

Inflorescence patterns within the genus *Portulaca* (Portulacaceae): analyses of anatomy and morphology, based on species occurring in Brazil

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Abstract

The inflorescences of Portulacaceae have traditionally been considered capitula and their morphology and architecture have not been studied in detail. The purpose of this study was to expand the knowledge on the inflorescences within this family, comparing members of distinct lineages of *Portulaca* occurring in Brazil, to understand some systematic and evolutionary patterns within this group. Morphological characteristics of the inflorescences were analyzed using a light stereomicroscope, and for anatomical studies, we made transversal and longitudinal sections along the entire inflorescence, including involucre bracts, analyzing them using an optical microscope. We confirmed that observed inflorescences are determinate, composed of a first-order dichasium, with second-order helicoidal branches forming a cephaloid structure. The involucre leaves differed from adjacent bracts, which did not display a constriction at the base, as commonly observed in leaves. Thus, we conclude that the congested inflorescence of *Portulaca* is not a capitulum, but a cephaloid with different degrees of branch reduction within the genus. The Pilosa clade displayed the most congested cephaloid compared to members of the other analyzed clades. We showed present to show a new interpretation of the congested inflorescences in *Portulaca* and reinforce the need to analyze solitary inflorescences to understand the importance of these data to systematics, evolution, and pollinator-plant interactions within Portulacaceae.

Introduction

Due to its wide diversity, inflorescence morphology is an important factor for understanding the extreme evolutionary and plasticity of reproductive structures in angiosperms. However, studies on this diversity are limited when compared to those on flower diversity. According to Endress (2010), inflorescences in several groups of angiosperms have complexities that are mainly related to a repetitive process of a basic branching pattern. The evolutionary processes involving branch-reduction events have been shown to lead to congested inflorescences, as demonstrated in Eriocaulaceae (Stutzel and Trovó 2013), Passifloraceae (Hernandes-Lopes et al. 2019), as well as in Euphorbiaceae, Maranthaceae and Poaceae (Sell and Cremers 1992).

The capitulum is one of the most studied types of congested inflorescence. It comprises a polytelic structure that is derived from a raceme and developed through compression and thickening of the inflorescence axis (receptacle), encircled by involucre bracts, also known as phyllaries (Weberling 1989). Other congested inflorescences could assume similar morphologies, such as racemose umbels, cymes, and racemes (Harris 1999), mainly by the presence of axes that are not extended during inflorescence development, such as in Araliaceae, Combretaceae, Eriocaulaceae, Fabaceae, Nyssaceae, Plantaginaceae, and Proteaceae (see table 2 in Harris 1999).

In Portulacaceae, the inflorescence morphology is difficult to interpret, mainly because of the abundant amount of woolly trichomes that often cover the flower buds in several species, in addition to the presence of congested branches. Currently, Portulacaceae includes only the pantropical genus *Portulaca* L (Nyffeler and Egli 2010), which displays inflorescences described as arranged in cymes,

"pseudocapitula", "metaxytriad", heads, or rarely solitary flowers (Legrand 1962; Geesink 1969; Carolin 1987; Nyffeler and Egli 2010; Ocampo and Columbus 2012). The term capitulum has been used to describe congested inflorescences that occur in American species of this genus, while the inflorescences of non-American species have been identified as non-congested cymes, solitary flowers, or rarely as capitula (Ocampo and Mair-Sánchez 2018).

The inflorescence in *Portulaca* is surrounded by a whorl of involucre leaves that morphology are similar to that of the stem leaves (Legrand 1962; Geesink 1969; Carolin 1987; Hofmann 1994). According to Legrand (1962), variations in the number of involucre leaves may be taxonomically relevant at the infrageneric level. In addition to these structures, bracts are observed preceding the flowers in this genus and can be found in groups of four (*P. digyna* F. Muell.) or often in a pair, which may be reduced to scales or trichomes (*P. wightiana* Wall. ex Wight & Arn.). Taxonomic studies including reproductive information in this genus are common (Legrand 1962; Geesink 1969; Carolin 1987; Hofmann 1994; Ocampo and Mair-Sánchez 2018); however, details on the development of flower organs and morphology of the inflorescences are scarce (Soetarto and Ball 1968).

Geesink (1969) presented the most detailed work on the reproductive structures of *Portulaca*, including a hypothesis on the morphological interrelationship and schemes; he argued that inflorescences in this family were derived from a hypothetical dichasium. For Geesink, *Portulaca* inflorescences are non-congested (a pattern common to members of *P.* subg. *Portulacella*, such as *P. oligosperma* F. Muell. and *P. cyclophylla* F. Muell), capitula (as in *P. wightiana*), or solitary flowers (*P. quadrifida* L.), which are both common in *P.* subg. *Portulaca*. Carolin (1987) analyzed Geesink's (1969) proposal and classified the inflorescence history as "metaxytriads," defined as an inflorescence derived from an ancestral panicle.

The molecular study that focused on the diversity of inflorescence types in *Portulaca* considered the capitulum in this group as homoplastic, evolving at least twice within the family (Ocampo and Mair-Sánchez 2018). Members of this genus, which have inflorescences in typical capitula, were recovered mostly in the clades Pilosa, Umbraticola, Oleracea, and Cryptopetala, all of which were included in the alternate to subopposite-leaved (AL) clade (Ocampo and Columbus 2012). In contrast, capitulum is uncommon in the opposite-leaved (OL) clade, occurring in the Old World, only found in *P. wightiana* (Ocampo and Columbus 2012).

Because inflorescence types were found to be homoplastic, in Portulacaceae, Ocampo and Mair-Sánchez (2018) also considered them as a character that does not provide information to establish evolutionary relationships within this family. They suggested new studies on inflorescence development and pollination biology, which may provide important information to increase the knowledge on inflorescence-type diversity in this group.

Another important question relates to the bracts and involucre leaves, which are common in other capitulum-like inflorescences and are treated as phyllaries by Weberling (1989) and Harris (1999). For instance, in Asteridae (Asteraceae), a group largely known by its high capitulum diversity, the involucre whorl can be mainly identified by its position, as it is distributed on the periphery of the receptacle as an

envelope (Zhu et al. 2011). This structure appears to be similar to that observed in *Portulaca*; however, in Asteraceae, these involucre leaves were similar (*Dimerostemma* Cass. - Moraes and Semir 2009) or different from the vegetative leaves (*Tridax* L. – Powell 1965), whereas in *Portulaca* this information has not previously been detailed.

The present study aims to expand the knowledge on the morphological diversity and anatomical patterns of the congested inflorescences of *Portulaca* by analyzing species of this genus belonging to different clades. We focused on species occurring in Brazil, all belonging to the AL clade. Based on this, answers to the following questions were sought: 1) Could congested inflorescences occurring in *Portulaca* be considered capitula? 2) Do these inflorescences vary within the genus? 3) Is the congested inflorescence of *Portulaca* similar to the capitulum of other plant families? 4) Do bracts and involucre leaves have similar morphological and anatomical structures?

Material And Methods

Sampling

We analyzed specimens belonging to eight species of *Portulaca* occurring in Brazil (Table 1) that have congested inflorescences traditionally described as capitula: *P. elatior*, *P. halimoides*, *P. hirsutissima*, *P. minensis*, *P. mucronata*, *P. oleracea*, *P. umbraticola*, and *P. werdermannii*. All those species were considered by Ocampo and Columbus (2012), except *P. minensis* and *P. werdermannii*. Anatomical and morphological studies were based on inflorescences obtained from two to three adult individuals collected during field trips or from plants cultivated in a greenhouse at the University of São Paulo (Fig. 1). Samples were obtained at distinct stages of development, including young flower buds, pre-anthesis flowers, young flowers, and mature capsules. Vouchers were deposited in the herbarium of the State University of Feira de Santana (HUEFS). To improve the morphological studies, we also analyzed herbaria materials, as indicated (Table 1).

Morphological And Anatomical Analysis

The entire set of inflorescences collected, including involucre leaves and bracts, were fixed in FAA 50 (formaldehyde, acetic acid, and 50 °GL ethanol) for 48 h and then conserved in 70% ethanol. The samples were dissected and photographed, dehydrated in an ethanolic/butanolic series and embedded in paraffin as part of the anatomical study (Ruzin 1999). Permanent slides were prepared from serial longitudinal and transverse sections (8–10 µm thick) using a rotary microtome. Sections were dewaxed with xylol and stained with 1% astra blue in 50% ethanol and 1% safranin in 50% ethanol (Kraus et al. 1998). Slides were mounted, analyzed, and photomicrographed using a Leica DMLB microscope with an attached camera.

Additionally, morphological analyses of the inflorescences were made by observing the structures using a stereomicroscope and focusing on the quantity and shape of involucre leaves, collaboration and texture

of the bracts, and the level of branch reduction of the congested inflorescence. The terminology used to classify them was that of Weberling (1989), Prenner et al. (2009), and Endress (2010). All studies were conducted at the Plant Anatomy Laboratory of the University of São Paulo (USP).

Table 1

Samples of *Portulaca* analyzed in the present work. *Cultivated in a greenhouse at the University of São Paulo (USP). **Phylogenetic relationship proposed by Ocampo and Columbus 2012, Ocampo *et al.* 2013, Santos et al. 2021.

Species	Voucher	Phylogenetic relationship**
<i>Portulaca elatior</i> Mart. ex Rohrb	T. Vieira 28, 153, 146 (HUEFS, Brazil)	Pilosa clade
<i>P. halimoides</i> L.	T. Vieira 10, 24, 30 (HUEFS, Brazil)	Pilosa clade
<i>P. hirsutissima</i> Camb.	T. Vieira, 161 (HUEFS, Brazil) D. Cardoso 3788 (HUEFS)	Cryptopetala clade
<i>P. minensis</i> Legr.	T. Vieira 158 (Brazil, HUEFS) A. Stadnik and A. Tuller 435 (Brazil, ALCB)	Possibly Cryptopetala clade
<i>P. mucronata</i> Link.	T. Vieira 11, 142, 149 (HUEFS, Brazil)	Cryptopetala clade
<i>P. oleracea</i> L.	T. Vieira 154 (HUEFS, Brazil) T. Vieira and R. Ferrari 168, 164* (HUEFS, Brazil)	Oleracea clade
<i>P. umbraticola</i> Kunth	T. Vieira 14, 25, 143 (HUEFS, Brazil)	Umbraticola clade
<i>P. werdermannii</i> Poelln.	T. Vieira 07, 16, 173 (HUEFS, Brazil)	Possibly Pilosa clade

Results

Involucral leaves and bracts

We observed a whorl of involucral leaves around the inflorescence in all samples of *Portulaca* (Fig. 1a-f). The number of involucral leaves varied from 2 to 4 in *P. oleracea* and *P. umbraticola* (Fig. 1a, b), to 8 or more in *P. hirsutissima* (Fig. 1c), *P. mucronata* (Fig. 1d), *P. elatior*, *P. halimoides* (Fig. 1e), *P. minensis*, and *P. werdermannii* (Fig. 1f). These involucral leaves were flat in *P. hirsutissima* (Fig. 1c), *P. mucronata* (Fig. 1d), *P. minensis*, *P. oleracea* (Fig. 1b), and *P. umbraticola* (Fig. 1a), and terete in *P. elatior*, *P. halimoides* (Fig. 1e), and *P. werdermannii* (Fig. 1f). Furthermore, a constriction was present at the base of each involucral leaf (Fig. 2a).

The inflorescences were surrounded by bracteoles in all analyzed species, subtending the flowers (Fig. 2a-f). These structures were thin, small, and translucent; they were exposed in *P. umbraticola*

(Fig. 2b) and *P. oleracea* or more commonly hidden among woolly trichomes in *P. mucronata* and *P. elatior*. Anatomically, the bracts of all species had a single central bundle (Fig. 2c, e) and did not show a constriction at the base (Fig. 2a, f).

Morphological Of The Inflorescences

Regarding the congested inflorescences, all analyzed species presented a terminal flower with lateral branches on opposite sides, similar to a dichasium. We identified three different branch reduction types, considering the studied inflorescences. Type 1 was identified in *Portulaca mucronata* (Fig. 3a-f), *P. hirsutissima*, *P. minensis*, and *P. umbraticola*. It is characterized by reduced branches in a receptacle (Fig. 3a), which seemed to be a dichasium with helicoidal branches towards lower orders (Fig. 3b) in representatives of *P. mucronata* (Fig. 3c) and *P. umbraticola* (Fig. 3d). The floral insertion was composed of a terminal flower, centrally placed, with lateral reduced branches supporting the flowers of the second order (Fig. 3e, f).

Type 2 was observed in *Portulaca oleracea* (Fig. 4a-e), with branches slightly congested, and the inflorescences partially included. These partial inflorescences displayed long peduncles, facilitating visualization of the main inflorescence (Fig. 4a-c). We observed flower insertion in the receptacle (Fig. 4d), forming a dichasium with branches of partial inflorescences that were elongated, emerging from the lateral position of the dichasium (Fig. 4d, e).

Type 3 occurred in members of *Portulaca elatior*, *P. halimoides*, and *P. werdermannii*. These species showed extremely short ramifications (Fig. 5a), with inflorescences grouped in the receptacle (Fig. 5b, c), that were formed by both main and partial inflorescences. We observed the inflorescence positions in the transverse view (Fig. 5d, e). The center of the receptacle had the eldest inflorescence and was surrounded by lateral, partial inflorescences (Fig. 5d, e).

Discussion

Involucral leaves and bracts structures

The analyzed congested inflorescences of *Portulaca* were characterized by the presence of an involucral whorl formed by vegetative leaves that preceded it, which were widely described as involucral leaves (Legrand 1962; Geesink 1969; Carolin 1987). We identified whorl arrangement as the only difference between involucral leaves and stem leaves.

In the studied species, the involucral leaves widely varied in number, sometimes even within the same species, and these leaves were morphologically similar to those of the stem. These results disagree with those found by Legrand (1962), and based on the analyzed species, this does not seem to be a character that aids to propose evolutionary relationships and taxonomic groups within the genus. The analyzed involucral leaves, which were flat or terete, followed the morphology found in stem leaves, which was

previously mentioned as indistinct by Eggli and Ford-Werntz (2002), even based on other representatives of this genus. This is similar to other groups that show indistinct involucre leaves compared to those of the stems, as is the case for members of the genus *Tridax* L. (Asteraceae - Powell 1965).

Our results confirm the presence of bracts in all analyzed species, without variation in relation to their number or position, in contrast from what is reported for the Paleotropical species *P. wightiana* and *P. digyna* (Geesink 1969). According to Weberling (1989), those structures fit into the concept of bracts and prophylls, i.e., leafy organs preceding the floral axis. More recently, Prenner et al. (2009) updated this concept, considering that these structures may be a flower-preceding prophylls (FPP) or a flower-subtending bract (FSB). For all species of *Portulaca* analyzed here, it was possible to identify FPPs, the thin leafy structures that internally subtend the inflorescences for the involucre leaves, or the FSBs, with similar structures that preceded the flowers individually.

Morphological Inflorescence's Comparisons

Three types of congested inflorescences were identified in members of the four clades analyzed. Type 1 was found in species of the Cryptopetala clade (*P. hirsutissima* and *P. mucronata*) the Umbraticola clade (*P. umbraticola*), and in *P. minensis*, which currently has no confirmed phylogenetic placement, but which probably has a phylogenetic relationship with Cryptopetala clade (Santos et al. 2021). Type 2 was observed only in the Oleracea clade (*P. oleracea*), and the most congested inflorescences (Type 3) were identified in members of the Pilosa clade (*P. elatior* and *P. halimoides*), as well as in *P. werdermannii*, which also has an undefined placement.

According to Hofmann (1994), congested inflorescences are not common in Caryophyllales and are observed as capituliform racemes in representatives of *Mirabilis* L. (Nyctaginaceae), and spike-like inflorescences in *Halophytum* Speg. (Halophytaceae), which is known to be the sister group of Basellaceae (Anton et al. 2014). Therefore, that author does not consider the inflorescence of *Portulacaceae s.l.* a congested structure, but a diachasium, monochasium, or double raceme.

The congested inflorescences of *Portulaca* are called capitula (Geesink 1969; Carolin 1987), a concept adopted by Muller-Doblies and Muller-Doblies (1987), of inflorescences with axes shortened in the branching region, as heads. For Endress (2010), heads may be considered a capitulum when they are opened and the first-order axis of the inflorescence is not terminated by a flower, as in Asteraceae (Harris 1999; Roque et al. 2009); on the other hand, it may be considered a cephaloid when it is closed, meaning that the main axis of the inflorescence shows a terminal flower with a dichasial structure. Therefore, the use of the term cephaloid (Muller-Doblies and Muller-Doblies 1987) seems to be more appropriate to describe the congested inflorescences of *Portulaca*, according to Endress's (2010) delimitation.

According to Ocampo and Mair-Sánchez (2018), two hypotheses on the evolution of the *Portulaca* inflorescence are possible, depending on the analyses used. Based on maximum likelihood, those authors stated that the congested inflorescences of *Portulaca* may be the ancestral condition for the suborder

Portulacineae. The analyses based on parsimony returned solitary flowers or non-congested inflorescences as the ancestral condition in this genus, in agreement with Geesink (1969) and our results.

In the present study, cephaloid patterns were distinct among the clades presented by Ocampo and Columbus (2012) and did not resemble other congested inflorescences of Caryophyllales. Cephaloid Type 1 is present in members of the *Cryptopetala* and *Umbraticola* clades (as well as in *P. minensis*); therefore, they may not have the same origin. As Oleraceae and *Umbraticola* clades are not sister groups (Ocampo and Columbus 2012) and they clearly differ in cephaloid patterns, information is still lacking regarding these structures in *Portulaca*. Our data also indicated that the "capitulum" treated as the same character state by Ocampo and Mair-Sánchez (2018) should be revised in further phylogenetic studies, considering the different branch reductions proposed here.

The cephaloid Type 3 is similar to the aggregate of cymose units observed in Calyceraceae (Asteraceae; Asterales), where several cymes are found in the same receptacle (Pozner et al. 2012). The similarity between the cephaloid of *Portulaca* and that of Calyceraceae may be due to the fact that both inflorescences are derived from an ancestral determinate, non-congested inflorescence. There are several arrangements of determinate congested inflorescences in both families, which are not observed in other representatives of the MGCA clade (Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae - Pozner et al. 2012), or previously reported for Caryophyllales.

Conclusions

We conclude that: 1) inflorescences traditionally recognized as a capitulum in *Portulaca* are actually a cephaloid, resulting from branch reduction of a dichasium, with helicoidal lateral branches; 2) three different degrees of branch reduction occurred in *Portulaca* inflorescences, with highly congested inflorescences recognized in the species of the *Pilosa* clade, differing from other clades with less congested terminal inflorescences; 3) the most congested cephaloid in *Portulaca* does not resemble other inflorescences in Caryophyllales; however, they are structurally similar to the aggregate of cymose units of Calyceraceae; and 4) the involucre leaves are morphologically and anatomically different from the bracts, based on the wide variation in the number of structures (*vs.* constant), similarity with the stem leaves (*vs.* thin), and opaque structure (*vs.* translucent), in addition to the presence of a constriction at the base of these structures (*vs.* absence). Further studies focusing on the inflorescence morphology of other *Portulaca* species, mainly those described as having solitary flowers, should reveal more information on the diversity and evolution of inflorescence in this group is necessary to increase the sampling to confirm the observed patterns.

Declarations

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Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical standards: The authors declare the compliance of ethical standards.

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Figures

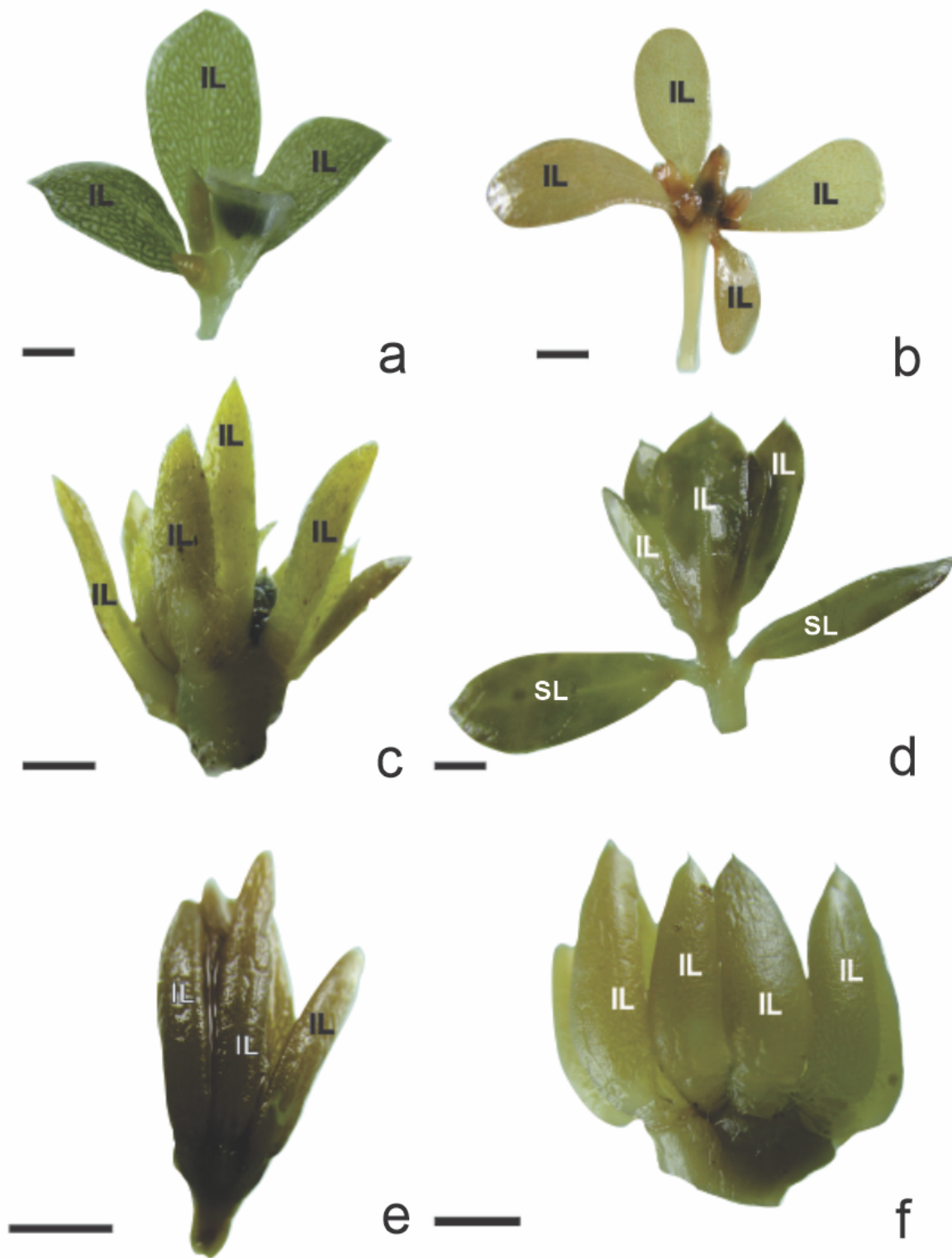


Figure 1

Morphology of congested inflorescences in *Portulaca*. **a.** *P. umbraticola*. **b.** *P. oleracea*. **c.** *P. hirsutissima*. **d.** *P. mucronata*. **e.** *P. halimoides*. **f.** *P. werdermannii*. scale bars= 1 cm; il= involucre leaves; sl= stem leaf.

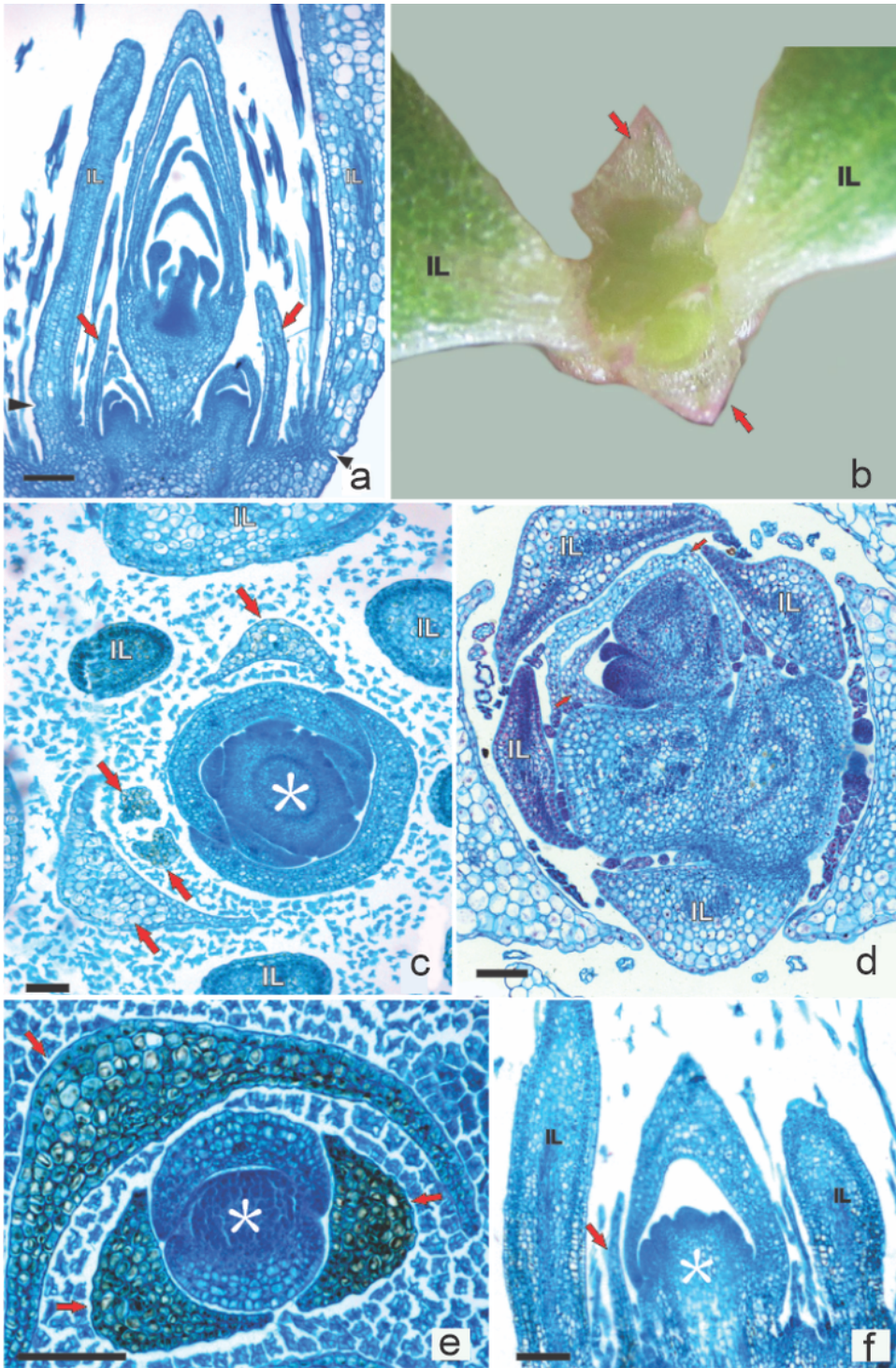


Figure 2

Morphology and anatomy of congested inflorescences in *Portulaca*. **a.** Longitudinal section of the inflorescence with a terminal flower and bracts of lateral (red arrow) flowers in *P. halimoides*. **b.** General view showing two bracts (red arrow) and involucral leaves (IL) in *P. umbraticola*. **c.** Transverse section of inflorescence. *P. oleracea*D – F. *P. werdermannii*. **d.** transverse section of inflorescence. **e.** transverse

section of young floral bud. **f.** longitudinal. scale bars= 100 μ m; white asterisk = young floral bud; black arrowhead = constriction at the base of leaf.

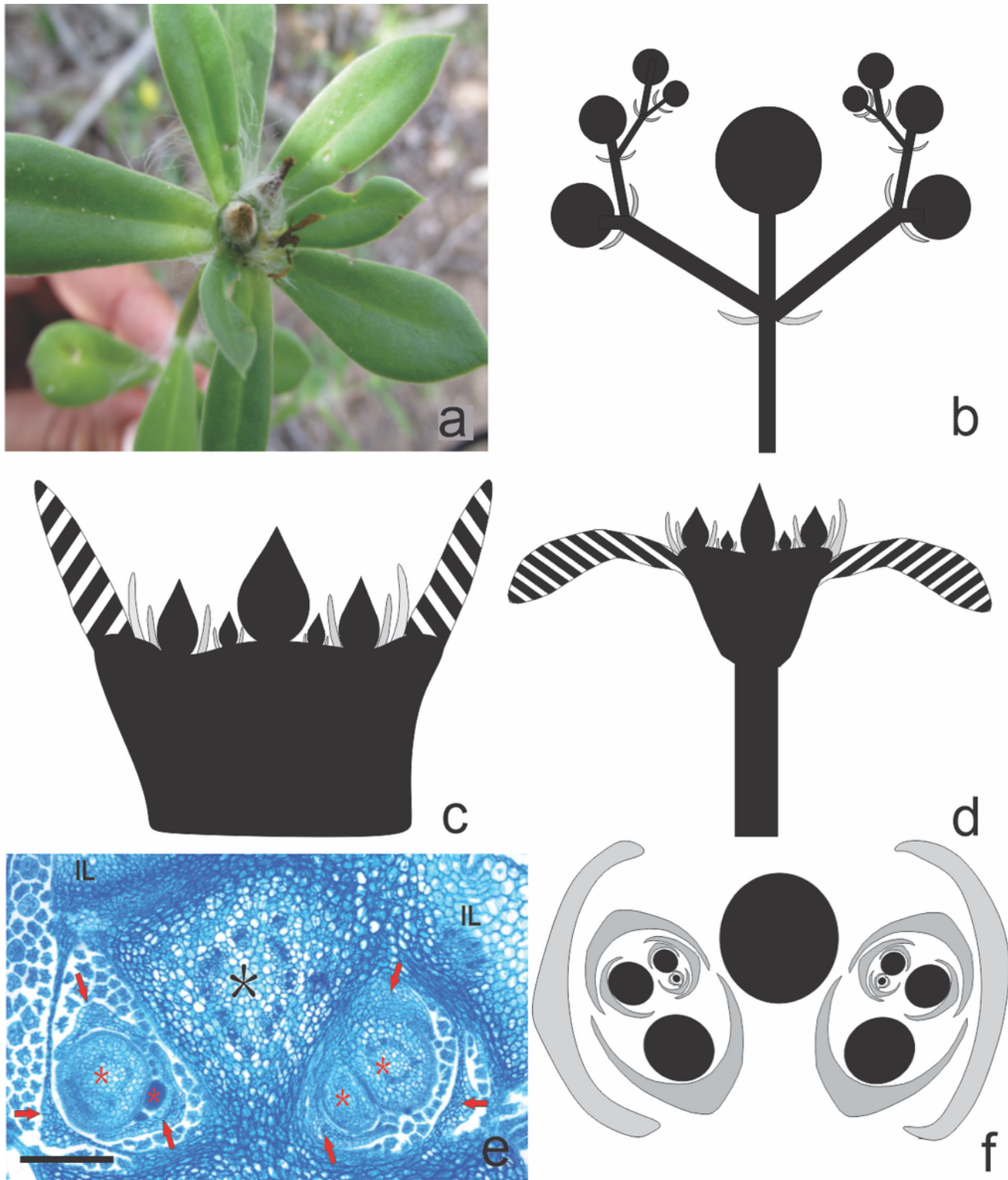


Figure 3

Morphology and anatomy of congested inflorescences in *Portulaca*: the cephaloid Type 1. **a.** Inflorescence in nature, *P. mucronata*. **b–d.** Schematic illustration of inflorescences, in longitudinal view.

b.Representation of elongated branches (exaggerated). **c.** Schematic of *P. mucronata*. **d.** Schematic of *P. umbraticola*. **e.** Transverse section of the inflorescence showing young floral bud, *P. mucronata*. **f.** Schematic illustration of inflorescences in transverse. scale bars= 100 μ m; black asterisk = terminal flower; red asterisk = flowers; red arrow = bracts; il = involucral leaves. Schematic legend: gray leaf structure = a pair of profiles; hatched leaf structure = involucral leaf; black circular structure = floral bud.

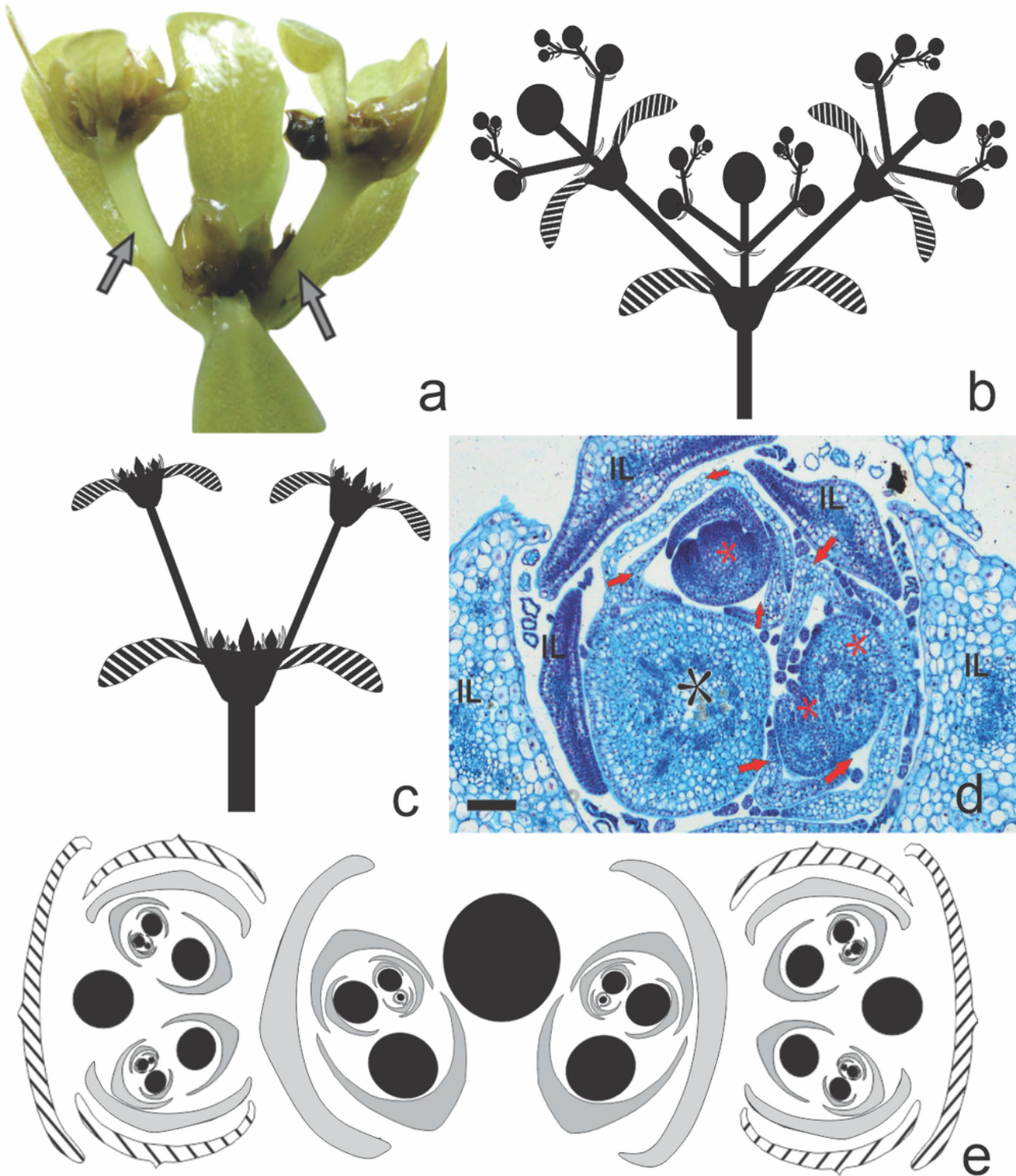


Figure 4

Morphology and anatomy of congested inflorescences in *Portulaca*: the cephaloid Type 2.

a. Inflorescence in nature, *P. oleracea*. **b–c.** Schematic illustration of inflorescences in longitudinal view. **b.** Representation of elongated branches (exaggerated). **c.** Representation of congested branches. **d.** Inflorescence anatomy cuts in the transverse section. **e.** Schematic illustration of the inflorescences, in transverse view. scale bars= 100 μm ; black asterisk = terminal flower; black arrow head = constriction at the base of the leaf; red asterisk = flowers; red arrow = a pair of profiles; il = involucre leaves. Schematic legend: gray arrow = branches; gray leaf structure = a pair of profiles; hatched leaf structure = involucre leaf, black circular structure = floral bud.

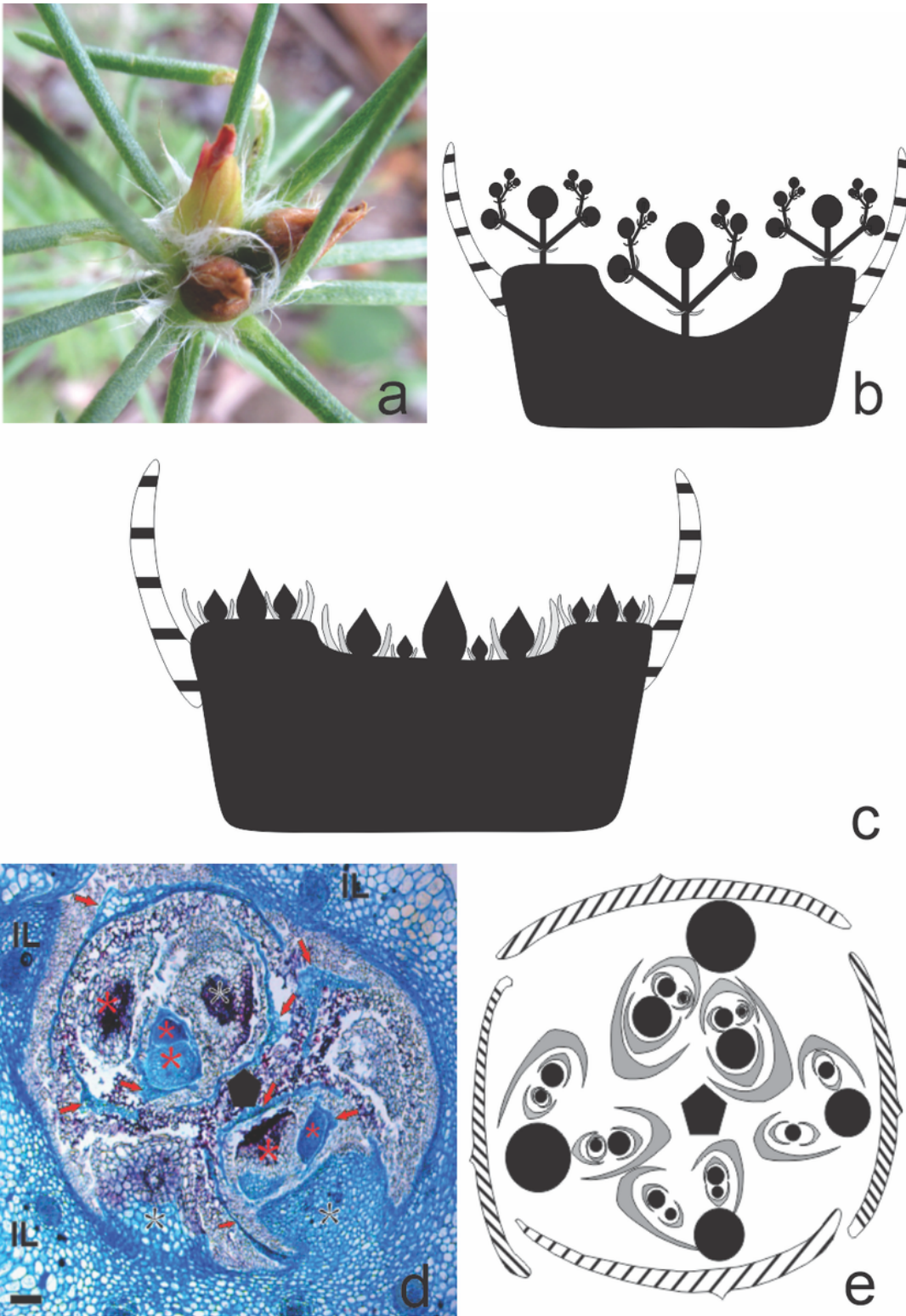


Figure 5

Morphology and anatomy of congested inflorescences in *Portulaca*: the cephaloid Type 3. **a.** Morphology of fresh inflorescence of *P. elatior*. **b–c.** Schematic drawings of inflorescences in longitudinal view. **B.** Representation of elongated branches (exaggerated). **c.** Representation of congested branches. **d.** Transverse section of the inflorescence showing young and mature flowers, *P. elatior*. **e.** Schematic illustration of inflorescences in transverse view. Scale bars= 100 μ m; black asterisk = terminal flower; red

asterisk = flower bud; red arrow = a pair of profiles; il = involucral leaves. Schematic legend: gray leaf structure = bract; hatched leaf structure = involucral leaf, black circular structure = floral bud, black polygon = gap left by the main inflorescence.