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Morphological Study on Some Taxa of Myoporaceae and Scrophulariaceae

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The taxonomic relationship between Myoporaceae and Scrophulariaceae has long been debated, historical systems kept Myoporaceae as a distinct family but combined morphological and" especially molecular evidences" resulted in the treatment of the Myoporaceae as a part of Scrophulariaceae. This study investigates the taxonomic delimitation between these families by examining macromorphological characters of the whole plant and micromorphological features of the stem, lamina, and flower. Six species from both families (three representing Myoporaceae and three representing core Scrophulariaceae) were collected and investigated using light microscopy to assess the diagnostic traits. A sum of 47 macro- and micromorphological traits was compiled into a comprehensive matrix and statistically analyzed using R software to evaluate the degree of similarity and potential phylogenetic closeness between the two families. Results revealed significant differences mainly in (plant habit, fruit type, number of ovules, mesophyll tissue, secretory system, and trichome types), which support the distinct separation of the two families. In contrast, the considerable similarity in floral vasculature patterns suggests a possible merger of the two families. Furthermore, the taxonomic placement of *Leucophyllum frutescens* is noteworthy, as it exhibits a high degree of similarity to the family Myoporaceae.

Keywords: Anatomy, Morphology, Myoporaceae, Scrophulariaceae, UPGMA

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INTRODUCTION

Myoporaceae R.Br. is a small flowering plant family, containing about five genera and 230 species (Chinnock, 2007). The family is distributed in temperate to tropical regions of the southern hemisphere especially Australia in arid and semi-arid regions (Theisen & Fischer, 2004). The habit of these plants are generally woody shrubs or small trees characterized by gland dotted, spirally arranged and often simple aromatic leaves with entire margin. The family includes various economically important species in horticulture applications, environmental contributions, and traditional usages, especially in arid and semi-arid areas. Some species are used for timber, some are ornamentals especially *Eremophilla*, some fruits are eaten locally (*Myoporum*), and some are commonly used in folk medicine. They can be also utilized as windbreaks in arid farming systems (Richmond & Chinnock, 1994; Theisen & Fischer, 2004; Chinnock, 2007). The Flowers of the family Myoporaceae are solitary or arranged in simple raceme inflorescence. Calyx is with five imbricated lobes. Corolla is zygomorphic, with mainly five united lobes. Stamens are four, and anthers are with longitudinal slits. Ovary superior, with two fused carpels, two locules each with one to two anatropous, unitegmic ovules pendulous from near apex. Style terminal. The fruit is drupe (Kadereit, 2004).

While Scrophulariaceae Juss. *sensu lato* (figwort family) is a cosmopolitan family; it includes about 200-220 genera and nearly 2600 to 3000 species (Rendle, 1952; Core, 1962; Lawrence, 1969; Heywood, 1979; Pandey, 1982; Willis, 1985). Recently according to APG (2016), the family comprises 62 genera and about 1830 known species (Christenhusz & Byng, 2016). In 2024, Plant of the World Online accepted 58 genera. These plants are

found primarily in temperate and tropical regions around the world. The family is characterized by its wide range of morphological forms, including herbs, shrubs, and rarely small trees. The family includes economically important species such as *Verbascum* species (mullein) which have been used for centuries for respiratory conditions in traditional medicine (Turker & Gurel, 2005). The flowers of Scrophulariaceae are bisexual with hypogynous discs. Calyx with five imbricate or valvate sepals. The corolla is commonly tubular, and zygomorphic except in *Verbascum*, composed of five imbricate united lobes. Stamens are commonly four, didynamous, epipetalous, and arising from the extreme base of the corolla tube, (stamens maybe five in *Verbascum*). The ovary is superior, mainly with a hypogenous disc, composed of two united carpels. Ovules are numerous, anatropous, and arranged on a thick axile placenta. Style one and terminal. Stigma bilobed. Fruits are capsules (Bailey, 1949; Rendle, 1952; Benson, 1957; Core, 1962; Lawrence, 1969; Heywood, 1979; Pandey, 1982; Willis, 1985; Kadereit, 2004).

Morphological characters are critical for identifying closely related taxa and understanding evolutionary relationships and biodiversity (Viscosi & Cardini, 2011; Salim et al., 2021). Morphology plays an essential role in the taxonomy of Myoporaceae helping as a major tool to discriminate species and comprehend evolutionary relationships within the family (Chinnock, 2007). Fowler et al. (2021) incorporated molecular phylogenetics with morphological characteristics to determine relationships within Myoporaceae; moreover, they demonstrated how morphological characteristics can support molecular data and provide insights into the evolutionary history of the group.

The anatomical characters are broadly utilized in studying taxonomic relationships at various taxonomic ranks (De Villiers et al., 2010; Liu & Zhu, 2011; Salim et al., 2025). Myoporaceae is characterized by the presence of secretory cavities lined with epithelial cells in leaves and young stems (Metcalfe & Chalk, 1950; Lersten & Betman, 1998). The occurrence of secretory cavities is also recorded in some Scrophulariaceae members; *Scrophularia*, *Verbuscum*, and *Leucophyllum* (Volkens, 1887; Metcalfe & Chalk, 1950; Lersten & Beaman, 1998; Lersten & Curtis, 2001). Several studies discussed the taxonomic relationship between Myoporaceae and Scrophulariaceae depending on anatomical characters, among others, Karrfalt & Tomb (1983) studied the relation between *Leucophyllum* and Myoporaceae by comparing the characters of air spaces in the isolateral leaves of *Leucophyllum* with that of *Bontia*. This study demonstrated an evolutionary association between Leucophyllaea and Myoporaceae. Also, Carlquist & Hoekman (1986) supported the taxonomic relationship between Myoporaceae and Scrophulariaceae based on the wood anatomical characters.

Henslow (1891) clarified the bases of floral anatomy as well as its significance in understanding flower morphology; moreover, he emphasized the importance of the vasculature pattern in the receptacular region. The floral vascular orientation is taxonomically and phylogenetically informative, as persistent internal vascular traces retain evidence of ancestral morphology and evolutionary relationships even when external organs are lost (Subramanyam, 1960). The floral anatomy solved various morphological, taxonomic, and phylogenetic problems in different plant families (Puri, 1951; Stebbins, 1974; Salim et al., 2016; Tantawy et al., 2021).

The advancement of molecular studies clarifies, updates, and alters the prior understandings of the classification of flowering plants, affording a clearer illustration of the relation between plant families. An example of this is the re-classification of the Myoporaceae family, which was considered a separate family but now is included in the family Scrophulariaceae. In the traditional angiosperm classification systems, Myoporaceae treated as a distinct family close to Scrophulariaceae and placed in order personales (Bentham & Hooker, 1862–1883), order Tubiflorae (Engler & Prantl, 1895; Wettstein, 1935) order Scrophulariales (Cronquist, 1981), order Lamiales or Scrophulariales (Bessey, 1915; Dahlgern, 1980). This separation was primarily based on morphological differences, such as variations in secretory structures, flower symmetry, and adaptations to arid environments. On the contrary, the modern classification systems beginning with Olmstead et al. (2001), nested the *Myoporum* within Scrophulariaceae *s.s*.. Then APG II (2003) and onward, APG III (2009) and APG IV (2016) merged Myoporaceae as a tribe (Myoporeae) under Scrophulariaceae within order Lamiales. Oxelman et al. (2005), supported that Buddlejaceae and Myoporaceae belong inside Scrophulariaceae. Villaverde et al. (2023), mentioned that Myoporeae is now often included under Scrophulariaceae. The scrophulariaceae *s.s*. comprise nine tribes Aptosimeae, Buddlejeae, Freylinieae, Hemimerideae, Leucophylleae, Manuleae, Myoporeae, Scrophularieae, and Teedieae (APG III, 2009). There are many

intersections between members of Myoporacae and Scrophulariaceae, especially *Leucophyllum* (Srophulariaceae) shows close relationship to Myoporaceae, which has led to numerous studies on this point (Niezgoda & Tomb, 1975; Karrfalt & Tomb, 1983; Young et al., 1999). While Henrickson & Flyr (1985) recognized *Leucophyllum* as a distinct genus separate from Myoporaceae.

To clarify all above, this work was done to investigate and collect the macromorphological characters of whole plant as well as the micromorphological features of stem, lamina, and flower of the studied species. The study is also done to discuss, analyze and evaluate whether these characters can provide a little further clarification regarding the closure relationship between the two families.

MATERIAL AND METHODS

Plant sources

In the present work, six species were collected from different localities (three species belonging to Myoporaceae and the other three representing the core Scrophulariaceae). The collection data are shown in Table 1. The wild species were identified according to Täckholm (1974) and Boulos (2002), while the ornamental species were identified by the aid of Bailey (1949) and Bailey & Bailey (1976). According to APG IV (2016) *Bontia*, *Eremophila*, and *Myoporum* belong to tribe Myoporeae, *Leucophyllum* belongs to tribe Leucophylleae, and *Scrophularia* and *Verbascum* under tribe Scrophularieae. The voucher specimens of the wild species were deposited in the Herbarium of the Botany Department, Faculty of Science, Ain Shams University (CAIA).

The macromorphological characters of the whole plant were investigated directly from the fresh specimens (at least four individuals per species).

Stem and lamina anatomical investigation

Segments from stem and lamina were taken and preserved in F.A.A. solution (Formalin. Glacial acetic acid. Alcohol). The cross section of the stem (between the fourth and fifth node) and the vertical section of the lamina (from the middle portion) were prepared using hand microtome at 10-20µm, double stained using safranin and light green then mounted by Canada Balsam according to the customary method of Johansen (1940). The sections were examined and photographed using an Olympus C.35AD-2 light microscope. The internal structures were described with the help of Eames (1929) and Metcalfe & Chalk (1950).

Flower anatomical investigation

The mature floral buds of the studied species were fixed and preserved in (F.A.A.), embedded in paraffin wax, and then serially sectioned at 10-15µ according to (Johansen, 1940). Sections stained by crystal violet- erythrosine combination. The floral serial cross sections were examined by an Olympus C.35AD-2 light microscope. The practical study was done at the Botany Department, Faculty of Science, Ain Shams University.

Table 1. List of the studied species and their localities.

No.	Species	Source/ locality
1	***Bontia daphnoides* L.** =*Bontia daphnoides* var. *minor* (C.F.Gaertn.) A. DC. =*Bontia minor* C.F.Gaertn.	Orman Botanical Garden, Giza, Egypt
2	***Eremophila purpurascens* Chinnock**	//
3	****Leucophyllum frutescens* (Berland.) I.M.Johnst.** =*Terania frutescens* Berland. =*Leucophyllum texanum* Benth.	//
4	***Myoporum laetum* G.Forst.** =*Myoporum crystallinum* Kunze =*Myoporum perforatum* Voss =*Myoporum pubescens* G.Forst.	Around irrigation canal and fields, Kafr El-Sheikh governorate, Egypt
5	****Scrophularia xanthoglossa* Boiss.**	Wadi Talaa, Saint Katherine protectorate, Egypt
6	****Verbascum sinuatum* L.** =*Celsia sinuata* (L.) Colla =*Lychnitis sinuata* (L.) Fourr. =*Thapsus sinuatum* (L.) Raf.	Wadi El-Arbeen, Saint Katherine protectorate, Egypt

(*): The core Scrophulariaceae taxa

Data analysis

The recorded macro- and micromorphological characters were scored and coded as multistate character. The un-weighted pair-group method (UPGMA) dendrogram, and heatmap generation were performed using R software (R Core Team, 2013) with the following packages: *ggplot2*, *readr*, *FactoMineR*, and *factoextra*.

RESULTS

The macromorphological characters of the whole plant and micromorphological features of stem, lamina, and flower were illustrated for each studied species. The flower anatomical characters (micro-photographs) were arranged and illustrated in Figures 1- 6. Some of the specific stem and lamina anatomical characters (micro-photographs) were arranged and illustrated in Figure 7.

***Bontia daphnoides* L.**

Whole plant: a shrub with simple, glabrous, alternate, elliptic to lanceolate, petiolate leaves. The lamina with entire margin, acuminate apex and symmetrical base. The flowers arranged in a simple raceme inflorescence, pentamerous, zygomorphic with bi-lipped corolla tube and four fertile stamens. Anther lobes dithecious. The fruit is a drupe with oval seeds.

Stem anatomy (Figure 7, $a_{1,2}$): stem outline is terete. The epidermis is papillose to radial in shape and covered with thin cuticle and sunken glandular trichomes. The cortex consists of five to seven rows of angular collenchyma followed by 17- 20 rows of polyhedral parenchyma and an incomplete ring of sclerenchyma (extra-xylary fibers). The vascular system is in the form of a continuous cylinder. Vessels are barrel-shaped and diffuse porous. Rays are uniseriate fascicular and interfascicular. Pith wide of thin-walled polyhedral parenchyma. Crystals are found as druses in the cortex and pith. The schizolysigenous duct is recorded in the cortex and pith.

Lamina anatomy (Figure 7, a_3): the epidermal cells in the midrib are radially arranged while those in the wings are tangentially elongated; both are covered with thin cuticles. Trichomes are sunken and glandular. Mesophyll is dorsiventral, consists of three rows of discontinuous elongated palisade cells adaxially extend to the midrib followed by six rows of spongy cells abaxially with small intercellular spaces. The Midrib region outline is straight adaxially and convex abaxially and occupied by angular collenchyma beneath the ad- and abaxial epidermis and polyhedral parenchyma. The vascular supply of the midvein is represented by a crescent-shaped central vascular bundle supported by sclerenchyma fibers abaxially and many small lateral vascular bundles distributed throughout the wing tissue. Druses of calcium oxalate crystals accumulated in the midvein region. Schizolysigenous ducts are recorded in the midrib and wings tissue.

Flower anatomy (Figure 1): the pedicel vasculature is in the form of a dissected siphonostele formed from ten masses; five outer and five inner (Photo1). The outer five masses migrate toward the sepal tissue as a sepal trace then divided into three bundles (one median and two marginal). At the same level, each of the inner five masses firstly gives two marginal sepal bundles (for the two adjacent sepals) and secondly reunited in the form of continuous siphonostele. From the central stele, five petal traces are cut then enter the corolla tube tissue as five petal bundles each ramifying into numerous bundles (Photos 2& 3). Upwardly, four staminal traces protrude from the central stele and then enter the corolla tube as four staminal bundles (Photos 4-6), after that, at the anther level each bundle bifurcates to feed the two anther lobes (Photos 7-9). The remaining central stele is differentiated into the following: two dorsal carpellary bundles, numerous lateral carpellary bundles, and four ventral bundles (Photos 7-10). The two dorsal carpellary bundles run longitudinally along the carpel and the style then fades out beneath the stigmatic level. The lateral carpellary bundles undergo further branching, then fade out beneath the style level. The four ventral bundles feed the four ovules and fade out beneath the compitum level (Photos 11& 12). The septum between the two locules is incompletely fused in the upper portion of the ovary and is called compitum (Photo 12).

***Eremophila purpurascens* Chinnock**

Whole plant: a sub-shrub with simple, glabrous, alternate, obovate, sessile leaves. The lamina with entire margin, acute apex and symmetrical base. The flowers arranged in a simple raceme inflorescence, pentamerous, zygomorphic with bi-lipped corolla tube and four fertile stamens. Anther lobes dithecious. The fruit is a drupe with oval seeds.

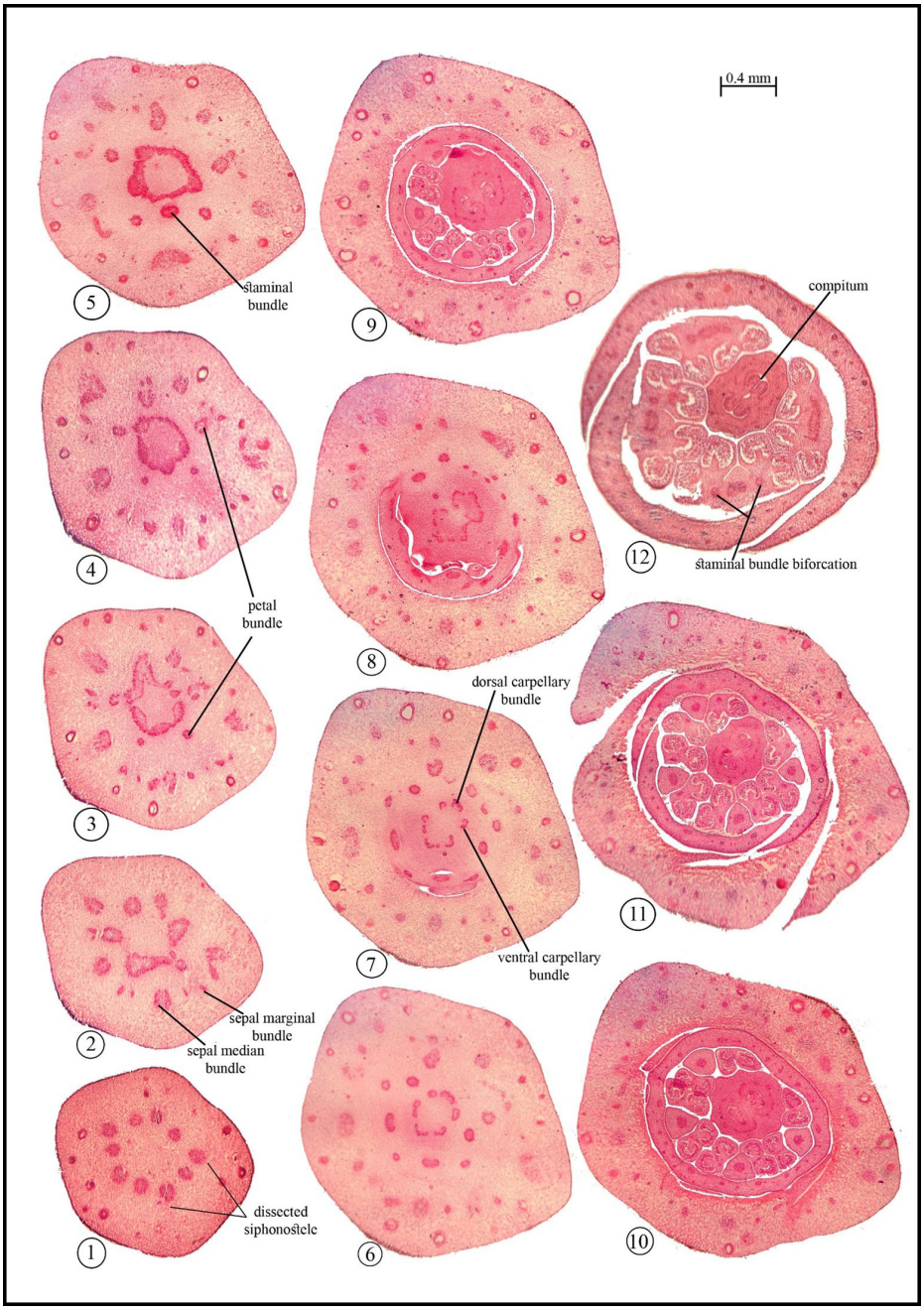

Figure 1 (Photos 1-12). Serial cross sections of a mature flower bud of *Bontia daphnoides* from pedicel upwards

Stem anatomy (Figure 7, $b_{1,2}$): stem outline is terete. The epidermis is papillose to radial in shape and covered with thin cuticle and two types of trichomes: uniseriate unbranched multicellular e-glandular and glandular capitate trichome. The cortex consists of two to three rows of angular collenchyma followed by four to six rows of polyhedral parenchyma and an incomplete ring of sclerenchyma (extra-xylary fibers). The vascular system is in the form of continuous cylinder. Vessels are barrel-shaped and diffuse porous. Rays are uniseriate fascicular and interfascicular. Pith wide of pitted thick-walled polyhedral parenchyma. Schizogenous duct is recorded in the cortex only.

Lamina anatomy (Figure 7, b_3): the epidermal cells in the midrib are radially arranged while those in in the wings are tangentially elongated; both are covered with thin cuticles. Trichomes are unbranched uniseriate multicellular e-glandular. Mesophyll is dorsiventral of three rows of continuous elongated palisade cells adaxially extend to the midrib followed by six rows of spongy cells abaxially without intercellular spaces. The midrib region outline is straight adaxially

and convex abaxially and occupied by polyhedral parenchyma. The vascular supply of the midvein is represented by a crescent-shaped central vascular bundle supported by sclerenchyma fibers abaxially and numerous small lateral vascular bundles distributed throughout the wing tissue.

Flower anatomy (Figure 2): the pedicel vasculature is a continuous siphonostelic structure (Photo 1). At a slightly higher level, ten protrusions arise from the central stele; five outer traces migrate toward the sepal tissue as sepal median bundles and undergo further ramification while the other inner five represents petal-sepal marginal complex. Each complex is divided into two outer sepal marginal bundles and one inner petal bundle (Photos 2-4). The latter enters the petal tissue and then undergoes further ramification giving numerous bundles. Upwardly, four staminal traces protrude from the central stele and then enter the corolla tube as four staminal bundles (Photos 6-9), after that at the anther level each bundle bifurcates to feed the two anther lobes (Photo 3). The remaining central stele is differentiated into the following: two dorsal carpellary bundles, numerous lateral carpellary bundles, and two ventral masses (Photos 7-9). The two dorsal carpellary bundles run longitudinally along the carpel and the style then fades out beneath the stigmatic level (Photo 13). The lateral carpellary bundles undergo further branching, and then fade out beneath the style level. Each ventral mass is formed from the fusion of two ventral bundles and is responsible for feeding the ovules (two ovules per locule) then at the final stage fades out beneath the compitum level (Photo 12).

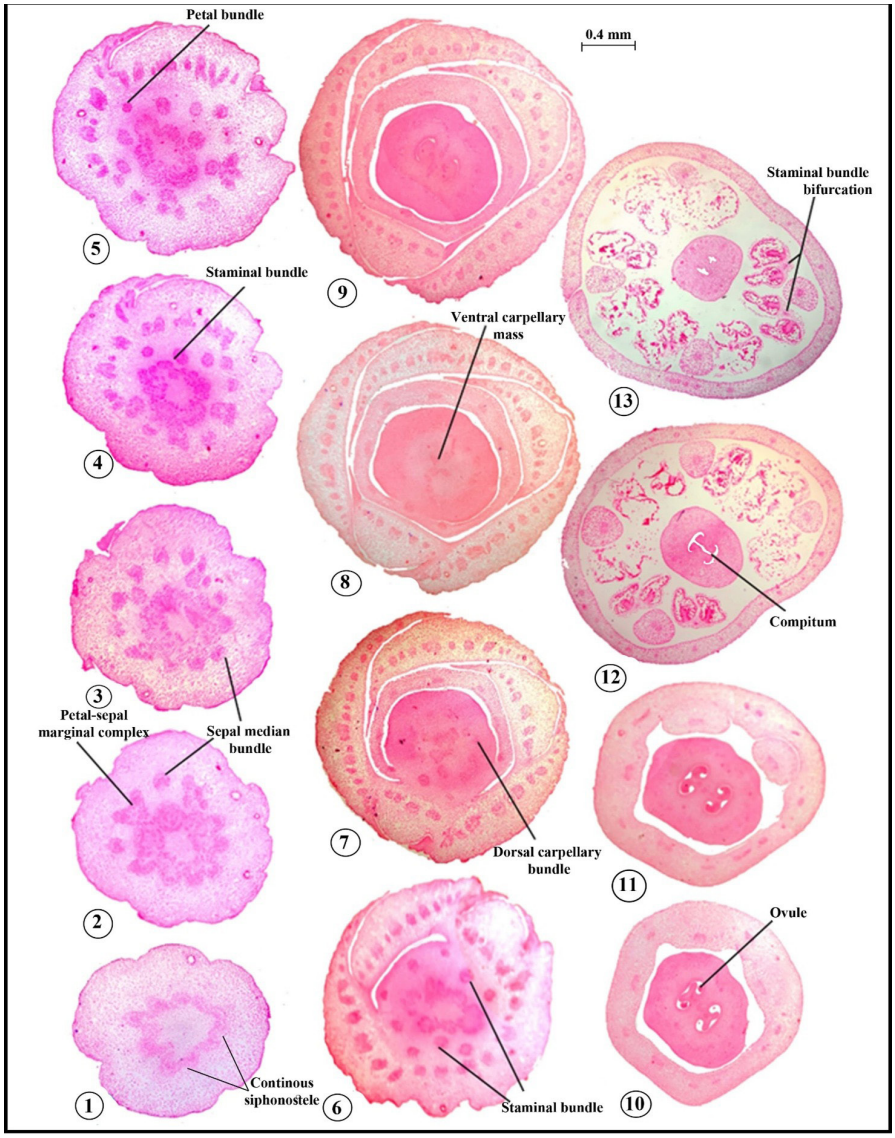

Figure 2 (Photos 1-13). Serial cross sections of a mature flower bud of *Eremophila purpurascens* from pedicel upwards

***Leucophyllum frutescens* (Berland.)**

Whole plant: a sub-shrub with simple, hairy, alternate, oblong ovate, petiolate leaves. Lamina with entire margin, acute apex and symmetrical base. The flowers arranged in a simple raceme inflorescence, pentamerous, zygomorphic with bi-lipped corolla tube and four fertile stamens. Anther lobes dithecious. The fruit is a capsule with oval seeds.

Stem anatomy (Figure 7, $c_{1,2}$): stem outline is terete. The epidermis is papillose to radial in shape and covered with thin cuticle and two types of trichomes: e-glandular branched tree-like multicellular and glandular capitate trichomes. The cortex has five to eight rows of polyhedral parenchyma and incomplete ring of sclerenchyma (extra-xylary fibers). The vascular system is in the form of continuous cylinder. Vessels are barrel-shaped and diffuse porous. Rays are uniseriate fascicular and interfascicular. Pith narrow of thin-walled polyhedral parenchyma. The idioblast is recorded in the cortex only.

Lamina anatomy (Figure 7, c_3): the epidermal cells in the midrib are radially arranged while those in the wings are tangentially elongated; both are covered with thin cuticles. Trichomes are two types: e-glandular branched tree like multicellular and glandular capitate. Mesophyll is isolateral, consists of two rows of palisade cells ab- & adaxially, the palisade cells adaxially extend to the midrib and discontinuous, at the middle of the wing there are two rows of spongy cells with large intercellular spaces. The midrib region outline is concave adaxially and convex abaxially and occupied by angular collenchyma beneath the ad- and abaxial epidermis and polyhedral parenchyma. The vascular supply of the midvein is represented by central rounded vascular bundle, and many small lateral vascular bundles distributed throughout the wing tissue.

Flower anatomy (Figure 3): the pedicel vasculature is a continuous siphonostelic structure (Photo1). At a slightly higher level**,** ten protrusions arise from the central stele; five outer traces migrate toward the sepal tissue as sepal median bundles while the other inner five represent petal-sepal marginal complex. Each complex is divided into two outer sepal marginal bundles to the adjacent sepals and one inner petal bundle (Photos 2& 3). The latter enters the petal tissue and later undergoes further ramification giving three to five bundles. Upwardly**,** four staminal traces protrude from the central stele and then enter the corolla tube as four staminal bundles (Photos 4-6), after that at the anther level each bundle bifurcates to feed the two anther lobes (Photo 11). The remaining central stele is differentiated into the following: two dorsal carpellary bundles, numerous lateral carpellary bundles, and two ventral masses (Photos 5-7). The two dorsal carpellary bundles run longitudinally along the carpel and the style then fades out beneath the stigmatic level (Photo 12). The lateral carpellary bundles undergo further branching and then fade out beneath the style level (Photo 11). The two ventral masses at the middle of the ovary are fused as a ventral cord (Photo 8) which is responsible for feeding the ovules (many ovules per locule) and fades out beneath the compitum level (Photo 10).

***Myoporum laetum* G.Forst**

Whole plant: a shrub with simple, glabrous, alternate, lanceolate, petiolate leaves. Lamina with slightly serrate margin, acute apex and symmetrical base. The flowers are arranged in a simple raceme inflorescence, pentamerous, actinomorphic with tubular corolla and four fertile stamens. Anther lobes dithecious. The fruit is a drupe with oval seeds.

Stem anatomy (Figure 7, $d_{1,2}$): stem outline is terete. The epidermis is papillose to radial shape and covered with thin cuticle and sunken, glandular trichomes. The cortex has 13- 15 rows of polyhedral parenchyma followed by an incomplete ring of sclerenchyma (extra-xylary fibers). The vascular system is in the form of continuous cylinder. Vessels are barrel-shaped and diffuse porous. Rays are uniseriate fascicular and interfascicular. Pith wide of pitted thin-walled polyhedral parenchyma. Crystals are found as druses in the cortex and pith. The schizolysigenous duct is recorded in the cortex and pith.

Lamina anatomy (Figure 7, d_3): the epidermal cells in the midrib are radially arranged while those in the wings are tangentially elongated; both are covered with thin cuticles. Trichomes are sunken, glandular. Mesophyll is dorsiventral of three rows of discontinuous elongated palisade cells adaxially extend to the midrib followed by six rows of spongy cells abaxially. The Midrib region outline is concave adaxially and convex abaxially and occupied by angular collenchyma beneath the ad- and abaxial epidermis and polyhedral parenchyma. The vascular supply

of midvein is represented by a crescent-shaped central vascular bundle supported by sclerenchyma fibers abaxially and numerous small lateral vascular bundles distributed throughout the wing tissue. Druses of calcium oxalate crystals are recorded. Schizolysigenous ducts are present in the wing.

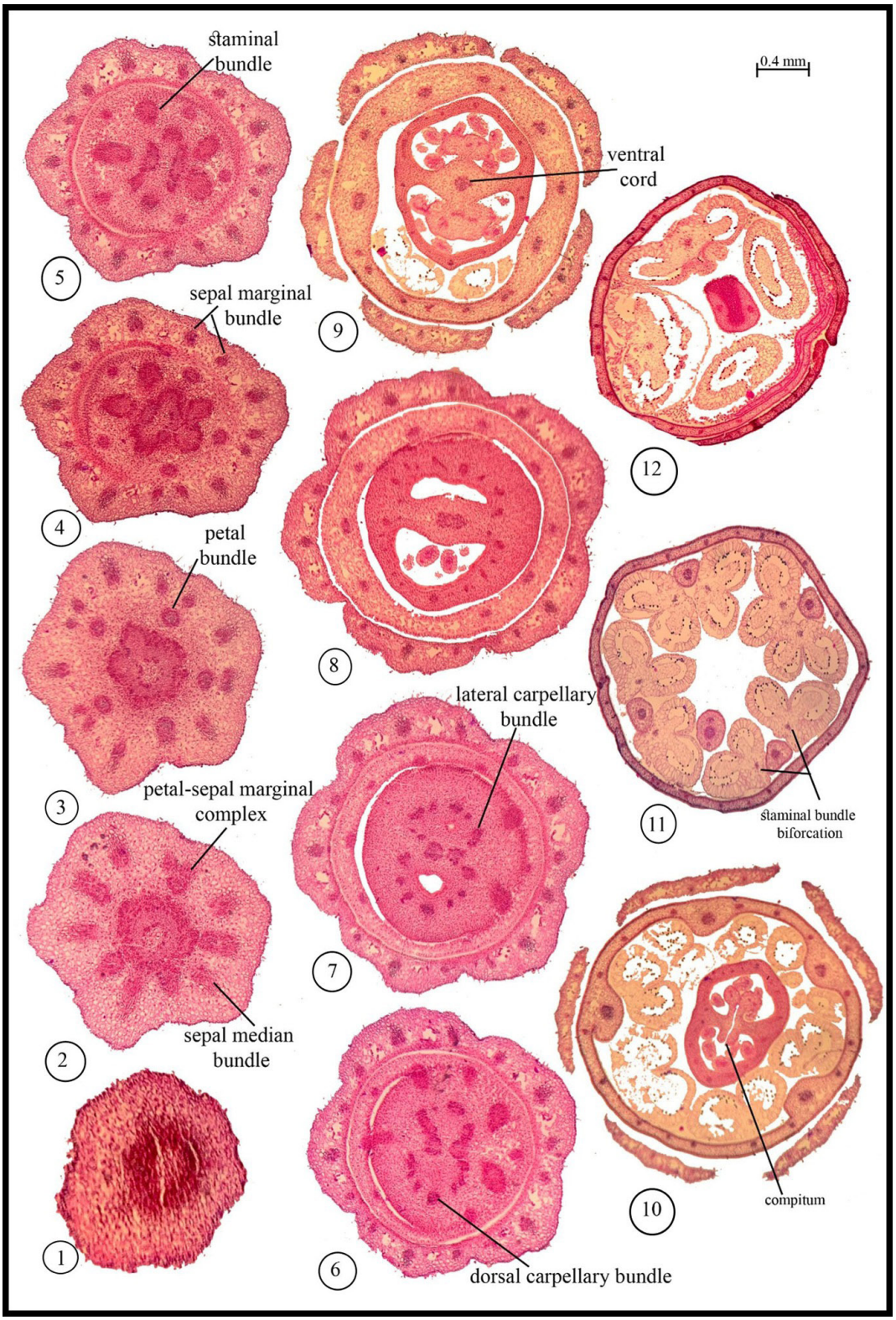

Figure 3 (Photos 1-12). Serial cross sections of a mature flower bud of *Leucophyllum frutescens* from pedicel upwards

Flower anatomy (Figure 4): the pedicel vasculature is a continuous siphonostelic structure (Photo 1). At a slightly higher level five protrusions emerge from the central stele representing sepal median bundles which cut, migrate then enter the sepal tissue as one bundle throughout (Photos 2& 3). At the same level, another five traces arise from the central stele, then divided into two, enter the sepal tissue as sepal marginal bundles to the adjacent sepals. At a mildly elevated level five traces cut, migrate then enter the corolla tube tissue as petal bundles then undergo further ramification (Photos 3-5). Upwardly**,** four staminal traces protrude from the central stele and then enter the corolla tube as four staminal bundles (Photos 4-6), after that at the anther level each bundle bifurcates to feed the two anther lobes (Photo 12). The remaining central stele is differentiated into the following: three dorsal carpellary bundles, numerous lateral carpellary bundles, and three ventral masses (Photos 7-9). The three dorsal carpellary bundles run longitudinally along the carpel and the style then fades out beneath the stigmatic level. The lateral carpellary bundles undergo further branching then fade out beneath the style level (Photo 12). The three ventral masses (each formed from two fused bundles) remain distinct and then fused at a slightly higher level giving a single ventral cord that feeds the three ovules (one per locule) and fades out beneath the style level (Photos 10-12).

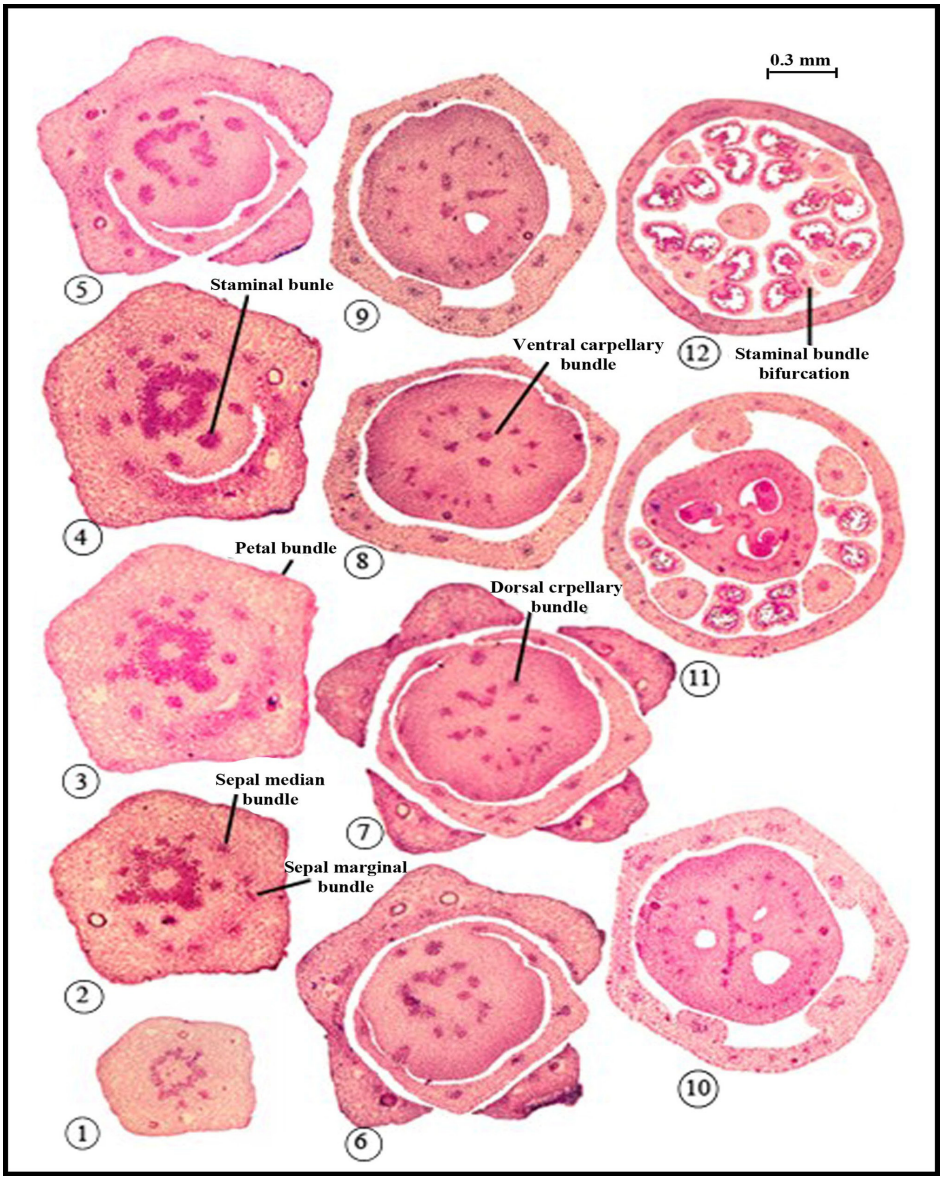

Figure 4 (Photos 1-12). Serial cross sections of a mature flower bud of *Myoporum laetum* from pedicel upwards

***Scrophularia xanthoglossa* Boiss.**

Whole plant: perennial herb, with pinnatisect, glabrous, opposite, ovate, sessile leaves. Lamina segments with serrate margin, acute apex and symmetrical base. The flowers arranged in a simple raceme inflorescence, pentamerous, zygomorphic with bi-lipped corolla tube and four fertile stamens. Anther lobes monothecious. The fruit is a capsule with oval to angular seeds.

Stem anatomy (Figure 7, $e_{1,2}$): stem outline is quadrangular. The epidermis is radial to tangential in shape and covered with thick cuticle. The cortex has lacunar collenchyma at corners followed by three to four rows of angular collenchyma and one row of polyhedral parenchyma then an incomplete ring of sclerenchyma (extra-xylary fibers). The vascular system is in the form of continuous cylinder. Vessels are rounded in shape and ring porous. Rays are uniseriate in the fascicular region while the interfascicular region occupied by fibers only. Pith wide of thin-walled polyhedral parenchyma.

Lamina anatomy (Figure 7, e_3): the epidermal cells in midrib and wings are tangentially elongated and covered with thin cuticle. Mesophyll is isolateral of six rows of continuous elongated palisade cells ad- and abaxially and two rows of spongy cells in-between with large air cavities. Midrib region outline is straight ad- and abaxially occupied by polyhedral parenchyma. Vascular supply of mid vein represented by round-shaped central vascular bundle and numerous small lateral vascular bundles distributed throughout the wing tissue.

Flower anatomy (Figure 5): the pedicel vasculature is a continuous siphonostelic structure (Photo 1). At a slightly higher level ten protrusions emerge from the central stele: five representing sepal median-staminal complexes and five petal-sepal marginal complexes (Photos 2-4). Each sepal median bundle from the former complexes cut, migrate and then enter the sepal tissue as one bundle throughout. Each sepal marginal bundle undergoes further ramification giving numerous sepal marginal bundles (Photos 3-5). At the same level**,** five petal traces (from petal-sepal marginal complexes) cut, migrate then enter the corolla tube tissue (Photos 3-9). Each petal bundle undergoes further branching giving three vascular bundles then numerous upward. After the differentiation of sepal median bundles, the base of each sepal median-staminal complex is differentiated into staminal bundles (Photos 5-9). The latter cuts, migrates then enters the corolla tube as one staminal bundle throughout. The four anterior-lateral staminal bundles enter the filaments as a single bundle throughout. The fifth posterior staminal bundle remains within the corolla tube tissue then fades out at a higher level (Photos 7-13). After the differentiation of sepal, petal, and staminal vascular supply, the remaining central stele is differentiated into the following: two dorsal carpellary bundles, numerous lateral carpellary bundles, and two distinct ventral masses (Photos 5-9). The two dorsal carpellary bundles run longitudinally along the carpel and the style then fades out beneath the stigmatic level. The lateral carpellary bundles undergo further branching, giving numerous small lateral bundles, then fade out beneath the style level (Photo 12). The ventral bundles (two fused at each side) remain distinct throughout, then fade out beneath the compitum level (Photos 8-10). The ovule number is numerous. A very thin non-vascularized parenchymatous nectariferous disc was recorded (Photos 9& 10).

***Verbuscum sinuatum* L.**

Whole plant: perennial herb, with lobed, tomentose, alternate, oblanceolate, sessile leaves. Lamina lobes with entire margin, obtuse apex and the symmetrical base. The flowers arranged in a simple raceme inflorescence, pentamerous, zygomorphic with tubular corolla and five fertile stamens. Anther lobes dithecious. The fruit is a capsule with oval to angular seeds.

Stem anatomy (Figure 7, $f_{1,2}$): stem outline is terete. The epidermis is radial to tangential in shape and covered with thick cuticle and e-glandular branched stellate multicellular trichomes. The cortex has two to three rows of chlorenchyma followed by two to four rows of angular collenchyma then one to two rows of polyhedral parenchyma and an incomplete ring of sclerenchyma (extra-xylary fibers). The idioblasts were recorded in cortex. The vascular system is in the form of continuous cylinder. Vessels are round-shaped and ring porous. Rays are uniseriate in the fascicular and interfascicular region. Pith wide of thin-walled polyhedral parenchyma.

Lamina anatomy (Figure 7, f_3): the epidermal cells in midrib are radially arranged while those in wings are tangentially elongated; both are covered with thin cuticle. Trichomes are e-glandular multicellular stellate. Mesophyll isolateral of six rows of discontinuous elongated palisade cells ad- and abaxially, extended to midrib and two rows

of spongy cells in-between with no intercellular spaces. Midrib region outline straight adaxially and convex abaxially, occupied by angular collenchyma beneath ad- and abaxial epidermis and polyhedral parenchyma. Vascular supply of mid vein represented by crescent-shape central vascular bundle supported by sclerenchyma fibers abaxially and numerous small lateral vascular bundles distributed throughout the wing tissue.

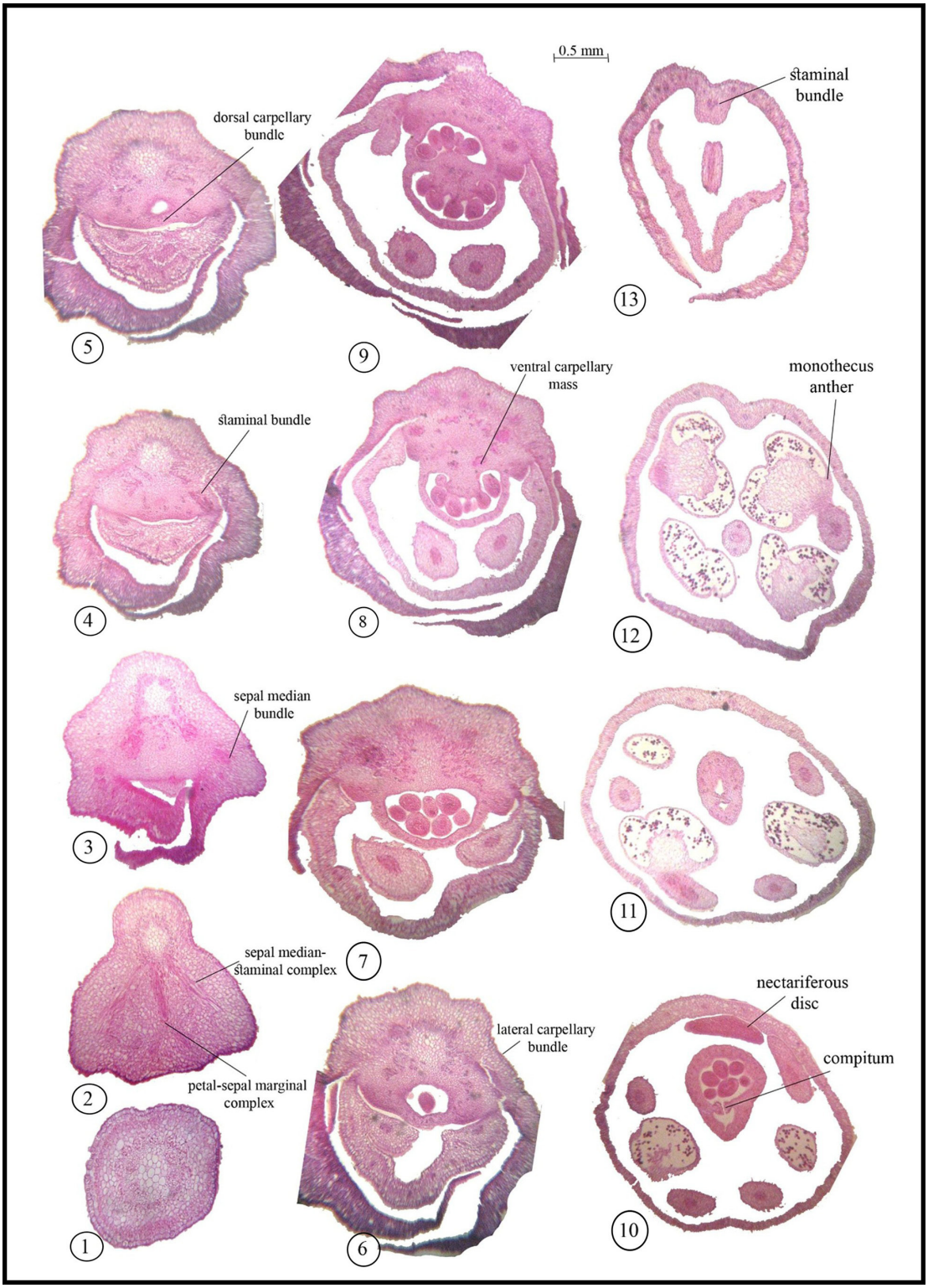

Figure 5 (Photos 1-13). Serial cross sections of a mature flower bud of *Scrophularia xanthoglossa* from pedicel upwards

Flower anatomy (Figure 6): the pedicel vasculature is a continuous siphonostelic structure (Photo 1). At a slightly higher level**,** ten protrusions; five representing sepal traces alternate with five petal-sepal marginal complexes beginning to emerge from the central stele (Photos 2-7). The formers differentiated into one large sepal median and two small sepal marginal bundles. Each of the petal-sepal marginal complex is differentiated into an outer numerous sepal marginal bundles and an inner petal vascular bundle. Each sepal is received finally one median and numerous lateral bundles. The base of each complex which represents the petal trace cuts, migrates then enters the corolla tube as a single unit (Photos 3-6). Through the corolla tube, each petal vascular bundle undergoes further branching giving three bundles of equal size then become numerous (Photos 6-10). After the departure of the petal vascular supply, five staminal traces are differentiated from the central stele (Photos 4-7). Each staminal trace cuts, migrates, and enters the corolla tube to the filaments as one bundle then bifurcates at the anther level (Photo 10). At the same level of the staminal trace differentiation, the remaining central stele is differentiated into two dorsal and several lateral carpellary bundles in addition to two distinct ventral carpellary masses (Photos 5& 6). The two distinct ventral carpellary masses fused at a slightly higher level giving a single ventral cord (Photo 7). The ventral cord feeds the numerous ovules and fades out beneath the compitum level (Photo 9). The dorsal carpellary bundles run through the stylar tissue then fade out beneath the stigmatic level. The lateral carpellary bundles fade out beneath the style level. A very thin non-vascularized parenchymatous nectariferous disc was recorded (Photos 7& 8).

Data analysis

The macro- and micromorphological characters were summarized, coded as multistate characters, and used for data analysis as shown in Table 2.

DISCUSSION

Macro- and micromorphological characters

this work aimed to assess the taxonomic relationship between Myoporaceae and Scrophulariaceae using macromorphological characters combined with micromorphological characters of stem, lamina, and flower of six studied species. The results strengthen the taxonomic importance of morphological and anatomical characteristics (such as habit, corolla shape, fruit type, number of ovules, secretory systems, mesophyll type, spongy layer, and the vasculature pattern of the flower).

As summarized in Table 2, macromorphological analysis showed variation in habit among the studied species as; shrub habit in *Bontia daphnoides* and *Myoporum laetum* while subshrub in *Eremophila purpurascens* and *Leucophyllum frutescens* whereas perennial herb in *Scrophularia xanthoglossa* and *Verbascum sinuatum*. The flower actinomorphic in *M. laetum* and zygomorphic in the other five species. Also, the corolla is tubular in *M. laetum* and *V. sinuatum* while bi-lipped in the remaining four species. The evolutionary move is from radial to bilateral symmetry, and the zygomorphic corolla is considered an adaptive mechanism for entomophily as discussed by Delevoryos (1962). The results recorded two types of fruit; drupe in *B. daphnoides*, *E. purpurascens* and *M. laetum* while capsule in *L. frutescens, S. xanthoglossa* and *V. sinuatum.*

The stem anatomical characters showed a clear distinctions, particularly in the type of epidermal cells and cuticle; the epidermis is radial to tangential with thick cuticle in *S. xanthoglossa* and *V. sinuatum* while papillose to radial with thin cuticle in the remaining species. The results recorded the total lack of trichomes in *S. xanthoglossa*, with their presence in form of e-glandular in *V. sinuatum*. Additionally, trichome types were observed as glandular in *B. daphnoides* and both glandular and e-glandular types in the remaining species. The occurrence of pitted parenchyma cells distinguished *E. purpurascens* and *M. laetum* from the other species. The secretory system recorded as; schizolysigenous duct that characterized *B. daphnoides* and *M. laetum,* schizogenous duct which distinguished *E. purpurascens,* moreover the idioblasts have been detected only in *L. frutescens* and *V. sinuatum,* the presence of idioblasts was previously mentioned by Lersten & Curtis (2001). The ring porous xylem vessels differentiated *S. xanthoglossa* and *V. sinuatum* from the other species. The presence of calcium oxalate crystals (druses) differentiated *B. daphnoides* and *M. laetum* from the remaining studied species.

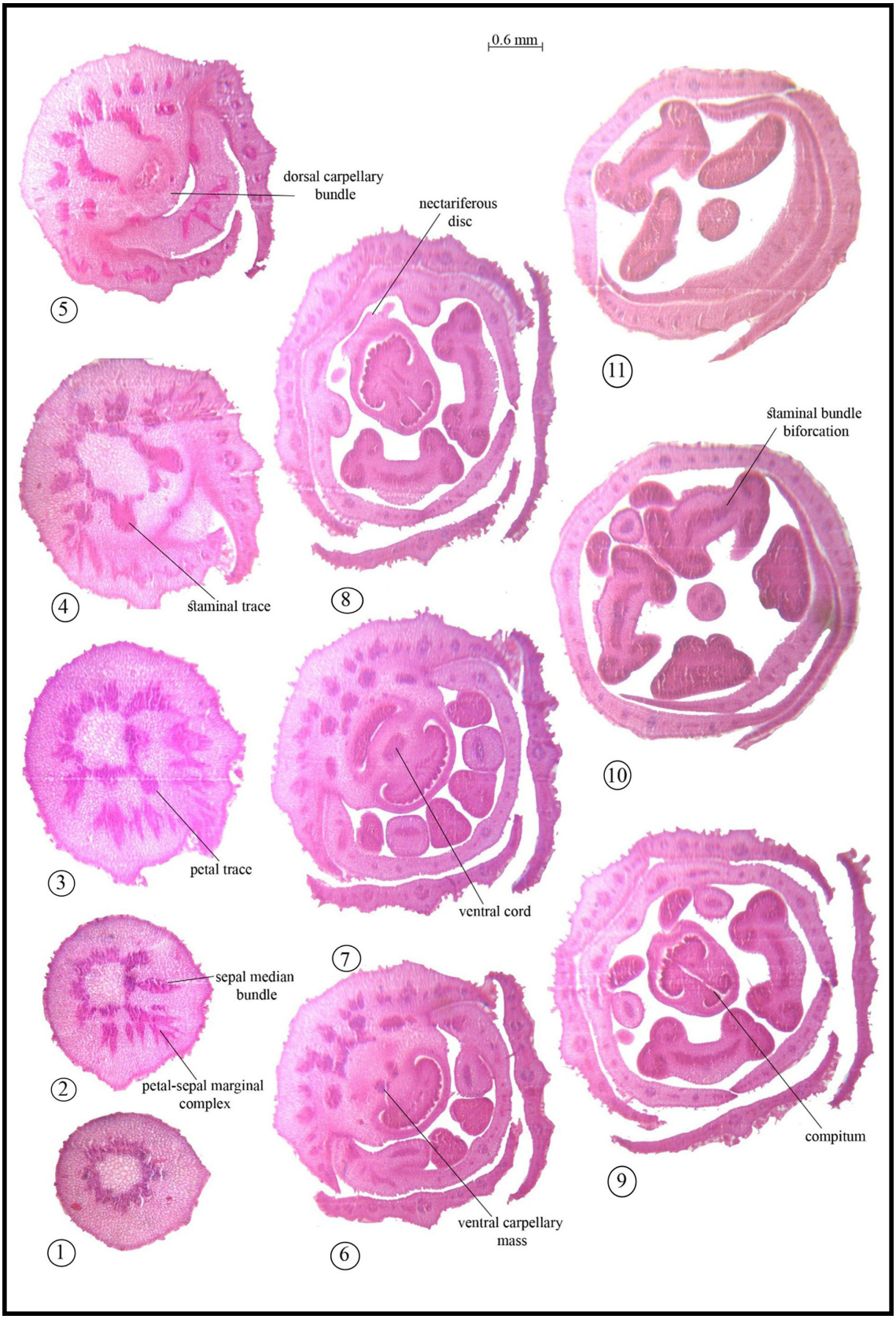

Figure 6 (Photos 1-11). Serial cross sections of a mature flower bud of *Verbuscum sinuatum* from pedicel upwards

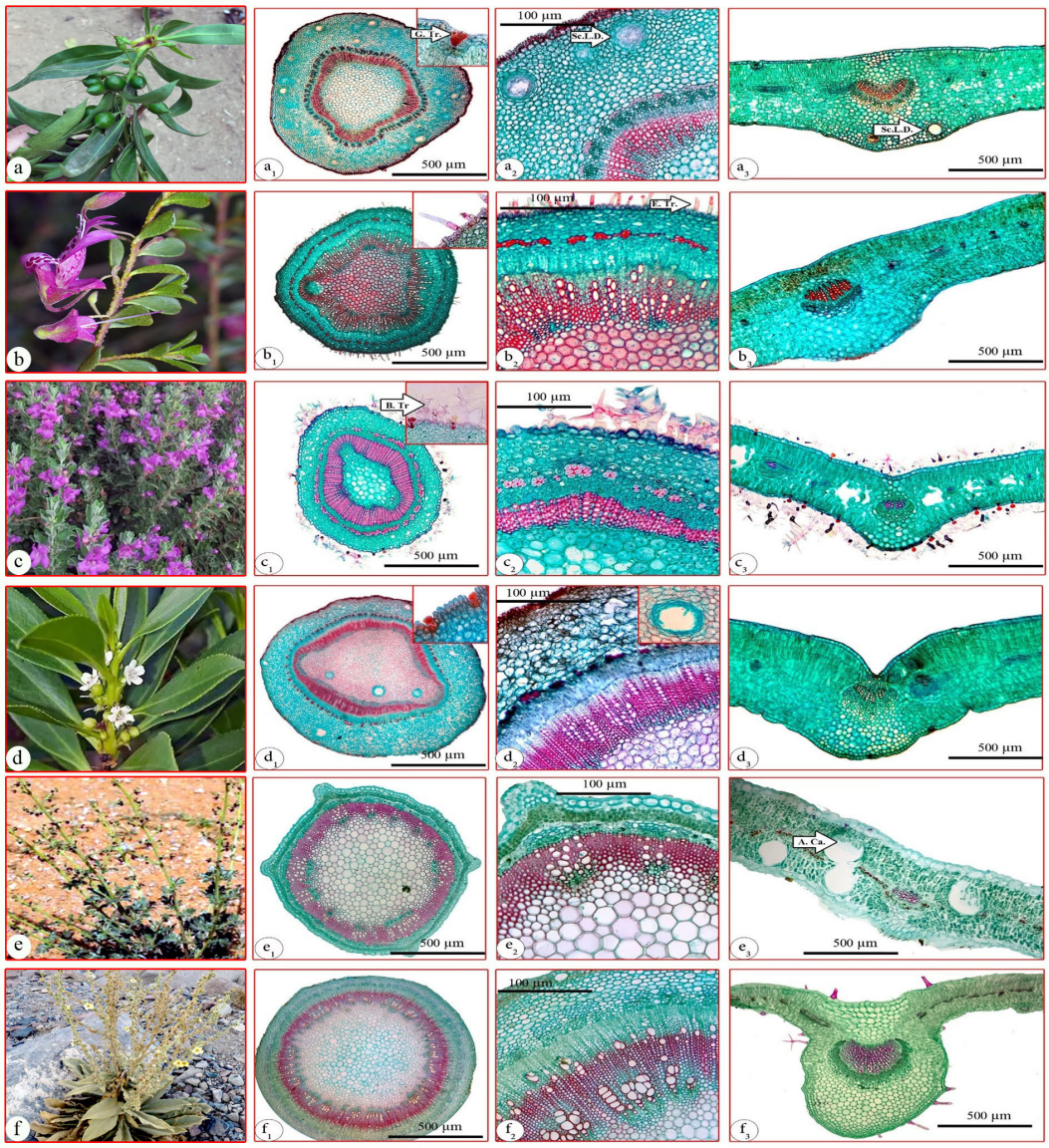

Figure 7. Micro-photographs show different growth aspects of the stem and lamina of the studied species. (a): *Bontia daphnoides*, (b): *Eremophila purpurascens*, (c): *Leucophyllum frutescens*, (d): *Myoporum laetum*, (e): *Scrophularia xanthoglossa*, (f): *Verbascum sinuatum* [A.Ca. Air cavity, B.Tr. Branched trichomes, E.Tr. E-glandular trichomes, G.Tr. Glandular trichomes, SC.L.D. Schizolysigenous duct]

On the other hand, leaf anatomical characters demonstrated distinct differences, as the mesophyll is dorsiventral in *B. daphnoides*, *E. purpurascens* and *M. laetum* while isolateral in *L. frutescens, S. xanthoglossa* and *V. sinuatum.* The palisade tissue is extended from the wing to the midrib in all the studied species but exhibit interconnection only in *E. purpurascens* and *S. xanthoglossa.* The spongy tissue recorded as two rows in *L. frutescens, S. xanthoglossa* and *V. sinuatum* while six rows in *B. daphnoides*, *E. purpurascens* and *M. laetum.* The study recorded the presence of large intercellular spaces in *L. frutescens* and *S. xanthoglossa* while small in *B. daphnoides* and completely absent in the rest of the species. The intercellular spaces were formerly declared by Lersten & Beaman (1998). The results noted sclerenchyma cells support the midvein in all the species under study except in *L. frutescens* and *S. xanthoglossa.* The presence of schizolysigenous duct and druses distinguish *B. daphnoides* and *M. laetum* from the remaining species. In some cases, these secretory structures go through developmental stages characteristics of both schizogenous and lysigenous patterns. For this reason, they are referred to as schizolysigenous ducts (Turner et al., 1998; Prado & Demarco, 2018).

Table 2. Macro- and micromorphological characters and the data matrix of studied species [The UPGMA (Un-weighted Pair Group Method with Arithmetic mean) hierarchical clustering and heat map based on the macro- and micromorphological traits are displayed in Figure 8; on the X-axis; each column represents a trait while on the Y-axis; each row represents one taxon and is hierarchically clustered based on all traits (using UPGMA clustering). The color from white to red, increased color intensity relates to more divergence in the trait]

Taxa / Characters and character states with their codes	*Bontia daphnoides*	*Eremophila purpurascens*	*Leucophyllum frutescens*	*Myoporum laetum*	*Scrophularia xanthoglossa*	*Verbascum sinuatum*
Habit: Shrub (1), Sub-Shrub (2), Perennial herb (3)	1	2	2	1	3	3
Leaf Insertion: Petiolate (1), Sessile (2)	1	2	1	1	2	2
Leaf composition: Simple (1), Pinnatifid (2), Pinnatisect (3)	1	1	1	1	3	2
Leaf Arrangement: Alternate (1), Opposite (2)	1	1	1	1	2	1
Lamina Margin: Entire (1), Serrate (2)	1	1	1	2	2	1
Lamina Apex: Acute (1), Acuminate (2), Obtuse (3)	2	1	1	1	1	3
Lamina Texture: Glabrous (1), Hairy (2), Tomentose (3)	1	1	2	1	1	3
Flower Symmetry: Zygomorphic (1), Actinomorphic (2)	1	1	1	2	1	1
Corolla shape: Bi-lipped corolla (1), Tubular (2)	1	1	1	2	1	2
Stamen number: four (1), Five (2)	1	1	1	1	1	2
Anther lobes: Dithecous (1), Monothecous (2)	1	1	1	1	2	1
Fruit Type: Drupe (1), Capsule (2)	1	1	2	1	2	2
Seed Shape: Oval (1), Oval to angular (2)	1	1	1	1	2	2
Stem anatomical characters						
Outline: Terete (1), Quadrangular (2)	1	1	1	1	2	1
Epidermis: Papillose to radial (1), Radial to tangential (2)	1	1	1	1	2	2
Cuticle: Thin (1), thick (2)	1	1	1	1	2	2
Trichomes: Glandular & e-glandular (1), Glandular (2), E-glandular (3), Absent (4)	2	1	1	2	4	3
Cortex: Four types of cells (1), Two types of cells (2), Three types of cells (3)	3	3	2	2	3	1
Pith size: Wide (1), Narrow (2)	1	1	2	1	1	1
Pitted parenchyma in Pith: Present (1), Absent (2)	2	1	2	1	2	2
Secretory system: Schizolysogenous (1), Schizogenous (2), Idioblast (3), Absent (4)	1	2	3	1	4	3
Xylem vessels distribution: Ring porous (1), Diffuse porous (2)	2	2	2	2	1	1

Table 2. Cont.

Taxa / Characters and character states with their codes	*Bontia daphnoides*	*Eremophila purpurascens*	*Leucophyllum frutescens*	*Myoporum laetum*	*Scrophularia xanthoglossa*	*Verbascum sinuatum*
Horizontal system: Uniseriate fascicular and interfascicular (1), Uniseriate fascicular only (2)	1	1	1	1	2	1
Crystals: Druses (1), Absent (2)	1	2	2	1	2	2
Lamina anatomical characters						
Trichomes: Glandular & E-glandular (1), Glandular (2), E-glandular (3), Absent (4)	2	3	1	2	4	3
Epidermis in midrib: Radial (1), Tangential (2)	1	1	1	1	2	1
Mesophyll Type: Isolateral (1), Dorsiventral (2)	2	2	1	2	1	1
Extended palisade in midrib continuity: Yes (1), No (2)	2	1	2	2	1	2
Spongy tissue rows: Two rows (1), Six rows (2),	2	2	1	2	1	1
Intercellular spaces in Spongy tissue: Small (1), Large (2), Absent (3)	1	3	2	3	2	3
Outline adaxial: Straight (1), Concave (2)	1	1	2	2	1	1
Outline abaxial: Straight (1), Convex (2)	2	2	2	2	1	2
Sclerenchyma cells: Present (1), Absent (2)	1	1	2	1	2	1
Collenchyma: Present (1), Absent (2)	1	2	1	1	2	1
Secretory system: Schizolysogenous (1), Absent (2)	1	2	2	1	2	2
Mid vein vascular bundle: Cresent shape (1), Rounded (2)	1	1	2	1	2	1
Crystals: Druses (1), Absent (2)	1	2	2	1	2	2
Flower anatomical characters						
Pedicle vasculature: Continuous (1), Dissected (2),	2	1	1	1	1	1
Sepal median vasculature: From stele (1), From complex (2)	1	1	1	1	2	1
Sepal marginal vasculature: From stele (1), From complex (2)	1	2	2	1	2	2
Petal vasculature: From stele (1), From complex (2)	1	2	2	1	2	2
Staminal vasculature: Four bundles (1), Four bundles and one vascular supply (2), Five bundles (3)	1	1	1	1	2	3
Bifurcation of staminal bundle: Present (1), Absent (2)	1	1	1	1	2	1
Ventral carpellary bundle: Ventral cord (1), Two masses (2), Four bundles (3)	3	2	1	1	2	1
Ovules number per locule: One (1), Two (2), Numerous (3)	2	2	3	1	3	3
Compitum: Present (1), Absent (2)	1	1	1	2	1	1
Nectariferous rim: Present (1), Absent (2)	2	**2**	2	2	1	1

Another aspect to be considered is the flower anatomical features; all the studied species display a largely similar floral vascular pattern, with only minor not vital variations detected among them. The receptacle in all studied species is continuous siphonostele but dissected only in *B. daphnoides*. Regarding to the sepals, the sepal median bundle departed from complex (sepal median-staminal complex) only in *S. xanthoglossa* or from the central stele in the remaining studied species. The sepal marginal bundles derived directly from the stele in *B. daphnoides* and *M. laetum*, while they come from petal-sepal marginal complex in the remaining species. The vasculature of the sepals may be derived from the same source which is stele and, in this case, considered as the primitive state as mentioned by Lindsey (1938) and Rao (1949), or considered advanced state when the vasculature comes from different sources such as complex, in other words, from more than one organ (Joshi, 1942). Each stamen received one vascular bundle, that is the dominant state in angiosperm (Esau, 1965), the present study recorded three different patterns in the androecium; five traces split directly from the central stele in *V. sinuatum* then enter the five fertile stamens, five traces diverged from sepal median staminal complexes then the posterior one remains as a supply in the corolla tube while the other four entered the four fertile stamens as in *S. xanthoglossa* and the last pattern, four traces splited directly from the central stele and entered the four fertile stamens as in the remaining species. In all the studied species the staminal bundle extended into the connective tissue between the two anther lobes except in *S. xanthoglossa* because the anther is monothecus, that agrees with Wilson (1942). The typical carpel vasculature in angiosperm is a three-traced organ; one dorsal and two ventral traces (Eames, 1929; Fraser, 1937). In the ovary, each carpel receives a single dorsal carpellary bundle and numerous lateral carpellary bundles, which are derived from the central stele, both run through the tissue of the style then fade out beneath the stigmatic level. In *B. daphnoides*, each carpel is supplied by two ventral carpellary bundles that feed the ovules, where as in *E. purpurascens* and *S. xanthoglossa*, a single fused vascular mass supplies each carpel, meanwhile in *L. frutescens , M. laetum* and *V. sinuatum* one ventral cord supply the entire ovary (even if it initially forms as two masses, it ultimately merges into a single ventral cord). The fusion of carpellary ventral bundles into a ventral cord represents an advanced evolutionary trait, derived from ancestral conditions with numerous separate bundles and this is accepted by Bessey (1915), Takhtajan (1969), Hutchinson (1973), Lawrence (1969), Stebbins (1974). In this study the number of ovules is effectively differentiates between Myoporaceae and Scrophulariaceae, it recorded the presence of only one ovule per locule in *M. laetum,* two ovules per locule in *B. daphnoides and E. purpurascens*, while many ovules per locule in *L. frutescens, S. xanthoglossa* and *V. sinuatum.* the number of ovules assists in the taxonomic discrimination and the evolution between the species under study (Marchenko & Kuzovkina, 2023). Unlike all the species under study, *M. laetum* lacks a compitum, the compitum may consists of a canal, pore or split in the septum between carpels as defined before by Esau (1965). The study recorded the presence of nectariferous rim (with receptacular nature: when the vasculature derived either from the central stele or lacking completely) only in *S. xanthoglossa* and *V. sinuatum* and this agrees with Eames (1961); Mourad et al. (2015).

For some selected characters, the weight of their states has been determined on the basis of the evolutionary dicta attained by several taxonomists as Bessey (1915), Hutchinson, (1948) and Stebbins (1974). The evolutionary shift is from woody to herb, simple to compound, leaves in pairs (opposite) to the solitary leaves at nodes (alternate), radial to bilateral symmetry, capsule fruit to drupe, the organ receives the vascularization from the same source (stele) to from different sources (complex), polystemonous to oligostemonous, numerous to few stamens. The fusion of the carpellary ventral bundles is an advance over their distinction. The advancement is toward the absence of a nectarifirous disc. The presence of compitum is more advanced than its absence. Although the general evolutionary trend according to Bessey (1915) is from numerous to few in general, Marchenko & Kuzovkina (2023) specifically considered the presence of numerous ovules as an advanced characteristic, due to its role in ensuring survival across generations. Furthermore, the structural complexity is more advanced like the presence of compitum since it allows a pollen tube to change carpels during its growth (Tcherkez, 2004). But the absence of a nectarifirous disc aligns with the evolutionary adaptation to anemophily (Hamed & Tantawy, 1994). *S. xanthoglossa* is the most advanced species among the studied species because it shows numerous advanced characteristics

such as herbaceous habit, pinnatisect leaf, bi-lipped corolla tube, monothecous stamens, the sepal median trace, sepal marginal trace and petal supply are derived from complexes (different sources), and presence of compitum (Mourad et al., 2015). *B. daphnoides* and *M. laetum* are considered the least evolutionary advanced species among the examined species, as they retain the highest number of primitive character states. The remaining species occupy an intermediate evolutionary position, as they exhibit a mixture of plesiomorphic and apomorphic characters. Ultimately no extant organism possesses exclusively plesiomorphic or exclusively apomorphic traits; instead, each exhibits a combination of ancestral and derived characteristics that reflect its unique evolutionary history.

Integration of multivariate analyses (UPGMA clustering and heat map)

The UPGMA and heat map

Figure 8 shows that *Bontia daphnoides, Eremophila purpurascens, Myoporum laetum,* and *Leucophyllum frutescens* are clustered together due to the shared characters and similarities. The most related species are *B. daphnoides* and *M. laetum* as they are linked at a very low height in the dendrogram they shared 35 similar characters out of the total 47 under study, at a slightly higher level, *E. purpurascens* joined to them (similar in 23 out of 47 characters) that agreed with Fowler et al. (2021). Later on, *L. frutescens* merged to the cluster as a result of sharing 16 characters out of 47. On the other hand, *Scrophularia xanthoglossa* joined *Verbascum sinuatum* at a high level due to its unique traits, and together formed a cluster distant from the rest of the studied species due to sharing 22 out of 47 characters, according to Riahi & Ghahremaninejad (2019) the genus *Verbascum* is strongly supported as monophyletic in relation to *Scrophularia*. . The UPGMA dendrogram and heat map highlighted the close affinity between *B. daphnoides* and *M. laetum* and the distinction of *S. xanthoglossa* and *V. sinuatum* in a separate lineage. Furthermore, a high degree of affinity was observed between *L. frutescens* and the family Myoporaceae, which aligns with the theory of Niezgoda & Tomb (1975), Karrfalt & Tomb (1983) and Young et al. (1999), which supposed that *Leucophyllum* may belong in Myoporaceae, or considered a sister group to Myoporeae depending on anatomical and palynomorphological evidence according to Oxelman et al. (2005), Gándara & Sosa (2013), Mosyakin & Tsymbalyuk (2015).

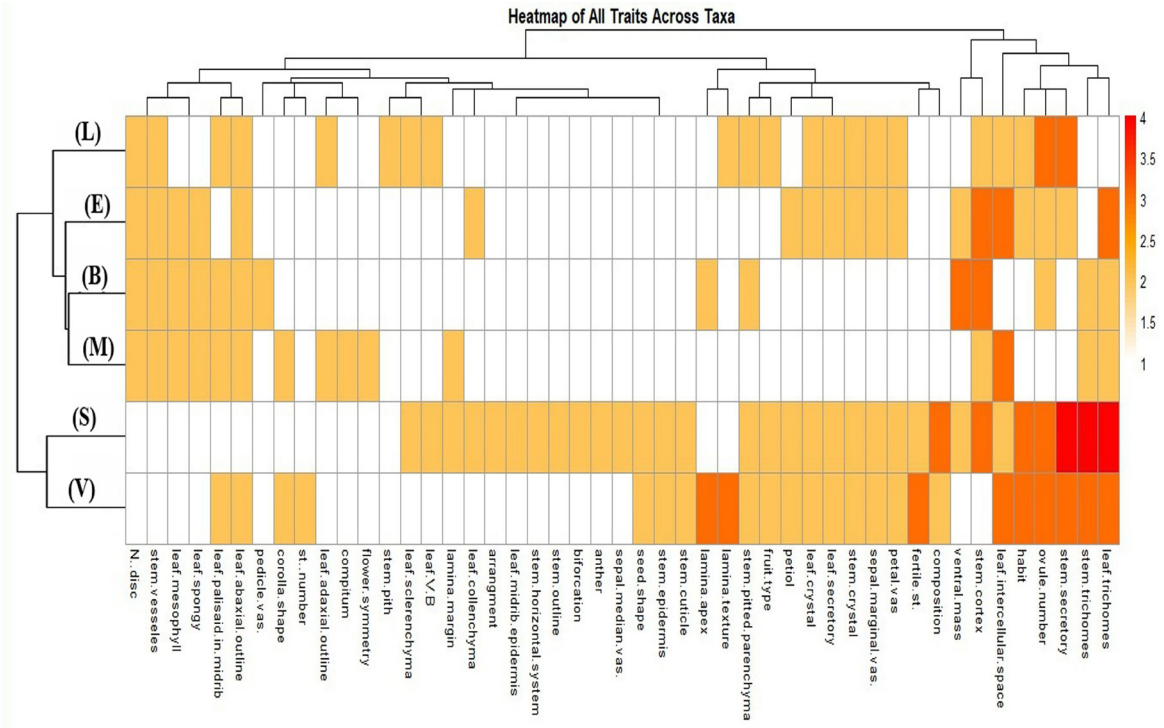

Figure 8. Dendrogram and heat map based on macro- and micromorphological characters of the studied species [(B): *Bontia daphnoides*, (E): *Eremophila purpurascens*, (L): *Leucophyllum frutescens*, (M): *Myoporum laetum*, (S): *Scrophularia xanthoglossa*, (V): *Verbascum sinuatum*]

CONCLUSION

The phylogenetic and taxonomic positions of the Myoporaceae and Scrophulariaceae are widely doubtful. This work clarifies the taxonomic relationships between Myoporaceae and Scrophulariaceae based on macro- and micromorphological characters. Fruit type, mesophyll anatomy, and the number of ovules per locule proved to be reliable diagnostic characters for distinguishing the examined species. Nevertheless, the integration of all investigated characters, particularly floral anatomical traits, does not sufficiently support the recognition of Myoporaceae as a separate family. Instead, the results favor the inclusion of the studied taxa within Scrophulariaceae, indicating closer evolutionary affinity between the two groups. Finally, Further investigations involving additional taxa and characters are recommended for achieving a more robust and comprehensive classification.

Conflicts of interests: The authors declare that there is no competing of interest.

Authors' contributions: Mohamed A. Salim: Conceptualization, Collecting plant material, Methodology, Writing original draft, Review & editing. Mariam I. Hussein: Methodology, Writing original draft, Investigation, Software, Review & editing. Nareman K. Hosney: Writing original draft, Review.

Ethical approval: Not applicable.

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