

## Morphoanatomical traits of *Solanum* L. seedlings and some taxonomic and evolutionary considerations

Caracteres morfoanatômicos de plântulas de *Solanum* L. e algumas considerações taxonômicas e evolutivas

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*Solanum* L. is the largest genus of Solanaceae and includes weedy species and plants of food interest to humans, such as tomato, peppers and potato. Structural study of seedlings is important for biology, ecology, agriculture and preservation of plant species, but has been little explored in the genus *Solanum*. In this paper, *Solanum* seedlings were morphoanatomically investigated and the characters were compared with *Capsicum annuum*, which has a phylogenetic relationship with the genus. The seedlings were grown in a greenhouse from seeds collected on vacant lots in urban areas or obtained commercially. Fragments of various parts of the seedlings were sectioned using a rotation microtome and analyzed under a light microscope. Seedlings are phanero-epigeal with foliaceous cotyledons. The primary root is diarch and the root-stem transition region begins at the root or hypocotyl and ends at the cotyledonary node. The cotyledonary node is unilacunar with a double trace. The epicotyl has a stem structure. The eophyll node is also unilacunar with 1-3 leaf traces. Cotyledons and eophylls are dorsiventral, generally with a spongy mesophyll and an adaxial layer of wide, elongated or funnel-shaped cells. Seedling analysis revealed characteristics that may be useful in distinguishing the investigated *Solanum* species, such as the shape of cotyledons and eophylls, the beginning of the root-stem transition zone, and the number of eophyll leaf traces.

Keywords: *Capsicum annuum*, root-stem transition, seedling leaves.

*Solanum* L. é o maior gênero de Solanaceae e inclui plantas daninhas e plantas de interesse alimentar para humanos, como o tomate, pimentas e batata. O estudo estrutural de plântulas é importante para a biologia, ecologia, agricultura e preservação de espécies vegetais, mas é pouco explorado no gênero *Solanum*. Nesse trabalho, plântulas de *Solanum* foram morfoanatomicamente investigadas e os caracteres foram comparados com *Capsicum annuum*, que tem relação filogenética com o gênero. As plântulas se desenvolveram em casa de vegetação, a partir de sementes coletadas em terrenos baldios de áreas urbanas ou obtidas comercialmente. Os fragmentos de várias partes das plântulas foram seccionados em micrótomo de rotação e analisados em microscópio de luz. As plântulas são faneroepígeas com cotilédones foliáceos. A raiz primária é diarca e a região de transição raiz-caule começa na raiz ou no hipocótilo e termina no nó cotiledonar. O nó cotiledonar é unilacunar com traço duplo. O epicótilo tem natureza caulinar. O nó do eófilo é também unilacunar com 1-3 traços foliares. Os cotilédones e eófilos são dorsiventrais, geralmente com mesófilo esponjoso e uma camada de células amplas, alongadas ou em forma de funil na face adaxial do mesófilo. A análise das plântulas revelou caracteres que podem ser úteis na separação das espécies investigadas de *Solanum*, como o formato dos cotilédones e eófilos, o início da região de transição raiz-caule e o número de traços foliares dos eófilos.

Palavras-chave: *Capsicum annuum*, transição raiz-caule, folhas da plântula.

### 1. INTRODUCTION

*Solanum* L. is one of the world's largest and economically most important plant genera comprising about 1500 species [1, 2]. According to Heigenhof et al. (2023) [2] cultivated *Solanum* species have served as a research model that uses morphological characters for the purpose of studying evolution, plant breeding and genetic control. In the phylogenetic analysis of *Solanum*, some characters were considered to be evolutionarily labile (for example, growth form and sympodial unit structure, glandular trichomes), and others with signs of evolutionary

lability (prickle type, trichome structure, leaf division) [2]. New taxa are constantly included in the genus *Solanum*, such as the integration of *Lycopersicon* and *Cyphomandra* through Spooner et al. (1993) [3] and Bohs (1995) [4] studies, bringing new perspectives on the phylogeny of this family and genus [5].

Invasive plants can be considered weeds when they occupy an area of human activity, causing some type of disorder [6]; they can negatively affect agricultural, forestry, ornamental and nautical activities, energy production and livestock farming [6]. On the other hand, these plants can act positively by providing structure to the soil, maintaining humidity and preventing water loss through evaporation [6]. They are pioneer plants of secondary succession, that is, they colonize places where some disturbance occurred, which eliminated the vegetation [6]. *Solanum* presents an enormous diversity of invasive species (weeds), which colonize different environments, such as agricultural areas, gardens and vacant lots [7].

Seedling structure presents a broad field of investigation that is still insufficiently explored, particularly in *Solanum*. A seedling can be considered a stage of plant development, beginning with germination and ending with the formation of the eophyll [8]. There are records of morphological studies of seedlings in *Solanum* [9], but seedling anatomy is a poorly explored subject. Structural characters of the seedling involving root, collet, hypocotyl, cotyledonary node, cotyledons, eophyll node and eophyll can be useful for characterizing *Solanum* species. At the beginning of the last century, it was demonstrated that the anatomy of the seedling, associated with the size, form, habit and general morphology of the species, can have significant taxonomic potential and can be of value in the phylogenetic study of angiosperms [10].

When analyzing *Solanum* seedlings, we found it interesting to compare them with *Capsicum annuum* L. seedling, a Solanaceae belonging to the Capsiceae clade. Both *Solanum* and Capsiceae clades are closely phylogenetically related [11]. *Capsicum annuum* is a domesticated species, and it is represented by peppers, sweet peppers (green pepper or American pepper) that present the greatest variability in color, size and shape of the fruits, being the most studied and used in programs genetic improvement [12].

In an attempt to search for morphoanatomical traits of seedlings that may be taxonomically and evolutionarily relevant in *Solanum*, five weed species were randomly selected for study. In this analysis, we included the characterization of seedlings of *Solanum lycopersicum* Lam. (tomato), which until recently belonged to the genus *Lycopersicum* Hill., and *Capsicum annuum*.

## 2. MATERIAL AND METHODS

### 2.1 Plant material

Five weed species of *Solanum* that occur in uncultivated lands and pastures in Maringá and Sarandi (municipalities located in the state of Paraná, Brazil) were selected for study. The morphoanatomical data of seedlings of weedy species were compared with seedlings of tomato and pepper plants (Table 1).

### 2.2. Obtaining seedlings

The seedlings were grown from collected seeds (weedy species) and store-bought seeds (cultivated plants). All seeds were washed in distilled water and sown in MecPlant substrate, which consists of an artificial mixture of organic matter (pine bark), a mineral component (vermiculite), and nutritional correctives and additives (limestone, single superphosphate, and NPK fertilizer). The seeds germinated and the seedlings grew in a greenhouse, with irrigation every two days. Seed germination was monitored daily and occurred at room temperature. The seedlings were kept in a greenhouse covered with 50% shade, until the complete expansion of the first eophyll.

Table 1 - *Solanum* and *Capsicum* species investigated with information on clade, plant habit, collection location and voucher (HUEM=Herbário da Universidade Estadual de Maringá).

| Species                             | <i>Solanum</i> clade* | Habit            | Plant collection location                   | Vouchers   |
|-------------------------------------|-----------------------|------------------|---------------------------------------------|------------|
| <i>Solanum americanum</i> Mill.     | Morelloid clade       | Herbaceous plant | Sarandi, Paraná, Brazil - uncultivated land | HUEM 40743 |
| <i>Solanum lycopersicum</i> Lam.    | Potato clade          | Herbaceous plant | (1)                                         | (1)        |
| <i>Solanum mauritianum</i> Scop.    | Brevantherum clade    | Arboreal plant   | Maringá, Paraná, Brazil - uncultivated land | HUEM 40742 |
| <i>Solanum sisymbriifolium</i> Lam. | Leptostemonum clade   | Herbaceous plant | Maringá, Paraná, Brazil - pasture           | HUEM 40741 |
| <i>Solanum torvum</i> Sw.           | Leptostemonum clade   | Shrub plant      | Sarandi, Paraná, Brazil - uncultivated land | HUEM 40744 |
| <i>Solanum viarum</i> Dunal         | Acanthophora clade    | Herbaceous plant | Maringá, Paraná, Brazil - uncultivated land | HUEM 40740 |
| <i>Capsicum annuum</i> L.           | -                     | Herbaceous plant | (1)                                         | (1)        |

(1) Store-bought seeds.

\*Clades *sensu* Gagnon et al. (2022) [13], Weese and Bohs (2007) [14].

### 2.3. Morphological analysis of the seedlings

The seedlings were classified and described morphologically according to the terminology adopted by different authors [8, 15-17]. The shape of the cotyledons and eophylls was based on Rizzini (1977) [18]. The seedlings were photographed with a digital camera.

### 2.4. Anatomical analysis of seedlings

Samples of the primary root, collet, hypocotyl, cotyledonary node, cotyledon, epicotyl, eophyll node and eophyll were fixed at 2.5% glutaraldehyde, 0.1 M phosphate buffer, pH 7.2 for approximately 48 hours, and preserved in 70% ethyl alcohol [19]. Then, these samples were dehydrated in ethyl alcoholic series, embedded in Leica® historesin, according to the norms specified in the product, and sectioned on a rotation microtome (10µm thick sections). The sections were subsequently stained in toluidine blue [20]. The illustrations of the anatomical sections were made with photomicrographs obtained with a digital camera attached to the Leica EZ4D microscope, whose images were processed using the Leica Application Suite Version 1.8 software.

## 3. RESULTS AND DISCUSSION

### 3.1 Seedling morphology

All seedlings of *Solanum* (Figures 1A and 2A) and *Capsicum annuum* (Figure 2B) are phanero-epigeal with foliaceous cotyledons. This type of seedling also found in other *Solanum* species [9]. The seedlings have an axial root (Figures 1A, 2A and 2B), and the collet (Figures 1A, 2A and 2B) can be identified by the difference in color and because it has a smaller diameter between the root and the hypocotyl. The hypocotyl (Figures 1A, 2A and 2B) is long in all species, green in color (pinkish-green in *Solanum lycopersicum*, Figure 2A), hairy (Figure 1D) in *Solanum* species and glabrous in *Capsicum annuum* (Figure 2B). Leaf-like cotyledons (Figures 1A, 1C-E and 2) are thin, green, and have a shape that varies from ovate to lanceolate (Table 2). The margin of the cotyledons (Figures 1 and 2) is entire (Figures 1C-E and 2) and the

cotyledonary apex is acute in most species or apiculate in *Solanum sisymbriifolium* and *Solanum torvum* (Table 2).

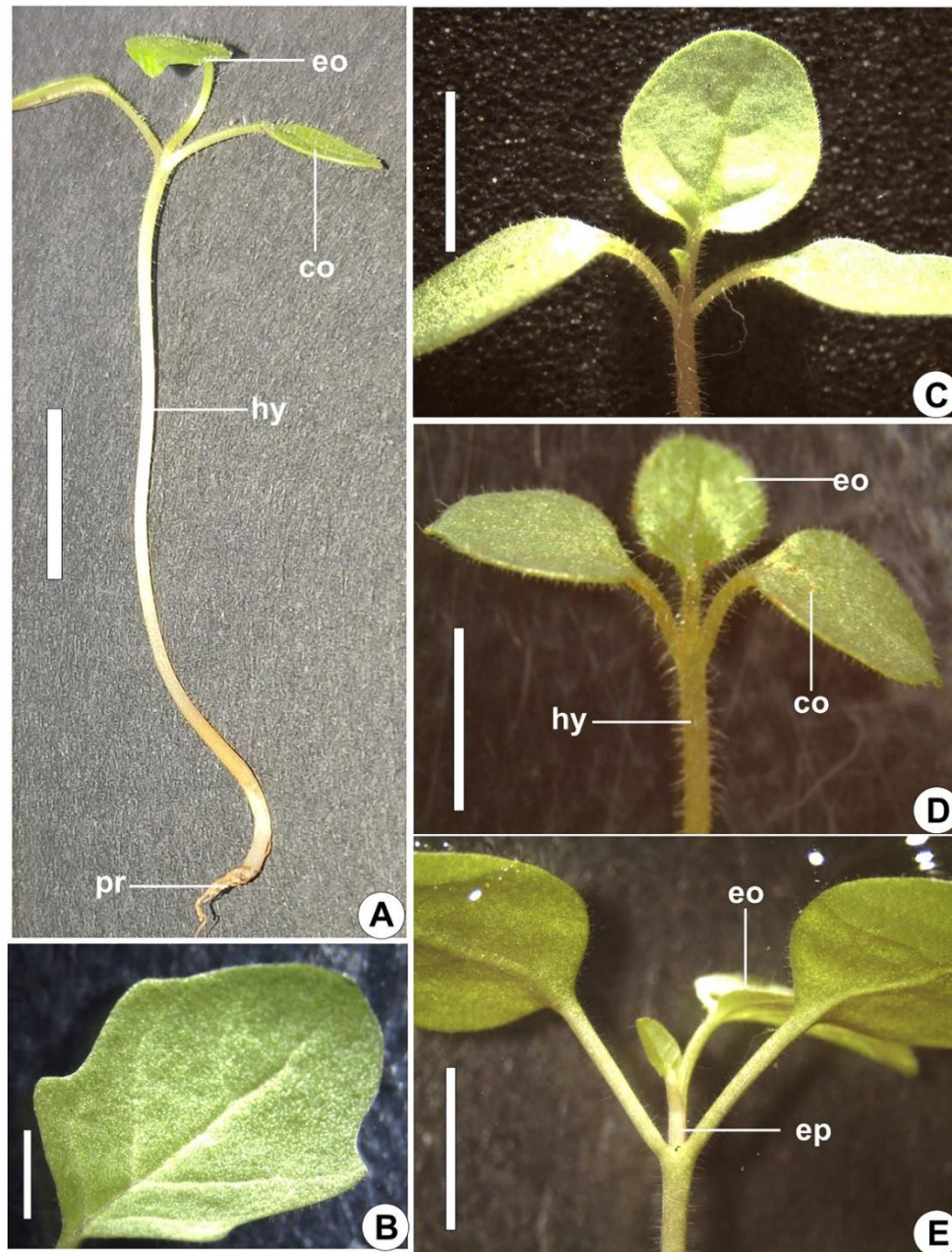


Figure 1 - Seedling morphology of *Solanum sisymbriifolium* (A,B), *Solanum americanum* (C), *Solanum torvum* (D) and *Solanum viarum* (E). A - Whole seedling. B - Eophyll. C,D,E - Seedling apices showing the upper part of the hypocotyl, cotyledons, eophyll and apical bud. (co=cotyledons; eo=eophyll; ep=epicotyl; hy=hypocotyl; pr=primary root). Scale bars: 1cm (A), 2mm (B), 4mm (C-E).

There is a single eophyll (Figures 1C-E and 2A) in seedlings (two in *Solanum lycopersicum*, Figures 2A and 2C), and it has a variable shape. The ovate shape of the eophyll is more common among species, and orbicular eophyll was registered in three *Solanum* species (Table 2). The eophyll margin is commonly entire (Figures 1C-E and 2B), but the eophylls of *Solanum lycopersicum* (Figures 2A and 2C) and *Solanum sisymbriifolium* (Figure 1B) have indentations on the leaf margin (Table 2). The eophyll apex is acute or obtuse, only *Solanum mauritianum* exhibits an indentation at the leaf apex (Table 2).

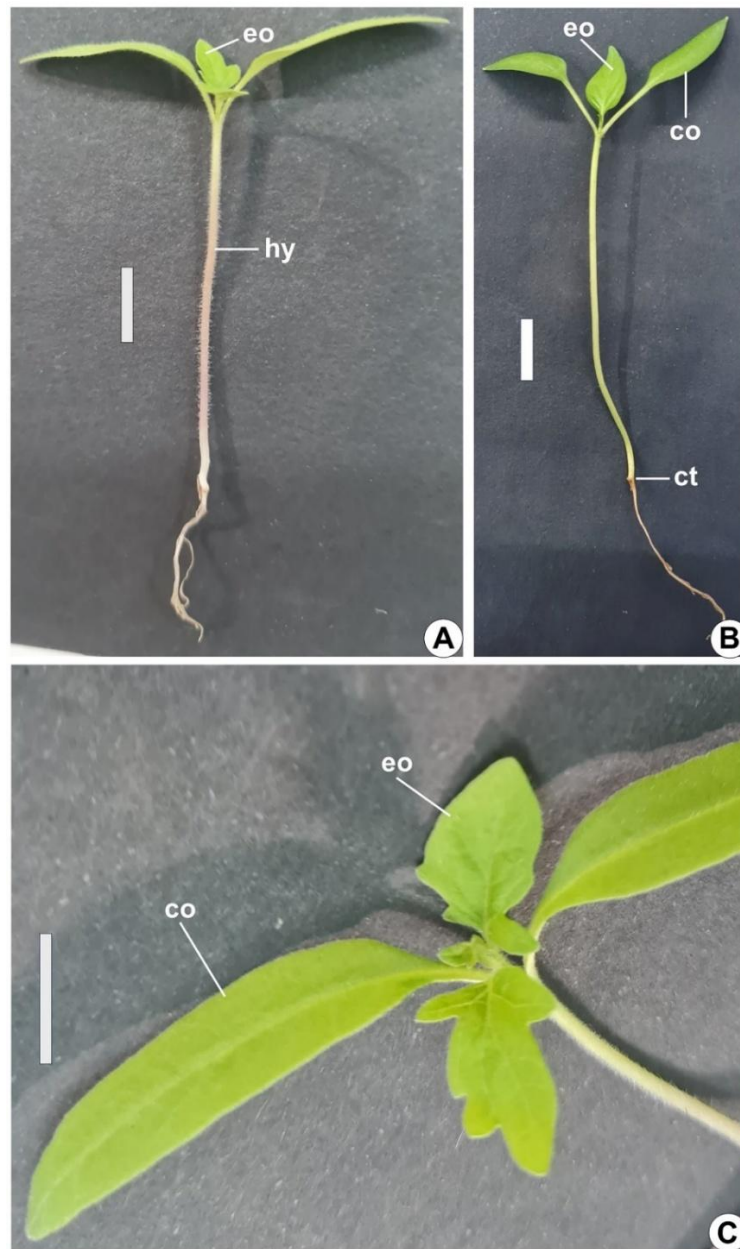


Figure 2 - Seedling morphology of *Solanum lycopersicum* (A,C) and *Capsicum annuum* (B). A,B - Seedlings. C - Detail of cotyledons and eophyll. (co=cotyledon; ct=collet; eo=eophyll; hy=hypocotyl). Scale bars: 1cm.

The seedlings of the six *Solanum* species and the *Capsicum annuum* seedling have a lot of morphological similarity, presenting some variations in the shape of the cotyledons and eophylls (Figures 1 and 2). All seedlings can be considered as belonging to the Macaranga type [15]. This type of seedling is characterized by being phanero-epigeal, and exhibiting leaf-like cotyledons and alternate eophylls (exceptionally two opposite eophylls [15], as in *Solanum lycopersicum*). The Macaranga is the most common seedling type, and in herbaceous eudicots only very few seedlings are not of the Macaranga type [15]. In Garwood's (1996) [16] seedling classification, all investigated species have PEF type seedlings (Phanerotylar, Epigeal, Foliaceous). PEF seedlings typically occur among pioneer species [16], where weedy *Solanum* species may be included.

Table 2 - Morphology of cotyledons and eophylls, and seedling structure (primary root, hypocotyl, leaf nodes, cotyledon and eophyll) of *Solanum* species and *Capsicum annuum*.

| Species                        | Cotyledon<br>(shape, margin, apex)         | Eophyll<br>(shape, margin, apex)                        | Primary root | Cotyledon (node, structure)                                                           | Eophyll (node, structure)                                                            |
|--------------------------------|--------------------------------------------|---------------------------------------------------------|--------------|---------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|
| <i>Solanum americanum</i>      | Ovate to lanceolate<br>Entire<br>Acute     | Orbicular<br>Entire<br>Obtuse                           | Diarch       | Unilacunar, double trace<br>Dorsiventral,<br>margin/rounded cells                     | Unilacunar, 1-traced<br>Dorsiventral,<br>margin/rounded cells                        |
| <i>Solanum lycopersicum</i>    | Lanceolate<br>Entire<br>Acute              | Ovate<br>Lobed<br>Acute                                 | Diarch       | Unilacunar, double trace<br>Dorsiventral,<br>margin/palisade and spongy<br>parenchyma | Unilacunar, 3-traced<br>Dorsiventral,<br>margin/rounded cells                        |
| <i>Solanum mauritianum</i>     | Ovate<br>Entire<br>Acute                   | Orbicular<br>Entire<br>Retuse (obtuse with indentation) | Diarch       | Unilacunar, double trace<br>Dorsiventral                                              | Unilacunar, 1-traced<br>Dorsiventral                                                 |
| <i>Solanum sisymbriifolium</i> | Lanceolate<br>Entire<br>Apiculate          | Oblong to ovate<br>Dentate<br>Obtuse to acute           | Diarch       | Unilacunar, double trace<br>Dorsiventral,<br>margin/palisade and spongy<br>parenchyma | Unilacunar, 1-traced<br>Dorsiventral,<br>margin/rounded cells                        |
| <i>Solanum torvum</i>          | Ovate to lanceolate<br>Entire<br>Apiculate | Orbicular<br>Entire<br>Obtuse                           | Diarch       | Unilacunar, double trace<br>Dorsiventral,<br>margin/rounded cells                     | Unilacunar, 1-traced<br>Dorsiventral,<br>margin/palisade and spongy<br>parenchyma    |
| <i>Solanum viarum</i>          | Ovate<br>Entire<br>Acute                   | Ovate<br>Entire<br>Obtuse                               | Diarch       | Unilacunar, double trace<br>Dorsiventral,<br>margin/rounded cells                     | Unilacunar, 1-traced<br>Dorsiventral,<br>margin with hydathode                       |
| <i>Capsicum annuum</i>         | Lanceolate<br>Entire<br>Acute              | Ovate<br>Entire<br>Acute                                | Diarch       | Unilacunar, double trace<br>Dorsiventral,<br>margin/rounded cells                     | Unilacunar,<br>2-traced<br>Dorsiventral,<br>margin/palisade and spongy<br>parenchyma |

### 3.2. Seedling anatomy

In four *Solanum* species (Table 2), the root-stem transition region (Figure 3) begins just below the collet, still at the root, in which a pith begins to appear. In the collet and base of the hypocotyl the xylem (metaxylem) is spread into two groups surrounding the pith, with two projecting protoxylems; in this region, each phloem strand subdivides into two strands, and the intraxylary phloem begins to appear (Figures 3B and 3C). This root-stem transition structure persists throughout the hypocotyl. The hypocotyledonary epidermis (Figure 3C) is uniseriate, regular, and has an evident cuticle. The hypocotyl cortex (Figure 3C) is made up of subepidermical collenchyma, parenchyma and endodermis with Caspary striae.

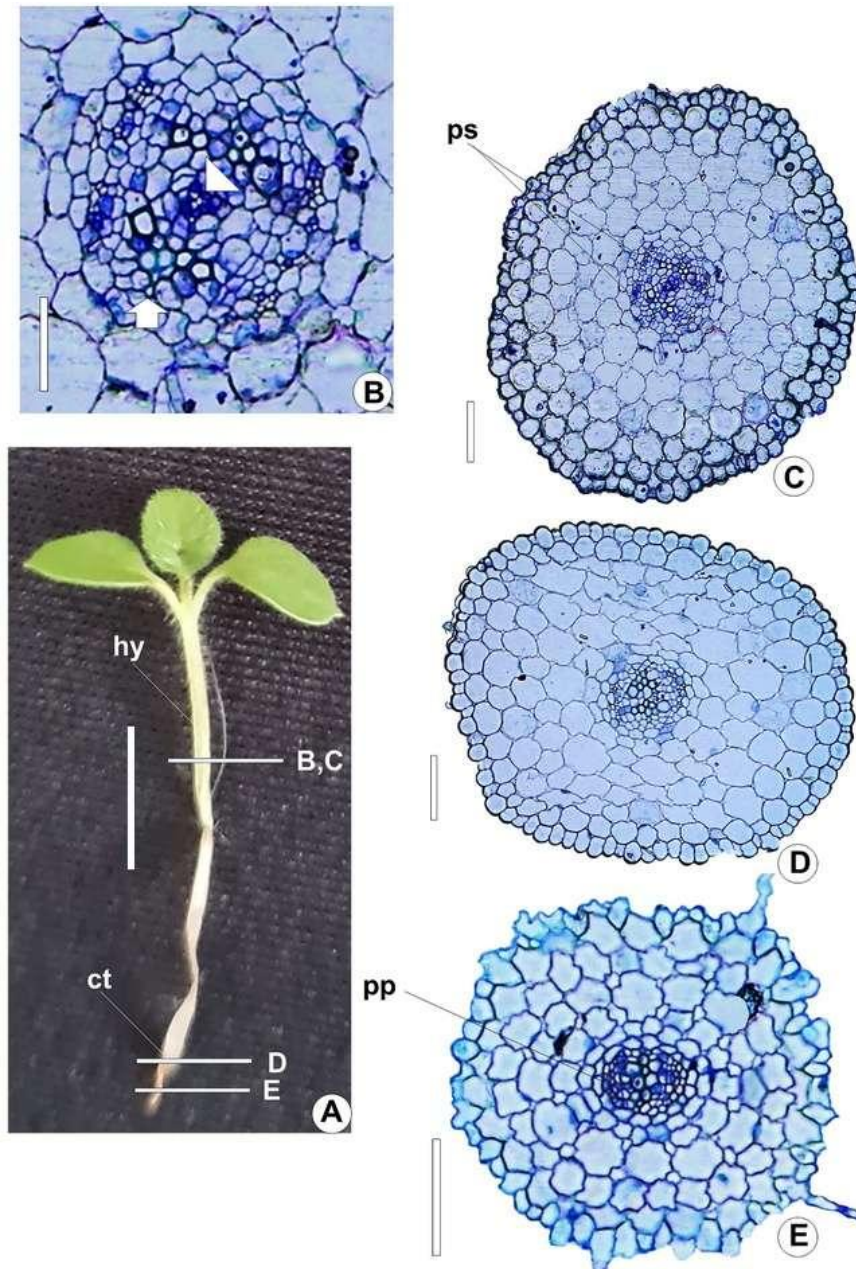


Figure 3 - Structure of the root, collet and hypocotyl of *Solanum torvum*, in cross-sections. A - Photograph of the seedling indicating the levels of the cross-sections. B,C - Hypocotyl sectioned in the middle region (C), evidencing details of the central cylinder (B) (arrowhead indicates intraxylary phloem and the arrow the protoxylem). D - Collet. E - Diarch root. (ct=collet; hy=hypocotyl; pp=primary phloem; ps= two strands of primary phloem). Scale bars: 0.5cm (A), 100 $\mu$ m (A-C), 50 $\mu$ m (D).

Primary roots (Figure 3E) of *Solanum* and *Capsicum annuum* seedlings are diarch, with two strands of primary xylem and phloem that alternate in the central cylinder. This cylinder is surrounded by the uniseriate parenchymatous pericycle (Figure 3E). The cambium of procambial and pericyclic origin is installed in the seedling phase. The cortex (Figure 3E) consists of exodermis, not always evident, parenchyma and endodermis with Caspary striae. The epidermis (Figure 3E) is uniseriate, irregular, and may exhibit unicellular hairs. Diarch and triarch roots are common in angiosperm seedlings [21, 22], but there is also a record of tetrarch and pentarch roots in seedlings of other angiosperm species, particularly in Bignoniaceae, Euphorbiaceae, Fabaceae, Meliaceae and Rutaceae [23].

In the proximities of the cotyledonary node, the vascular structure of the hypocotyl is composed of the two double traces of the cotyledons, which maintain vascular continuity with the root, and the traces of the epicotyl appear (Figure 4G). Thus, in the region of the cotyledonary node, the transition between the root and stem (epicotyl) ends, that is, the exarch condition of the root passes to the endarch condition of the stem. In the case of *Solanum americanum* and *Solanum lycopersicum*, the root-stem transition region begins more or less in the middle of the hypocotyl and also ends close to the cotyledonary node. The *Capsicum annuum* seedling has a root-stem transition structure similar to that of *Solanum* seedlings (it begins at the root and ends at the cotyledonary node), with a unilacunar cotyledonary node and a double trace.

Compton (1912) [10] proposed a classification of the various types of root-stem transition zone that he found in Leguminosae seedlings, suggesting three types called high, low and intermediate (subtypes high and low) types. The four *Solanum* species (Table 2) and *Capsicum annuum* belong to the intermediate high type, in which the transition phenomenon begins in the collet and ends close to the cotyledonary node. *Solanum americanum* and *Solanum lycopersicum* were classified as high type (Table 2), with the root-stem transition starting in the middle of the hypocotyl. The intermediate type of root-stem transition appears to be common in seedlings that have long, epigeal hypocotyls [23], as seen in *Solanum*. This type of transition was also found in species of Annonaceae, Asteraceae, Bignoniaceae, Clusiaceae and Fabaceae [23, 24].

The epicotyl of *Solanum* and *Capsicum annuum* (Figures 4C-E and 4H) has a stem structure with uniseriate and cuticularized epidermis, collenchymatous and parenchymatous cortex (the epicotyl may consist only of parenchyma depending on the stage of development), central cylinder with vascular bundles with intraxylary phloem, and a parenchymatous pith. Trichomes include a considerable diversity of glandular and no-glandular forms in the epicotyl epidermis. Intraxylary phloem, which is very evident in the epicotyl (Figure 4C), arises in the hypocotyl in the seedlings studied here, already referred to Solanaceae in the last century [25]. The author reports that in Convolvulaceae, which he considers a family related to Solanaceae, the intraxylary phloem arises in the stem above the level of the hypocotyls [25]. Additional phloem strands, penetrating more deeply into the pith were seen in *Solanum americanum*, and has already been registered for *Solanum* [26]. The *Solanum* eophyll node is unilacunar 1-traced (Figures 4B and 4H) that exhibits intraxylary phloem. The eophyll nodes of *Capsicum annuum* (Figure 4D) and *Solanum lycopersicum* (Figure 4E) are also unilacunar, but 2-traced and 3-traced, respectively.

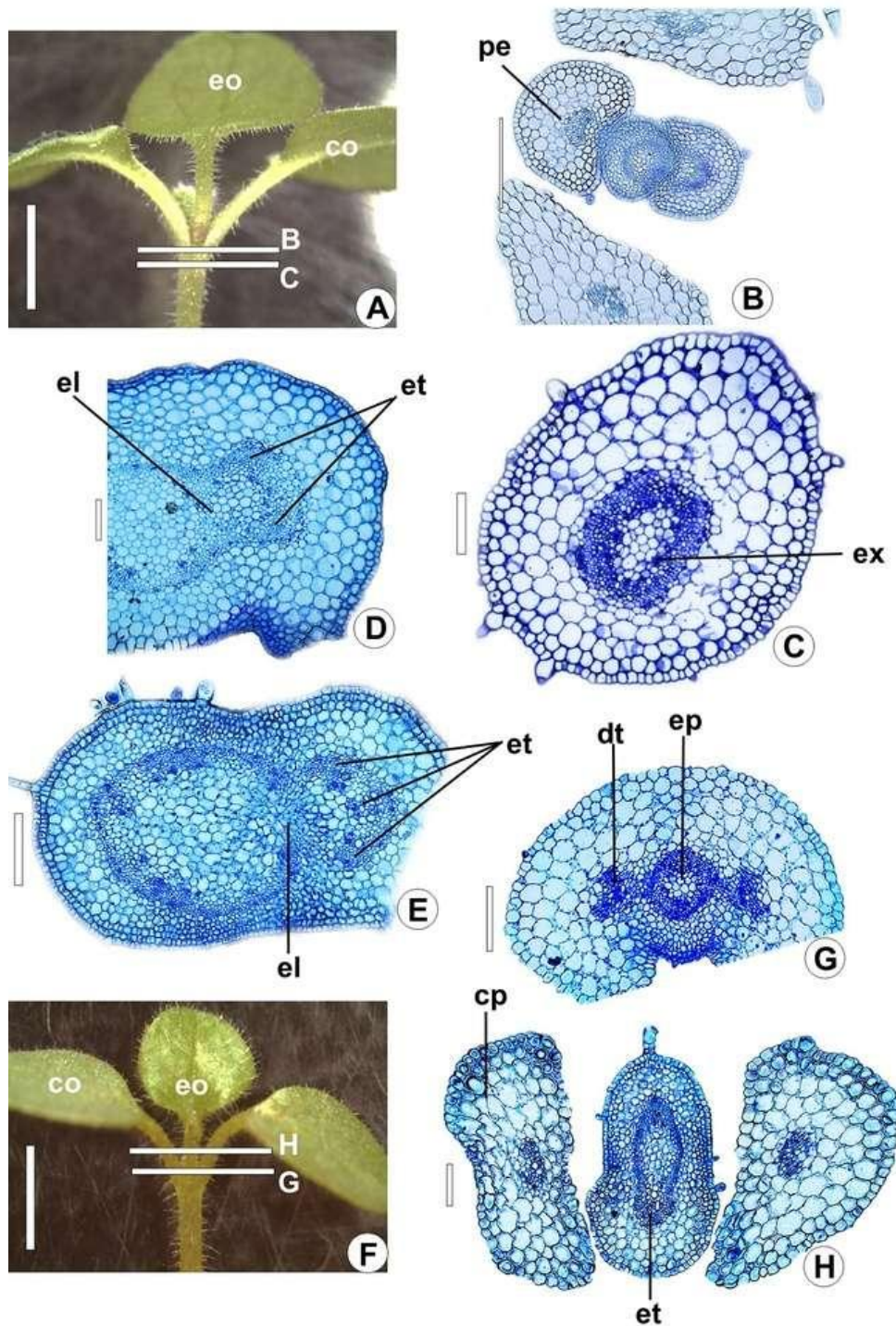


Figure 4 - Structure of the cotyledon and eophyll nodes of *Solanum mauritianum* (A,C), *Capsicum annuum* (D), *Solanum lycopersicum* (E) and *Solanum torvum* (B,E-G), in cross-sections. A,E - Upper portion of the seedlings with cotyledons and eophyll. B - Seedling apex showing the cotyledonary petioles (outermost figures) and the epicotyl with the bases of two leaves. C - Epicotyl. D,E - Unilacunar nodes of eophylls with two and three traces, respectively. G - Cotyledonary node with double trace and epicotyl already outlined in the center. H - Cotyledonary petioles and epicotyl showing a trace and a lacuna of the eophyll. (co=cotyledon; cp=cotyledonary petiole; dt=double trace of the cotyledon; el=eophyll lacuna; eo=eophyll; ep=epicotyl; et=eophyll trace; ex=extraxylary phloem; pe=petiole of eophyll). Scale bars: 3mm (A,E), 300 $\mu$ m (B), 100 $\mu$ m (C,G,H), 150 $\mu$ m (D,E).

The leaves of the *Solanum* seedlings, cotyledons and eophyll, can be considered dorsiventral (Figure 5), like the foliage leaves of most Solanaceae species [26]. Foliage leaves (nomophylls)

of numerous *Solanum* species, including *Solanum sisymbriifolium*, have been investigated more recently, and most species exhibit dorsiventral mesophyll [27]. The mesophyll (Figure 5) of cotyledons and eophylls consists of typical spongy parenchyma, but the parenchyma on the adaxial surface of the mesophyll commonly exhibits anticlinally elongated and wide cells or funnel-shaped cells, eventually interspersed with rounded cells. The condition of the mesophyll of the *Solanum lycopersicum* eophyll (Figures 5F and 5G) is somewhat different, in that there is a typical palisade parenchyma layer. The epidermis (Figure 5) of the cotyledons and eophylls is uniseriate, amphistomatic, and may present non-glandular and glandular trichomes.

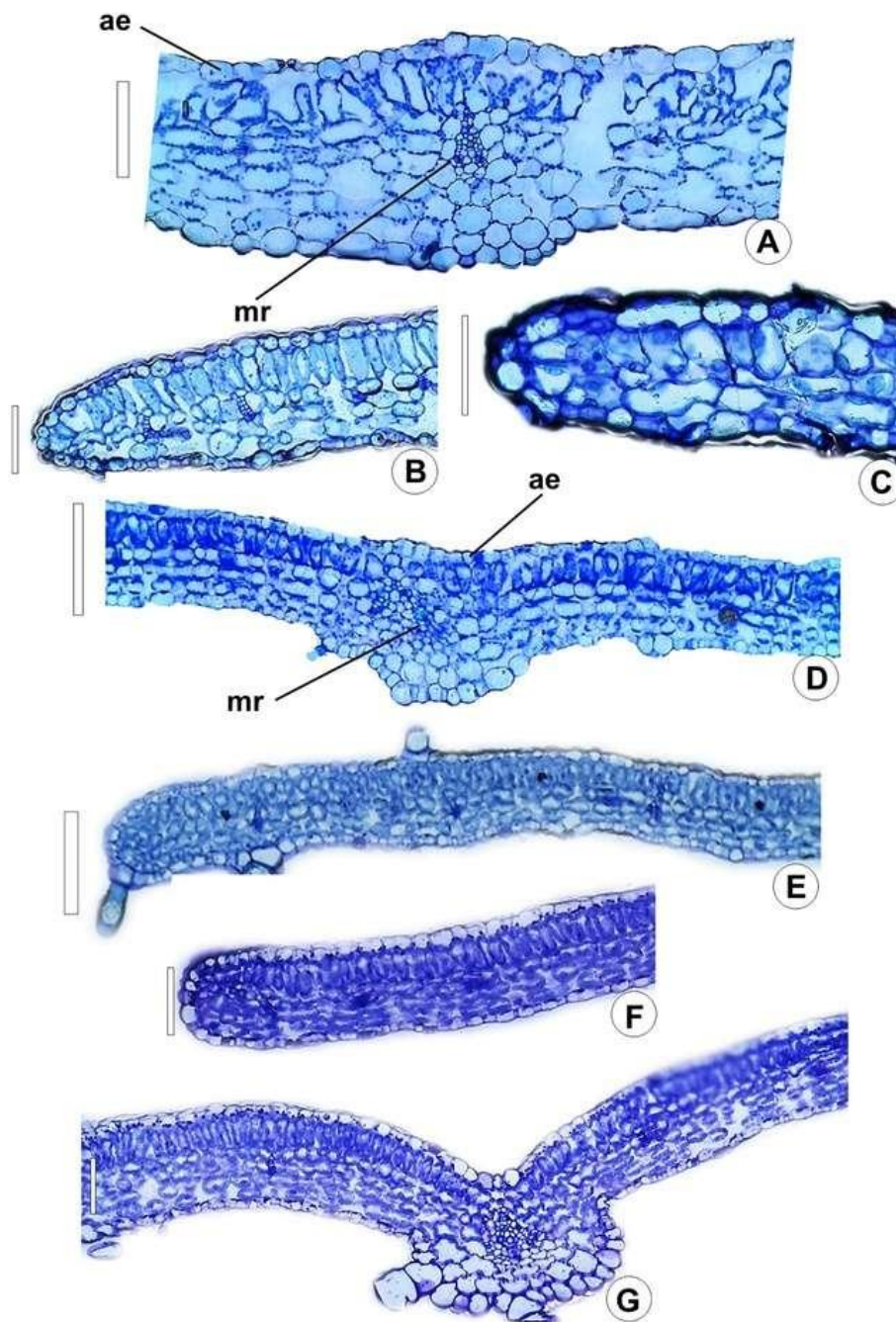


Figure 5 - Structure of cotyledons and eophylls of *Solanum torvum* (A, D), *Solanum sisymbriifolium* (B), *Solanum americanum* (C), *Solanum viarum* (E) and *Solanum lycopersicum* (F, G) seedlings, in cross-sections. A - Lamina and midrib of the cotyledon. B, C - Lamina and margin of the cotyledon. D, G - Lamina and midrib of the eophyll. E, F - Lamina and margin of the eophyll. (ae= adaxial surface epidermis; mr=midrib). Scale bars: 100 $\mu$ m (A, D, F, G), 50 $\mu$ m (B, E), 10 $\mu$ m (C).

The midribs of the cotyledons (Figure 5A) and eophylls (Figures 5D and 5G) are composed of a single vascular bundle, with phloem on both sides of the xylem. They may exhibit collenchyma and parenchyma on the adaxial surface and may show prominence on one (Figures 5D and 5G) or both surfaces (Figure 5A). The margin of the cotyledons and eophylls consist of palisade and spongy parenchyma (Figure 5B) or present more or less rounded cells (Figures 5C, 5E and 5F). At the margin of the eophyll of *Solanum viarum* there is a hydathode structure, with spongy parenchyma, vein termination and stomata.

### 3.3 Taxonomic and phylogenetic considerations

Morphological traits of the seedlings showed significant taxonomic potential for *Solanum*. The morphological variation of cotyledonary leaves and eophylls between investigated species is evident (Table 2), but it is necessary to emphasize that leaf morphology can be commonly affected by environmental factors [28]. Studies of morphological trait evolution in *Solanum* foliage leaves have revealed some controversy in the evolution of the leaf in the genus. There is an author who considers the leaves as ancestrally simple and entire [29], while another considers the compound (deeply pinnatifid) leaf to be ancestral [2]. Compound and pinnatifid foliage leaves can be found in *Solanum lycopersicum* and *Solanum sisymbriifolium*, respectively, whose eophylls already exhibit leaf margins with more or less deep indentations (Figures 2C and 1B; Table 2).

Among *Solanum* species, *Solanum americanum* and *Solanum lycopersicum* exhibit the beginning of the root-stem transition zone in the middle region of the hypocotyl (high type), all other species (including *Capsicum annuum*) begin this region in the root. Some authors at the beginning of the last century speculated on the value of the root-stem transition region in plant evolution. The high transition type (large part of the hypocotyl with structure indistinguishable from the root) was considered as basal (primitive) among the ancient dicots [10]. This view generated a lot of doubt among researchers at the time and, since then, it has not prospered.

The nature of the hypocotyl deserves some attention. In the species investigated here, the transition structure between the root and the stem is located throughout the hypocotyl, except in *Solanum americanum* and *Solanum lycopersicum*. The importance of the hypocotyl is emphasized as a structure related to the root and stem and its connection with the seed-leaves [10]. The hypocotyl should not be considered as a root or stem, nor as an organ composed partly of root or partly of stem, but as a specialized region of a primitively undifferentiated axis [10].

The node found in the eophylls of the investigated *Solanum* seedlings is unilacunar with only one leaf trace (Figures 4B and 4H) or three leaf traces seen on *Solanum lycopersicum* (Figure 4E). *Capsicum annuum* has the unilacunar eophyll node with two leaf traces (Figure 4D). The unilacunar node of foliage leaves characteristically occurs in orders considered advanced, such as the Scrophulariales (Solanales) order, to which Solanaceae belongs [30]. The unilacunar type of nodal structure is secondary in flowering plants, having originated from the basic tri-pentalacunar type [25, 31]. The nodal anatomy was investigated in 26 species of Solanaceae, and it was found that all of them have a unilacunar node and 1-traced [31]; the authors [31] concluded that unilacunar 2-traced and unilacunar 3-traced are the basic types in the family. It is important to emphasize that the anatomy of the cotyledonary nodes does not necessarily reflect ancestral conditions in the mature stem [25, 30]; for the authors [25, 30] the unique seedling morphology and decussate insertion of cotyledons make this unlikely.

## 4. CONCLUSION

The phanerocotylar and epigeal seedlings of *Solanum* species and *Capsicum annuum* have morphology typical of herbaceous and subshrub eudicots, and pioneer species. Primary roots of all species are diarch and the root-stem transition region occurs in the hypocotyl. Cotyledonary node exhibits double traces, and the eophyll node is unilacunar with 1-3 leaf traces. Cotyledons and eophylls are dorsiventral, with the parenchyma of the adaxial side of the mesophyll not always represented by typical palisade cells.

Morphological characters related to the shape of the cotyledons and eophylls are useful in separating the species investigated. Anatomical characters of the analyzed seedlings were very uniform among the species, with the beginning of the root-stem transition region (root or hypocotyl) and the number of leaf traces of the eophyll standing out as differential characters.

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