (Fig 11.). Save for small occasional breaks in which the space is filled with parenchyma, this collenchyma stretches the entire perimeter of the stem (Fig. 12). Inwards of the angular collenchyma in both the face and the corner is a thin region of closely packed parenchyma, with few to no air spaces.
Inwards of the parenchyma in the corners is a long u-shaped vascular bundle (Fig. 13). The vascular bundle spans the entirety of the bulge outwards, and ends suddenly when the convex corner becomes the concave face. The vessel elements of the vascular bundle are loosely arranged into imperfect rows separated by other tracheary elements. The innermost portion of the corner vascular bundle contains the largest vessel elements. Inwards of the parenchyma along the faces is vascular cambium connecting the corner vascular bundles. Within the vascular cambium may sometimes be found a small vascular bundle. These small vascular bundles consist of a single row of several vessel elements.

Inwards of both the corner vascular bundle and the vascular cambium is the pith. The pith is technically hollow, but the pith cavity is very small. The edge of the pith cavity is bordered by cellular debris.

*Physostegia virginiana*

*Physostegia virginiana*, also known as obedient plant, is an herbaceous perennial that produces rhizomes. Its leaves are narrow-lanceolate and sharply toothed, and its flowers are tubular and bloom in upright terminal spikes. It is native to North America from Florida to New Mexico and as far north as Quebec and Manitoba. It is a hardy plant that grows in a diverse range of habitats.[16]

*P. virginiana* has a stem that adheres to the classic Lamiaceae shape. Its edges are straight (Fig. 14) and its corners are rounded (Fig. 15). It has few, if any, trichomes upon its epidermis. Inwards of the epidermis in the corner is a region of angular collenchyma (Fig. 16). The angular collenchyma region is thin, only five to ten cells in thickness, and it is not long enough to span the whole of the corner vascular bundle. Inwards of the angular collenchyma is a region of aerenchyma (Aer.). The air spaces are long, but very
thin and compressed, and directly inwards of the aerenchyma is a very thin section of packed parenchyma. Inwards of the parenchyma is the corner vascular bundle. *P. virginiana* has a relatively large corner vascular bundle, with an overall rounded and domed shape. The vessel elements are arranged loosely into imperfect rows, separated from each other by regions of other tracheary elements. Inwards of the corner vascular bundle is the pith, which is solid but filled with a number of small air spaces.

Inwards the epidermis along the face of the *P. virginiana* stem is a region of aerenchyma (Fig. 17). The air spaces of the aerenchyma are separated from one another by a thickness of one or two cells. Inwards the aerenchyma is the vascular cambium. Within the vascular cambium are small vascular bundles, up to three per face (Fig. 18). These vascular bundles are rounded in shape, and when there are three, the center bundle will be the largest. Inwards of the vascular cambium is the pith.

*Stachys caroliniana*

*Stachys caroliniana* is an herbaceous perennial plant. Its leaves are lanceolate to lance-elliptic, and its flowers are white to pinkish. Current studies show that it is native only to the Santee River Delta area of South Carolina.\[^{13}\]

*S. caroliniana* follows closely the classic Lamiaceae shape. Its faces are flat (Fig. 19), and its corners are sharp (Fig. 20). Its epidermis is covered in a number of lignified, unbranched trichomes. The majority are multicellular and non-glandular, though there are rare unicellular glandular trichomes as well. Just within the epidermis in the corners is a band of angular collenchyma (Fig. 21). Inwards of the angular collenchyma is a region of aerenchyma cells. The air spaces of the aerenchyma are numerous, but relatively small, often not larger than the cells which border them. Inwards of the aerenchyma is the
corner vascular bundle (Fig. 22). The corner vascular bundle of *S. caroliniiana* is domed or crescent-shaped, tapering off at either end, and its variously sized vessel elements are arranged in irregular, but compact rows. Inwards of the vascular bundle is a region of pith cells. The majority of the pith is hollow, and the edges of the pith cavity are marked by cellular debris.

Directly inwards the epidermis along the face of the stem is a region of aerenchyma (Fig. 23). The spaces of the aerenchyma are variable in size, sometimes larger than the cells that surround them, and irregular. Air spaces are separated from each other by single cells. Inwards of the aerenchyma is the vascular cambium, which may contain very small vascular bundles. These smaller vascular bundles are generally composed of four to five vessel elements and are round in shape. Inwards of the vascular cambium is the pith and pith cavity.

*Stachys floridana*

*Stachys floridana*, also known as Florida betony, is an herbaceous perennial commonly treated as a weed. It has pink flowers, and produces tubers that resemble the rattles of a rattlesnake.\[^{5}\] It is widespread throughout the southeastern United States and California.\[^{25}\]

The shape of *S. floridana* conforms well to the classic Lamiaceae stem shape, with some small exceptions. The faces of the stem bulge outwards, giving the square shape a bloated appearance (Fig. 24). The corners are very sharp (Fig. 25). Most prominently, the epidermis tends to pull away from the faces of the stem, leaving long air spaces between the epidermis and the cortex within. The pulled-away epidermis is two cell layers thick, and may tear away entirely under stress. The epidermis does not usually
pull away in the corners, however, because of a small region of angular collenchyma. The angular collenchyma forms the point of the sharp corner shape, and its placement halts the line of fracture the epidermis tends to follow. Just within the angular collenchyma in the corner of *S. floridana* is a region of aerenchyma (Fig. 26). The cells of the aerenchyma are large, relative to the angular collenchyma, and the air spaces between the cells are small. Inwards the aerenchyma is the corner vascular bundle, which has a compact oval shape (Fig. 27). The vessel elements of the corner vascular bundle are arranged in irregular, yet compact rows. Inwards of the vascular bundle is a thin region of pith cells. The pith is hollow, and the pith cavity is bordered by cellular debris.

Inwards of the separated epidermis and the air space it leaves, the face of *S. floridana* contains aerenchyma with small yet frequent air spaces (Fig. 28). Inwards of the aerenchyma is the vascular cambium, within which may be found small vascular bundles. Inwards of the vascular cambium is a thin region of pith tissue and the pith cavity.

*Stachys tenuifolia*

*Stachys tenuifolia* is also known by the common name of smooth hedge nettle. It is an herbaceous perennial plant that grows in wet, partially shady conditions, such as stream banks. It has narrowly ovate or lanceolate leaves, with serrate or crenate margins, and flowers that range from light pink to white. It is native to the eastern and parts of the Midwestern United States, and to the southeastern territories of Canada.

*S. tenuifolia* follows the classic Lamiaceae stem fairly well, with some exceptions. The faces are straight (Fig. 29) and the corners, while defined, bulge out slightly with the vascular bundle (Fig.30). Trichomes occur rarely, and usually only on the corners. The
entire stem is dry and fragile, tearing easily during the sectioning process. Just within the epidermis in the corner is a region of angular collenchyma (Fig. 31). The angular collenchyma forms a cap upon the corner of the stem, distorting the square shape. While the shape of the region itself is symmetrical, its placement atop the corner is off-center. Within the angular collenchyma is a thin section of aerenchyma. The air spaces of this aerenchyma are compressed, particularly close to the vascular bundle. Inwards of the aerenchyma is a compact, oval corner vascular bundle, with vessel elements arranged in imperfect rows and the larger vessel elements positioned more inwards of the stem. Inwards of the corner vascular bundle is a region of pith cells. The pith is hollow, and the pith cavity is surrounded by debris from cells broken by apoptosis.

Within the epidermis along the face of *S. tenuifolia* is a region of aerenchyma (Fig. 32). The air spaces in the aerenchyma may be large, but for the most part their sizes are compressed, and they are almost always longer than they are tall. Inwards the aerenchyma is the vascular cambium. Embedded within the vascular cambium may be vascular bundles, but these vascular bundles are very small, so much that only the largest can be readily noticed at lower magnifications. Inwards of the vascular cambium is the pith and pith cavity.

*Melissa officinalis*

*Melissa officinalis*, also known as lemon balm, is a bushy perennial plant. It has wrinkled, green ovate leaves that exude an aromatic oil. It is native to Southern Europe, but it is found in gardens the world over as a culinary herb, and has been naturalized in many new locations.\footnote{12}
*M. officinalis* overall adheres to the classic Lamiaceae stem (Fig. 33). It has straight faces (Fig.34) and defined corners (Fig. 35). The epidermis rarely has small, non-glandular trichomes. Just within the epidermis in the corner is a region of angular collenchyma (Fig. 36). This region does not blend with the shape of the underlying parenchyma, but forms a cap that in some cases warps the shape of the stem. The cap of angular collenchyma is, however, relatively centered upon the corner. Inwards of the angular collenchyma is a region of parenchyma, with long and compressed cells. There are a few air spaces within the parenchyma, as flattened as the cells which surround them, but they are not frequent enough to warrant the term aerenchyma. Inwards of the parenchyma is the corner vascular bundle. The corner vascular bundle of *M. officinalis* has an asymmetrical renal shape, with the larger vessel elements arranged in rows near the innermost portion of the bundle. The corner vascular bundle tends to taper off on either side with evidence of extra secondary growth, though this may simply be due to the maturity of the sectioned stem. Inwards of the corner vascular bundle is the pith. The cells of the pith are relatively large, and though there is the rare air space, the pith overall is solid.

Inwards the epidermis of the face of the stem is a cortex of compact parenchyma, with few to no air spaces (Fig. 37). Inwards the parenchyma is the vascular cambium. The vascular cambium contains small vascular bundles, up to two per face, consisting of a few vessel elements. Inwards of the vascular cambium is the solid pith.

*Rosmarinus officinalis*

*Rosmarinus officinalis*, commonly known as rosemary, is an evergreen perennial shrub. It has aromatic, grey-green needlelike leaves, which are commonly used as
culinary herbs. It is native to Africa, Europe, and parts of western Asia, though has been naturalized in many other parts of the world. *R. officinalis* grows best in moderately dry, sunny habitats.\[18\]

The stem of *R. officinalis* has little in common with the classic Lamiaceae stem. It is round in shape instead of square, and its structure is the same all over instead of differing between corners and faces (Fig. 38). The epidermis and the parenchyma are difficult to differentiate, because there is so little of the parenchyma and because any tissue aside from the lignified xylem tears away easily. Within the epidermis and parenchyma, however, is a region of active phloem arranged into neat rows (Fig. 39). Within the active phloem is the heavily lignified vascular tissues that make up most of the stem. In the center of *R. officinalis* is a very small, solid pith.

*Salvia coccinea*

*Salvia coccinea*, also known as Texas sage, is an herbaceous plant that may grow as an annual or perennial, depending on its habitat. It has ovate to lanceolate, toothed, pubescent green leaves, and red flowers that bloom in loose racemes. It is native to North America from Mexico and Texas east to Florida and South Carolina.\[19\]

*S. coccinea* in general follows the classic Lamiaceae stem structure, but the square shape is somewhat distorted. The corners bulge outwards in rounded knobs that contain the angular collenchyma and the vascular bundle (Fig. 40). The faces of the square bulge outward slightly as well around the small vascular bundles embedded in the vascular cambium (Fig. 41). The epidermis of the stem is covered in small multicellular and unicellular trichomes, which may be either glandular or non-glandular. Inwards of the epidermis in the corners is a region of angular collenchyma, which follows the bulging
shape of the corner and tapers out as the corner becomes the face (Fig. 42). Inwards of the angular collenchyma is a cortex of compact parenchyma, with no air spaces. Inwards of the cortex is a crescent-shaped corner vascular bundle. The vessel elements of the corner vascular bundle are arranged into fairly regular rows, which are themselves broken up at times by sections of other lignified xylem elements. The phloem fibers of the corner vascular bundle are not lignified. Inwards of the corner vascular bundle is a solid pith comprised of relatively large parenchyma cells.

Inwards the epidermis of the face of *S. coccinea* is a cortex of small, compact parenchyma cells with no air spaces (Fig. 43). Inwards the parenchyma is the vascular cambium, which may contain one or a few small vascular bundles (Fig. 44). If there is only a single vascular bundle, it will be larger than if there are few, and the face of the square shape will bulge outward to accommodate it. Inwards of the vascular cambium is the solid pith.

*Salvia guaranitica*

*Salvia guaranitica*, also known as anise-scented sage, is an herbaceous perennial subshrub. It has ovate, toothed leaves, and produces deep blue flowers. It is native to Brazil, Paraguay, and northern Argentina, but can grow in a variety of habitats, and has been naturalized in many other parts of the world.\[20\]

*S. guaranitica* has a stem that follows the structure, though not exactly the shape, of the classic Lamiaceae stem. Its corners are large, rounded, and bulge outwards in knobs that contain both the angular collenchyma and the corner vascular bundle (Fig. 45). Its faces are similarly warped outwards around smaller vascular bundles, creating an overall bumpy shape (Fig. 46). The epidermis does not have many trichomes, but the
trichomes it does have may be extremely long. Inwards of the epidermis in the corners is a thin, wide region of angular collenchyma (Fig 47). The angular collenchyma follows the shape of the outward bulge, and tapers off as the corner becomes the face of the square. Inwards of the angular collenchyma is an extremely thin cortex of parenchyma, only two or three cells thick. This thin cortex is solid, with no air spaces. Inwards of the cortex is a wide, crescent-shaped corner vascular bundle. The vessel elements of the corner vascular bundle are arranged into irregular rows, separated by wide regions of other tracheary elements. Inwards of the vascular bundle is a pith with relatively large cells. While there is a pith cavity, it is small, and not always present in every sample of the stem. This may be due to the immaturity of the internode space examined.

Inwards the epidermis along the face of *S. guaranitica* is a thin, broken region of angular collenchyma, which seems to only be present above small vascular bundles (Fig. 48). Inwards of the angular collenchyma is a cortex of solid parenchyma. This cortex is thin, though not as thin as the cortex within the corners. Directly within the parenchyma is the vascular cambium. The vascular bundles within the cambium may be extremely large, with as many vessel elements per row as the corner vascular bundles, and visible lignified phloem fibers. Inwards of the vascular cambium is the pith and, when present, the pith cavity.

*Salvia involucrata*

*Salvia involucrata*, also called roseleaf sage, is an herbaceous perennial plant. Its flowers are red and have particularly colorful, showy bracts. The petioles and veins of the green leaves are vaguely red as well. *S. involucrata* is native to the Mexican provinces Puebla, Tamaulipas, and Veracruz, but it has been naturalized to a number of new
locations and has been bred into a number of cultivars. It is commonly found in shady habitats, such as the edges of forests.[4]

*S. involucrata* has a stem that follows closely the classic Lamiaceae shape. It has rounded corners (Fig. 49) and straight faces (Fig 50). Its epidermis is covered in a number of very small, mainly unicellular trichomes, which may be either glandular or non-glandular. Directly inwards of the epidermis in the corner is a wide region of angular collenchyma. This region of angular collenchyma is thin, about five or six cell layers thick, but it is wide enough to span the entirety of the rounded corner. Inwards of the angular collenchyma is a very thin cortex of compact parenchyma, with no air spaces. Inwards of the cortex is a long, thin corner vascular bundle. It has an almost linear shape, curving gently with the bend of the corner. Inwards of the vascular bundle is a region of relatively large pith cells. The pith is hollow, with cellular debris along the edge of the pith cavity.

Inwards of the epidermis along the face of *S. involucrata* is a cortex of parenchyma cells. The parenchyma is relatively compact, though there are a few air spaces. Inwards of the parenchyma is the vascular cambium, which may have one or two small vascular bundles embedded within it (Fig. 51). Though smaller than the corner vascular bundles, these vascular bundles may be large enough to contain several rows of vessel elements and visible lignified phloem fibers. Inwards of the vascular cambium is the pith and pith cavity.

*Salvia madrensis*

*Salvia madrensis*, also known as forsythia sage, is an herbaceous perennial plant. It has cordate green leaves, which may be separated by relatively long internodes. It has
yellow flowers, held in aromatic calyces covered in glabrous trichomes. It is native only to the Sierra Madre Oriental in Mexico, at elevations of 1200-1500 meters, but it has been cultivated in other parts of the world. It grows best in warm, wet habitats.[4]

The stem of *S. madrensis* bears little resemblance classic Lamiaceae shape. Its corners are unusually long and drawn out, and its faces pinch inwards toward the center of the stem. The overall form may be described as cross-shaped or x-shaped. Even with these differences, however, the overall structures of the corners and faces are similar to that of the classic Lamiaceae stem. The epidermis has few, if any, trichomes. Inwards of the epidermis in the corner is a large section of angular collenchyma that forms the whole of the tip of the corner (Fig. 52). Inwards of the angular collenchyma is a thick cortex of compact parenchyma, with no air paces. Inwards of the parenchyma is a u-shaped vascular bundle (Fig. 53). The vessel elements of the vascular bundle are arranged into relatively neat, loose rows separated by other tracheary elements. The active phloem and the lignified phloem fibers do not form a continuous band, but are arranged in clumps above the rows of vessel elements. Inwards of the corner vascular bundle is a solid pith with relatively large pith cells.

Inwards the epidermis along the faces of *S. madrensis* is a very thin cortex of small, compact parenchyma cells (Fig. 54). Inwards the cortex is the vascular cambium, which may have a number of smaller vascular bundles embedded within it (Fig. 55). These bundles, while smaller than the corner bundles, are large enough to have several rows of vessel elements and visible lignified phloem fibers. They are round in shape. Inwards of the vascular cambium is the solid pith (Fig. 56).
*Salvia nemorosa*

*Salvia nemorosa*, also known as purple sage, is an herbaceous perennial that grows in woody-based clumps. It has green or grey-green, ovate-lanceolate leaves, and small purple flowers that grow densely on long, spike-like racemes. *S. nemorosa* is native to Europe and west-central Asia, but has been naturalized in many other parts of the world.[21]

*S. nemorosa* follows the classic Lamiaceae shape almost exactly (Fig. 57). Its faces are straight, and its epidermis is covered in a number of multicellular non-glandular trichomes. Directly inwards of the epidermis in the corner, however, is a cap of angular collenchyma that bulges outward from the rest of the square shape (Fig. 58). Inwards of the angular collenchyma is a cortex of compact parenchyma cells with no air spaces (Fig. 59). Inwards of the parenchyma is the corner vascular bundle. The corner vascular bundle has an uneven renal shape, caused by a gap between vessel element rows and a decrease in vessel element row size at one end of the vascular bundle. Vessel elements tend to decrease in size in the innermost portion of the vascular bundle. The active phloem and lignified phloem fibers do not form a continuous band above the xylem, but are broken up frequently into small clumps. Inwards of the vascular bundle is a region of relatively larger pith cells. The pith is hollow, and the border of the pith cavity is marked by cellular debris.

Directly within the epidermis along the face of *S. nemorosa* is a thin cortex of parenchyma (Fig. 60). Inward the parenchyma is the vascular cambium, which is studded throughout with a large number of smaller vascular bundles (Fig. 61). The broken clusters of phloem elements continue along the length of the face over these numerous
vascular bundles, giving the whole stem an impression of continuous vascular activity and secondary growth. The smallness of the vascular bundles and the continued presence of cambium, however show that in spite of this no significant secondary growth has occurred. Inwards of the vascular cambium is the pith and pith cavity.

Ocimum basilicum

*Ocimum basilicum*, also known as basil, is an herbaceous annual plant native to tropical parts of Asia and Africa. It is sensitive to cold temperatures and prefers habitats with well-drained soil. It is highly aromatic, has been domesticated by humans for several centuries. Due to the selective breeding performed on *O. basilicum*, the plant is available in several anatomically distinct cultivars.[14] In this study, two separate cultivars were studied: sweet basil and purple ruffles basil.

Sweet Basil

Sweet basil is the most common, basic form of basil. It has wrinkled green leaves and small white flowers.[1]

Sweet basil has a stem that overall adheres to the classic Lamiaceae shape, with a few small exceptions. The corners are fairly rounded (Fig. 62), and the faces of the square curve inward slightly (Fig.63). The stem is mainly glabrous, with a few trichomes. Inwards of the epidermis in the corners is a region of angular collenchyma (Fig. 64). The angular collenchyma follows the curve of the rounded corner shape, and tapers off into the parenchyma at either end. Inwards of the angular collenchyma is a cortex of parenchyma, with a few small air spaces. Inwards of the parenchyma is a wide, thin, and curving vascular bundle. The vessel elements of the vascular bundle are loosely arranged, and may be
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relatively small compared to the other tracheary elements surrounding them. The active phloem and the lignified phloem fibers are broken into many small clumps outward of the xylem. Inward from the vascular bundle is a solid pith of relatively large pith cells.

Inward from the epidermis along the side of sweet basil is a small amount of angular collenchyma, which may not be present around the entire perimeter of the stem (Fig. 65). Inwards of the angular collenchyma is a cortex of compact parenchyma with no air spaces. This cortex may be very thin, or it may be quite vast and contain within it unusual bundles of tissue (Fig. 66). These bundles are circular in shape and consist of parenchyma surrounding a center of lignified cells (Fig. 67). It is unclear what these bundles may be, but it is hypothesized that the sections were taken unusually close to the node, and that these bundles may represent undeveloped leaves or petioles still enclosed within the main stem. Inwards of the parenchyma is the vascular cambium. The vascular cambium may have small vascular bundles embedded within it, though these vascular bundles consist of only one to a few vessel elements. Inwards of the vascular cambium is the solid pith.

Purple Ruffles Basil

Purple ruffles basil, sometimes differentiated from other basils as *O. basilicum var. purpureascens*, has dark purple foliage with “ruffled” edges. It produces light purple flowers.[1]

Purple ruffles basil overall adheres to the classic Lamiaceae stem, though it has faces which curve inwards slightly and bulge outwards around their
vascular bundles (Fig. 68). It has rounded corners and rare, multicellular, glandular trichomes (Fig. 69). Directly inwards of the epidermis in the corner is a region of angular collenchyma, which curves with the shape of the corner and tapers out as the corner becomes the face (Fig. 70). Inwards of the angular collenchyma is a cortex of solid, compact pith cells. Inwards the cortex is a long, curving corner vascular bundle. The vessel elements of the vascular bundle are loosely arranged and may be separated from one another by sections of other tracheary elements. Inwards the vascular bundle is a solid pith with relatively large cells.

Inwards the epidermis along the face of purple ruffles basil is a very thin section of angular collenchyma, the presence of which may be patchy. Inwards of the angular collenchyma is a very thin cortex of parenchyma, sometimes only two or three cell layers thick. Inwards the cortex is the vascular cambium, which may contain one small vascular bundle per face within it. These vascular bundles are roughly round or oval, and contain only a few vessel elements. Inward the vascular cambium is the solid pith.

Plectranthus scutellarioides

_Plectranthus scutellarioides_, also known as coleus, is an herbaceous evergreen perennial. It is native to Southeast Asia and Malaysia, but has been cultivated and naturalized as a garden foliage plant. Its leaves are showy and multicolored, with particular color combinations varying widely between cultivars, and its flowers are small and blue to white.¹¹⁷
P. scutellarioides follows very closely the classic Lamiaceae shape. It has rounded yet defined corners (Fig. 71), and straight faces (Fig. 72). Its epidermis is covered in a number of small, unicellular glandular and non-glandular trichomes. The structure of P. scutellarioides differs from the classic shape, however, in that significant amounts of angular collenchyma may be found directly inwards the epidermis all around the perimeter of the stem, not simply in the corners. The angular collenchyma in the corners is thicker (Fig. 73), but angular collenchyma a few cell layers thick can be found within the faces. Inwards the angular collenchyma both in the corners and in the faces is a cortex of compact parenchyma, with no air spaces.

Inwards the cortex in the corners is a long, curving corner vascular bundle. The vessel elements of the corner vascular bundle form long, imperfect rows separated in places by other tracheary elements. The active phloem becomes unusually thick at the apex of the corner, giving the illusion that the vascular bundle is drawn up to a sharp point. Inwards the vascular bundle is a solid pith with relatively large pith cells.

Inwards the cortex along the face of P. scutellarioides is the vascular cambium, within which may be two or three vascular bundles per face. These small vascular bundles are usually very thin, as small as a single row of vessel elements, but they may be very long as well. Inwards the vascular cambium is the solid pith.

Scutellaria integrifolia

Scutellaria integrifolia, also known as rough skullcap or helmet-flower, is an herbaceous perennial plant. The leaves located near the bottom of the plant tend to be coarsely toothed, while upper leaves lack teeth and are generally narrower. Its flowers are generally bluish-lavender. Its preferred habitat is clearings and open woodland, generally
containing moist soil.\textsuperscript{[23]} It is native to the southeastern and Midwestern United States, and parts of New England.\textsuperscript{[22]}

\textit{S. integrifolia} is a dry and brittle plant that breaks easily in the sectioning process, but it does exhibit a stem that closely matches the classic Lamiaceae shape. It has relatively sharp corners (Fig. 74) and straight faces (Fig. 75). Occasionally it displays small unicellular trichomes, mainly on the corners of the stem. A small divergence from the classic Lamiaceae shape occurs in the angular collenchyma just within the epidermis in the corner. The region of angular collenchyma is small in relation to the size of the corner vascular bundle, but it forms a cap atop the corner of the stem and pushes outward against the basic square shape (Fig. 76). Inwards of the angular collenchyma is a cortex of aerenchyma with large, irregular air spaces. Inwards the cortex is the corner vascular bundle. The corner vascular bundle is relatively compact and rounded in shape, tapering off into the vascular cambium on either side. The largest vessel elements are concentrated at the innermost portion of the vascular bundle. Inward of the vascular bundle is a thin section of large pith cells. The pith is hollow, though it is unknown how much of this is due to the overall fragile nature of the stem.

Inward the epidermis of the face of \textit{S. integrifolia} is a cortex of aerenchyma with large, irregular air spaces (Fig. 77). Inward from the cortex is the vascular cambium, which in \textit{S. integrifolia} exhibits a significant amount of secondary growth. No discernable side bundles are present. Inwards of the vascular cambium is the pith and pith cavity.
Scutellaria racemosa

*Scutellaria racemosa* is an herbaceous plant native to southern Mexico, eastern Brazil, northern Argentina, and the Andes. It is commonly found in damp habitats and alongside bodies of water. It has consistently hastate leaves and small flowers.[15]

*S. racemosa* is a dry and fragile plant, which makes it difficult to section. It only somewhat follows the classic Lamiaceae stem structure. Its stem is mainly glabrous with few trichomes. Its edges are straight and the overall shape is square, but each of its corners is tipped in a hornlike or spike-like outgrowth (Fig. 78). Inwards the epidermis in these corner growths is not angular collenchyma, but rows of lignified cells. Inward these lignified cells is a cortex of compact parenchyma. This parenchyma develops air spaces and becomes aerenchyma at the base of the spike-like growth. Inwards the cortex is the corner vascular bundle, which is compact and domelike in shape (Fig. 79). The vessel elements of the xylem are clustered at the innermost portion of the vascular bundle. Inward the vascular bundle is a region of large pith cells. The pith is hollow, and the pith cavity is bordered by cellular debris.

Inwards the epidermis of the face of *S. racemosa* is a cortex of what may be very loosely packed parenchyma or very tightly packed aerenchyma (Fig. 80). Air spaces may be large and frequent in one section of the face, and entirely nonexistent in another. In the outmost portion of the cortex are occasional lignified cells, similar to the ones found in the hornlike corner growths. Inward the cortex is the vascular cambium, which may contain a few extremely small, poorly distinguished vascular bundles. Inwards the vascular cambium is the pith and pith cavity.
**Vitex agnus-castus**

*Vitex agnus-castus*, also known as lilac chaste-tree, is a deciduous shrub, which may grow up to 3 meters tall. It has grey-green palmately compound leaves with lanceolate leaflets, and pale lavender or violet flowers that grow in loose panicles. *V. agnus-castus* is native to Asia and the Mediterranean.[29]

*V. agnus-castus* does not follow at all the classic Lamiaceae shape. Its stem is round, though the pith suggests an underlying square figure, and there is no complex structure of vascular bundles and cambium (Fig. 81). Inwards the epidermis all around the stem is a thin cortex of compact parenchyma with no air spaces (Fig. 82). Inwards of the cortex is the vascular tissue, which forms a large portion of the stem. The larger vessel elements of the xylem are concentrated in the innermost portion of the vascular tissue. Inwards the vascular tissue is a large, solid pith comprised of large cells. The pith’s shape is that of a bulging square, and the corners of this square push outwards to affect the shape of the vascular tissue (Fig. 83). Overall, however, the shape of the stem remains rounded.

**Discussion**

Comparing the 19 species, it is clear that whatever patterns may arise, each species has a unique stem anatomy. This indicates that stem anatomy may be used to classify members of Lamiaceae at the level of species. Such classification would be useful in determining new species, and in identifying individuals of known species that appear similar to others in the field.

Four of the most visible features exhibited by the Lamiaceae stems—the shape of the vascular bundle, the placement of angular collenchyma in the corners or around the perimeter of the stem, the bulging or non-bulging shape of the corners, and the presence or absence of a pith
cavity—were compared between species within Lamiaceae to examine the presence of patterns within current classifications (Chart 2). Each of these four categories was very general; no distinction was made, for example, for the differences between sharply angled or smoothly rounded corners. These were intended to be very broad categories, by which overarching patterns may begin to emerge. Some traits were more common in some areas of the family than others. The subfamily Nepetoideae, for example tended have to have u-shaped vascular bundles and bulging corners, while the subfamily Lamioideae tended to have more rounded or elongated vascular bundles and angular or rounded corners. These could not be called true patterns, however, for each family had multiple exceptions to these trends. The rarest trait, the presence of angular collenchyma around the perimeter of the stem, was examined because it was thought that such a rare and unusual divergence from the classic Lamiaceae stem structure may have a basis in phylogeny, but this trait displayed no traceable pattern.

The lack of overreaching patterns in the stem anatomy of Lamiaceae suggests one of two things. It may be that stem anatomy is indeed a valid method of classifying subfamily relations, and that the relationships the family is currently thought to contain are in fact artificial. Alternatively, and far more likely, established subfamily relationships within Lamiaceae are mainly correct, and stem anatomy is too imprecise and variable to form a basis for classification. Furthermore, it may be that only the examined features of the stems do not show patterns, and that other features must be used instead. Some other features that may be examined for patterns include the shape of angular collenchyma in the corner of the stem, or the presence of aerenchyma versus packed parenchyma in the cortex. Alternately, patterns might be found if some features of the family examined in this paper were made narrower and more precise.
Comparing the exact shape of corner vascular bundles closely may show more patterns than simply classifying them into broad categories of shapes.

Two taxa in particular exhibited noteworthy trends: _Salvia_ and _Stachys_. Out of the five species of Salvia observed, there were none that exhibited all four traits similarly. In fact, species of Salvia were as dissimilar from each other as they were from species in different genera. Five specimens is a small sample group, and it may be that more Salvia species would need to be observed for recognizable patterns in stem structure to emerge. However, the amount of variation observed within five species suggests that Salvia could be divided into subgenera. If this is the case, then stem anatomy may form a basis upon which such subdivision might occur.

The three species of _Stachys_, on the other hand, were all very similar to each other. Each exhibited the same combination of the four observed traits, and in fact held similarities beyond these four. Their corner vascular bundles, for example, were not only round, but round in a similar way to each other, which other species with round vascular bundles did not exhibit. This suggests that, in some cases, stem anatomy may be used to classify specimens to the level of genus. More research will be necessary, however, to determine if these trends continue beyond the three species examined in this study.

This study was limited by not only the small size of the sample, but by the fact that only a single individual of each species or cultivar was examined. Stems are highly variable, not only between species, but within a species as well. Environmental factors such as moisture levels are known to have a marked impact on the stem anatomy of a plant, and the same species grown in different locations may exhibit significant anatomical variation. More research on the impact of environmental conditions on stem anatomy, and on the amount of variation found within single species, will be necessary to confirm the concepts suggested by this study.
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