Morphological and Anatomical Adaptations of Halophytes: A Review

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Constantin Toma is deceased.

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Abstract

The nature of many morphological and anatomical adaptations of halophytes is xeromorphic, because of the physiological drought occurring in saline environments. Succulence may have a dilution effect on accumulated toxic salts within plant tissues and plays a water storage role during dry periods. Intense lignification linked to successive cambia activity in roots and stems of halophytic chenopods could be also related to salinity and aridity. Salt secretion is an important strategy of recretohalophytes (crynohalophytes); salt glands and salt bladders are involved in the secretion of salt excess from aerial organs toward the exterior of halophytes. Kranz anatomy pattern occurs in C_4 halophytes as a physical support for physiological and biochemical processes typical for C_4 pathway. Bulliform or motor cells act in "amphibious halophytes" for rolling up the leaf during extended drought periods. In respect with special or local environmental factors (tropical halophytes), halophytes have special adaptations, as is the case of mangroves (aerial prop roots, pneumatophores, viviparity, aerenchyma).

Keywords

Mangroves · Salt glands · Succulence · Mangroves · Tropical

1 Introduction: Halophytes as an Ecological Group of Plants

Most of morphological and anatomical adaptations of halophytes are xeromorphic by their nature. Dealing with halophytes as a special case of xerophytes is an old idea promoted by the subtle observations of plant ecologists from the end of the nineteenth century, especially Warming (1897, 1909) and Schimper (1891, 1903) who emphasized the hypothesis of "physiological dryness" (see extensive discussions in: Grigore 2008; Grigore and Toma 2010a, b, c, 2011a, 2017; Grigore et al. 2014 and the references therein).

Botanists have noticed long time ago that adaptations of halophytes are similar with those found in xerophytes, and these features are strictly correlated with physiological drought of saline habitats (Henslow 1895; Grigore's chapter on ▶ "Definition and Classification of Halophytes as an Ecological Group of Plants," this handbook). If xerophytes and halophytes would be considered as distinct ecological groups of plants, it would be striking to find out that they share the same adaptations, as they would have something in common. While for some authors the position of halophytes within other ecological groups of plants may be confusing, for others it seems logical and natural to deal with halophytes under the umbrella of xerophytes. Actually, the reason for the common origin of morphological and anatomical adaptations of halophytes and xerophytes is mainly the drought of soils in which both groups vegetate – a physical drought in the case of xerophytes and physiological drought in the case of halophytes, as described by Schimper (1903) and especially by Warming (1909).

According to Schimper (1903), the major natural regions and environments where physiological drought is prevalent and consequently only xerophytes can survive are grouped (according to their physical characteristics) as follows:

1. Deserts, steppes, and other areas with a dry substratum and dry air, occasional or persistent great heat, and intense illumination (Fig. 1)
2. The bark of trees and rocks where there is rapid drying of the substratum, owing to deficient depth (Fig. 2)
3. Sandy soil, gravel, and the like, on account of the rapid drying of the substratum, owing to its great permeability (Fig. 3)
4. Seashores and solfataras, which have an abundance of soluble salts in the soil (Fig. 4)
5. Peat bogs, because of the humic acids in the soil (Fig. 5)
6. Polar zones and vicinity of glaciers in high mountains, where the temperature of the soil is low (Fig. 6)
7. Alpine highlands, which experience rarefied air and the strong insolation characteristics of the alpine climate (Fig. 7)

At a glance, it is rather surprising that such habitats – so diverse by their geography and ecological conditions – can induce similar adaptations in plants

Fig. 1 *Alhagi maurorum* from Sahara desert (Schimper 1903) (xerophytic habitus)

Fig. 2 Xerophilous structure – dry substratum of bark tree and rocks. *Octomeria* ssp. (left) and *Cattleya bicolor* (right) (Schimper 1903)

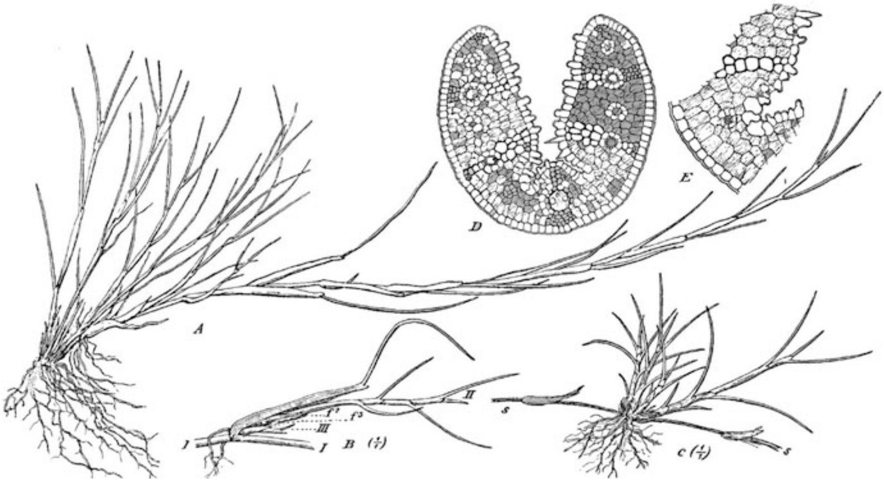


Fig. 3 *Glyceria maritima* – sand plant; (**A–C**), repent stem, general view (**A**) and details (**B, C**); (**D** and **E**), cross section through lamina (**D**, general view; **E**, detail) (Warming 1906)

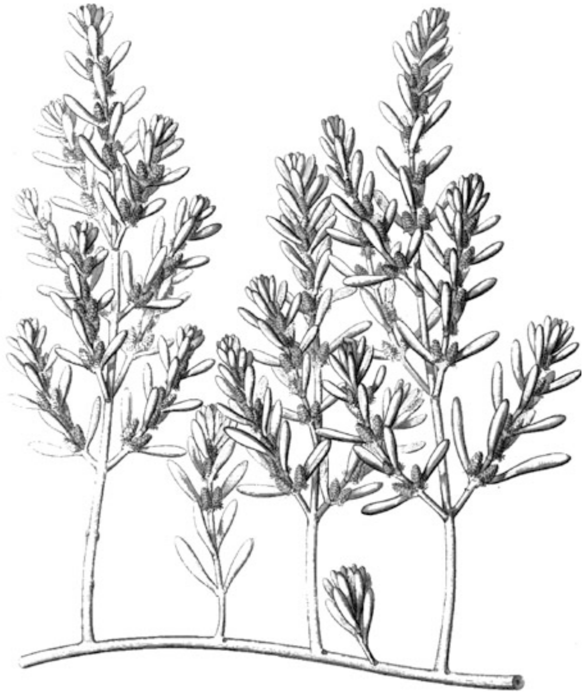


Fig. 4 *Batis maritima*; xerophilous structure; wet, saline soil of tropical shores. Plant with succulent leaves (Martius and Eichler 1844)

that belong to different ecological groups but that are, in fact, so closely related to the nature of their adaptations (Figs. 1, 2, 3, 4, 5, 6, and 7).

The idea of "physiological drought" has been adopted by many authors who have subscribed to Warming's and Schimper's hypothesis, approaching the adaptations of halophytes and xerophytes. They realized that there is a phenomenon of convergence: drought conditions (either physically or physiologically considered) induce in plants the need for conjoint features, despite they vegetate in very diverse and heterogeneous environments.

Moreover, even before the promoting of this idea by Schimper (1891, 1903) and Warming (1909), some botanists observed that species from different regions and habitats of the world – of course, included in different ecological groups – may display similar (convergent) morphological features and anatomical adaptations.

Henslow (1895) noticed that there are certain peculiarities of halophytes (maritime plants) common with desert plants as well as with some alpine and subalpine species. Hooker (1891) noticed a certain general correspondence between the climate of some countries at the sea level and that of the Himalaya, both in the absence of animal life and in lacking certain natural orders of plants. He thus compares New Zealand, Fuegia, and Tasmania with Scotland and Norway. He attributes the absence of life to the moist and cold atmosphere. Following Hooker's observation, Henslow pointed that several maritime plants are also found in mountains or certain varieties of them; despite that

Fig. 5 *Vaccinium oxycoccos*, a peat bog species (Fitch and Smith 1880)

not all the mountains are characterized by a high intense aridity, he mentioned several species that illustrate “this coincidence”: *Draba incana*, *Cochlearia officinalis* ssp. *alpina*, *Silene maritima, Plantago maritima*, and *Hieracium* species.

Henslow pointed that the resemblances which may be seen in plants from such widely different localities as our seashores, alpine regions, and desert countries are readily explicable that *certain elements of the environment are in excess*; these act upon the plants in question, and the latter respond accordingly, so that much the same results occur. Thus, if hairiness be due to a check in the development of cellular tissue, it may arise from too much heat, as in the deserts of Africa, or from too great a degree of cold, as in Alpine and Arctic regions; both conditions are causing great aridity. Succulence in the deserts, especially where the soil is saline, arises from identically the same cause as in plants on our own seashores (see the Figs. 1, 2, 3, 4, 5, 6, and 7). Since the moisture of the air and soil is more charged with saline matters in maritime regions and salt marshes, it was a reasonable inference that the presence of salts was in some degree responsible for the remarkable succulence of such plants as *Crithmum maritimum*, *Salicornia herbacea*, and many others.

Lots of experiments supported that some morphological and anatomical features of maritime plants can be lost or diminished, under different ecological conditions, as the salinity influence; these is a complicate discussion about different species,

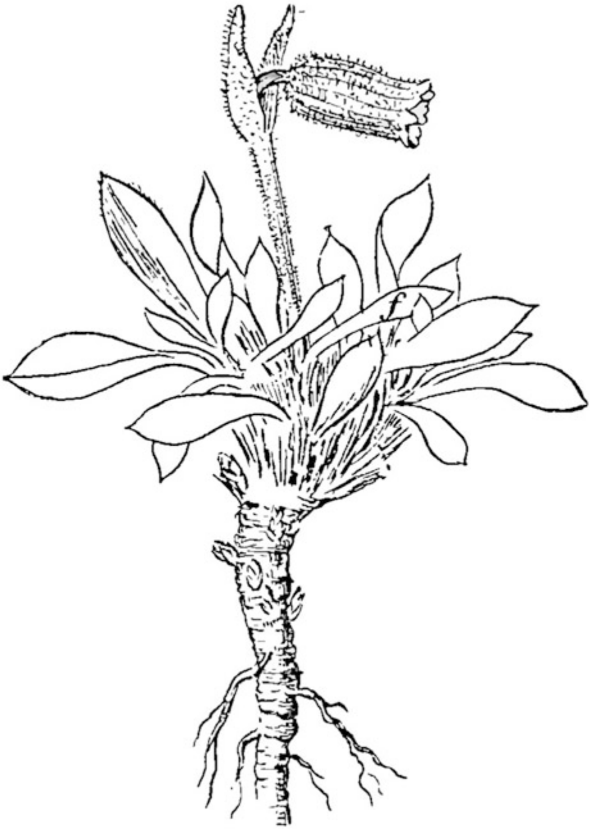


Fig. 6 *Melandrium apetalum* ssp. *artcticum*, arctic region (Warming 1906)

“forms” (inland and maritime) of the same species – with particular features on the shore and in inland areas – or ecotypes of the same species. Iconic experiments and observations of Lésage (1890) (see extended discussions in Grigore and Toma 2017) confirmed that salt addition or its removal from cultivation conditions may induce the presence or absence of a morphological character.

For this chapter, two ideas must be underlined in order to discuss morphological and anatomical features of halophytes:

1. A halophytes is here regarded and approached as a special case of xerophytes, because of physiological drought of saline environments; other groups of plants are under the multiple influence of this ecological situation, a fact that explains the presence of similar morphological and anatomical adaptations in desert plants, alpine plants, peat bog plants, epiphytes, and arctic (polar) plants.
2. The climatic (biogeographical) and ecological diversity of saline habitats would add something particular to halophytes. Halophytes vegetating on seashore, saline deserts, saline steppes, tropical shores (mangroves), and inland saltmarshes

Fig. 7 *Coprosma cuneata*, a New Zealand alpine plant (Schimper 1903)

> are – according to first sentence and our vision about halophytes – xerophytic by the nature of their adaptations. However, each mentioned saline habitat brings something new and particular, an ecological scenario that would induce particular adaptations. If to use a plastic definition, a halophyte should then considered a *general xerophyte plus something in addition*, *originated from individual ecological conditions of a given ecosystem.* Indeed, looking at the diversity of saline habitats, it is obvious that a halophyte from a saline steppe and another from a mangrove plant community would have different adaptations, added to a common xeromorphic profile (both of them must face physiological drought, however).

The position of halophytes within other ecological groups of plants is thus tricky; Coulter (1900) considered that the classification of plants into hydrophytes, xerophytes, and mesophyte would be artificial, if based on the criterion on water accessible for plants. However, halophytes seem to have a special position as, according to the amount of water supply, they could be classified within xerophytes or hydrophytes groups; in fact, the water contains certain salts, notably common salt, gypsum, and magnesia. The water may be abundant enough to represent hydrophyte conditions, or it may be scanty enough to represent xerophyte conditions, but if these salts are present in the soil in sufficient abundance to strongly affect the water, the plants are halophytes.

According to Coulter (1900), such areas occur in various positions:

1. In the vicinity of the seashore, where there are salty beaches, and swamps and meadows
2. The margins of salt lakes, such as the Great Salt Lake, the Dead Sea, or Caspian Sea, and a host of smaller lakes
3. About saline springs, which are common among the numerous medicinal springs of watering places
4. Certain interior arid wastes, which probably mark the position of old sea basins.

2 Review of General Morphological and Anatomical Adaptations of Halophytes

The main morphological and anatomical features in halophytes are listed below. In this subsection morpho-anatomical adaptations are approached as major, "general" to have an accurate picture on their xeromorphic nature. Differences between different groups of halophytes – or to be more precise – special features found in halophytes vegetating in different saline environments, will be discussed in the next subsections. For this purpose, contributions of Henslow (1895), Warming (1877, 1891, 1906, 1909), Chermezon (1910), Grigore (2008, 2011), Grigore and Toma (2005, 2006a, b, 2007a, b, c, 2008a, b, c, 2010a, b, c, 2011a, b, 2014, 2016), Grigore et al. (2011a, b, 2012a, b, 2012c, 2013), Safiallah et al. (2017), and Kherraze et al. (2018) were followed here.

2.1 Succulence

Succulence – first morphologically noticed by botanists – seems to be the early important adaptation observed and discussed within the halophyte group by botanists (Grigore and Toma 2017). Perhaps the most obvious feature among halophytes is that they are nearly all succulent plants: the leaves are thick, fleshy (containing water storage tissues), and more or less translucent (Grigore 2008). This is due partly to the great amount of cell sap and lack of chlorophyll but partly to the small size of the intercellular spaces. In many cases, it has been a long time indicated that species present two ecological forms: the maritime or halophytic form, which has succulent, thick leaves, and the inland form, which has thin leaves (Lésage 1890; Holtermann 1907, Chermezon 1910 – see Grigore and Toma 2017 for extensive discussions). Such examples are *Lotus corniculatus*, *Geranium robertianum*, *Convolvulus arvensis*, *Matricaria inodora*, *Hieracium umbellatum*, and *Solanum dulcamara*. Experiments with culture substratum have demonstrated that certain halophytes cultivated on ordinary soil with little or no salt achieve thinner leaves and lose other characteristics; such is the case with *Cakile maritima*, *Cochlearia officinalis*, *Salicornia herbacea*, *Spergularia media*, and *Salsola soda*.

Conversely, certain inland species acquire thicker leaves when cultivated in a substratum treated with common salt, as is the case with *Lotus corniculatus* and *Plantago major*. This thickness of leaf is induced by an increase in volume of mesophyll cells that become large and roundish; in the interior of the leaf, poor in chlorophyll, thus making the leaf hyaline, a genuine water storage tissue can form. In some species, a typical water storage tissue occurs and is surrounded by palisade tissue, for instance, in *Salsola kali*, *Batis maritima*, and *Salicornia europaea*.

Lésage (1890) projected a very interesting and well-designed experiment regarding the modifications of leaves in species having two ecoforms: maritime (halophytes, *varieté maritime*) and inland varieties (*varieté terrestre*); he tested his hypothesis dealing with individuals collected from nature and in experimental conditions. Finally, he compared several histological parameters in leaves of plants collected near to the sea (maritime plants) and their variants from inland nonsaline area. This study looks like a very modern and complex study of experimental plant anatomy (Grigore and Toma 2017).

The background idea of Lésage study is that every species able to vegetate in both considered environments (maritime and inland) would modify more or less following the influence of environments where they develop. He further divides this idea in several hypotheses:

1. Living usually on seashore, a species will have succulent (fleshy) leaves.
2. If the same species is moved toward interior (on inland, nonsaline areas), it will develop thin leaves.
3. If the species that usually vegetates in interior (nonsaline) environments is moved on seashore, it will acquire thicker leaves than those it has in inland areas.

Lésage suggested that seashore has, among other effects, the capacity of increasing leaf thickness. He took into his study 90 species collected from nature and finally compared the leaves of 85 species having two mentioned varieties (maritime and inland) and concluded that 54 of species are thicker in maritime form, 27 are indifferent, and 4 species are thicker in inland variant. He clustered these findings in several groups.

First group – Species that displayed a thicker leaf on seashore may be further divided in:

1. Plants that are often found in interior than on littoral: *Osmunda regalis*, *Ruscus aculeatus*, *Polygonum aviculare*, *Atriplex hastata*, *Beta vulgaris*, *Ranunculus sceleratus*, *Nasturtium officinale*, *Spergularia rubra*, *Samolus valerandi*, *Linaria vulgaris*, *Senecio vulgaris*, etc.
2. Littoral plants: *Salicornia herbacea*, *Atriplex portulacoides*, *Beta maritima*, *Cakile maritima*, *Eryngium maritimum*, *Crithmum maritimum*, *Glaux maritima*, *Armeria maritima*, *Plantago maritima*, *Inula crithmoides*, etc.

Second group – Species that remained indifferent:

1. Inland (interior) plants: *Scolopendrium officinale*, *Festuca rubra*, *Alisma plantago*, *Triglochin palustre*, *Hypericum perforatum*, *Lamium purpureum*, *Betonica officinalis*, and *Plantago major.*

2. Littoral plants: *Psamma arenaria*, *Spartina stricta*, *Glyceria maritima*, *Ruppia maritima*, *Triglochin maritimum*, *Suaeda maritima*, *Althaea officinalis*, and *Euphorbia peplis*.

Third group – Species that have a thicker leaf for inland (interior) variant: *Asplenium trichomanes*, *Medicago lupulina*, *Convolvulus arvensis*, and *Galeopsis ochroleuca*.

From this classification, he concluded that, in case of first group, an interior (inland) plant growing on seashore achieves thick leaves; conversely, a plant from seashore when cultivated in interior (nonsaline) area acquires thinner leaves.

Lésage included then in his study the following histological features in relation to leaf anatomy: epidermis, the external cell wall of epidermal cells (here including the thickness of cuticle), mesophyll (to check which tissue of it is involved in conferring thickness), nervures, vessels (their diameter), secretions, chlorophyll, and its distribution within cells. In respect with compared anatomical observations, he concluded that:

1. Epidermal cells (as well as stomata and trichomes) have no clear relevance in relation to the influence of sea. The single exception is the vezicular hairs (nominated by Lésage as *papilles*, but they represent without doubt the well-known vezicular hairs of halophytic chenopods).
2. The external cell wall of epidermal cells shown no clear differences in maritime and inlands forms.
3. Mesophyll (and palisade tissue) can increase its thickness by enlargement of volume of all cells or by formation of a large number of cell layers; these variations may affect all mesophyll or a part of it (palisade tissue). Within the 54 species found to have thicker leaves, 11 species presented an equal development of all elements; 7 species indicated a development in volume and length of palisade tissue, without increasing the number of leaf layers; 5 species recorded an increase in number of palisade layers; and 31 species shown an increase in volume and length of palisade tissue as well as a higher number of palisade layers. He concluded that the thickness of leaves of maritime variants is based on the large development of palisade tissue.
4. Nervures show nothing but a discrete increase in dimensions in the case of thicker leaves.
5. Vessels diameter revealed very subtle or no differences between maritime and inland individuals.
6. Secretions (calcium oxalate, tannin) do not shown significant differences between the two variants.
7. Amount of chlorophyll generally recorded no important differences between maritime and inland individuals; in the rare situations were differences were significant, the maritime variants have the tendency of having less chlorophyll.

Lésage (1890) shown that in *Eryngium maritimum*, *Aster tripolium*, *Thesium humifusum* (Fig. 8), and *Linum grandiflorum*, the leaves are more succulent in individuals collected from littoral than from inland (nonsaline areas) cells.

Lésage concludes his study as follows:

1. Plants that vegetate on seashore acquire thicker leaves than would in inland (nonsaline) areas. Nevertheless, he concludes that this rule does not apply to all species.
2. In plants that manage to deal with salinity of sea, palisade cells are very developed. The thickness of leaf increases, following the extension of palisade cells; accordingly, the number of mesophyll layers may increase or can remain unchanged. If the leaf maintains more or less the same thickness in different situations, the palisade develops in such manner in which the ratio between palisade tissue and mesophyll is greater on seashore.
3. Intercellular spaces greatly reduce in leaves of littoral plants.
4. Chlorophyll tends to be less abundant in cells of plants vegetating on seashore. However, this finding is less rigorous than previous conclusions, as it applies to plants that subjected often to the influence of sea tide.

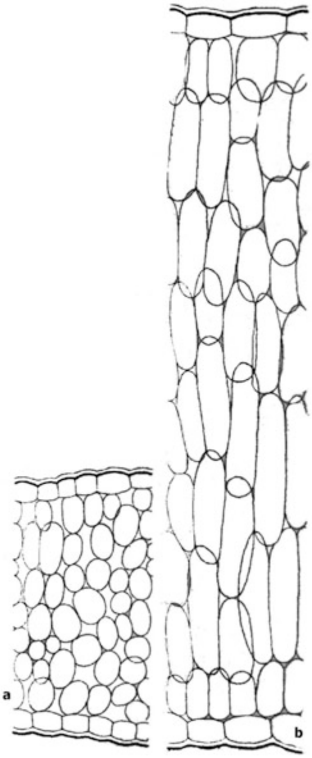


Fig. 8 Cross sections through the leaves of *Thesium humifusum*: (**a**) plants collected from inland, nonsaline areas and (**b**) maritime plants (Lésage 1890)

5. Leaf modifications, such as succulence, development of palisade tissue, and reduction of meatuses and chlorophyll, can be replicated under experimental conditions, using cultures with different salt concentrations.

Warming (1897) evidenced succulence in various species of halophytes; many of investigated species have succulent or narrow-reduced leaves (Fig. 140), a xeromorphic adaptation (Grigore et al. 2014). Warming (1897) found water storage tissue in the leaf structure of many halophytes: *Tournefortia gnaphalodes*, *Scaevola plumieri*, *Borrichia arborescens*, *Philoxerus vermiculatus*, *Remirea maritima*, *Euphorbia buxifolia*, and *Haloxylon ammodendron*.

He described several types of water storage tissue, based on his anatomical observations on investigated species:

(a) The epidermis is, after Westermaier (1881), commonly perceived as a water tissue. However, it is weakly chlorophyll-containing in many of the investigated species, as far as can be seen on the analyzed cross sections, for example, *Heliotropium curassavicum*. In some few cases, epidermis becomes particularly tall with large cell, so it can be assumed that it works especially as a water tissue, e.g., *Juncus gerardi*, *Ionidium buxifolium* (Fig. 9), *Dolichos axillaris* (Fig. 10), *Ruellia monanthos*, *Canavalia obtusifolia*, and *Diodia radicans*. However, following Westermaier's opinion, Warming has not observed such epidermis,

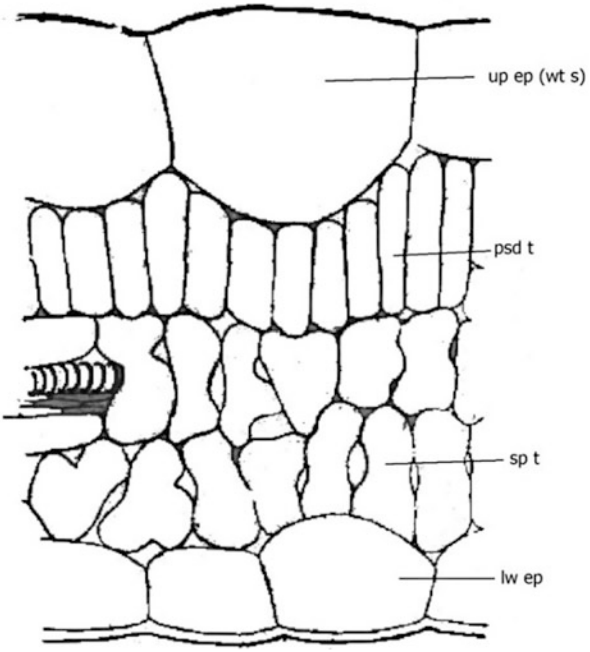


Fig. 9 Cross section through the leaf of *Ionidium buxifolium* (up ep wt s, upper epidermis with water storage function; psd t, palisade tissue; sp t, spongy tissue; lw ep, lower epidermis) (Denis 1919)

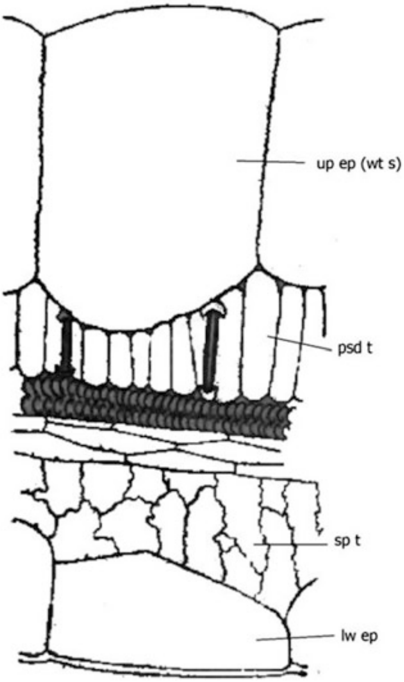


Fig. 10 Cross section through the leaf of *Dolichos axillaris* (up ep wt s, upper epidermis with water storage function; psd t, palisade tissue; sp t, spongy tissue; lw ep, lower epidermis) (Denis 1919)

and only in two species he found mucous membranes. These building conditions appear more significant to xerophytes. Water-storing hairs (salt hairs, vezicular hairs) are found in *Atriplex* species (Figs. 90, 91, 92, 93, 94, 95, 99, 100, 101, 174, and 175).

(b) Hypodermic water tissue occurs in certain species, usually only on one side, rare on both. On the upper side, water tissue is present in slight extent in *Lippia nodiflora* (Fig. 177) and *Erithalis fruticosa* and well-developed in *Remirea maritima* (Fig. 176). On lower side of epidermis, hypodermic water tissues occur in *Euphorbia buxifolia* (Fig. 172) and *Philoxerus vermiculatus* (Fig. 173). On both sides, hypodermic water tissue is found in *Eryngium maritimum* (Fig. 161) and *Atriplex halimus*.

(c) The water tissue extends between the two epidermises, surrounding the nervure network. This building condition is found in *Poaceae*, *Chenopodiaceae*, and other plants that have Kranz anatomy type in the leaf.

(d) The water tissue is in the middle of the leaf surrounded by all sides by chlorenchyma *Acicarpha spathulata* (Fig. 148), *Atriplex hastata*, *Alisne (Halianthus) peploides*, *Silene nicaeensis*, *Conocarpus erecta* (Fig. 149), *Inula crithmoides* (Fig. 27), *Aster tripolium* (Figs. 150 and 152 – where the isolateral character of the leaf may vary depending on the level of cross section through the leaf), *Suriana maritima* (Fig. 153), *Beta vulgaris*, *Cakile aequalis* (Fig. 154), *Cakile maritima* (Fig. 155), *Crambe maritima*, *Heliotropium currasavicum*, *Polygonum* *maritimum*, *Bupleurum tenuissimum*, *Silene otites*, *Crucianella maritima*, *Statice limonium*, *Statice rariflora*, *Medicago marina* (Fig. 156), *Malcolmia littorea*, *Polygala cyparissias*, *Convolvulus soldanella*, *Sedum anglicum*, *Halocnemum strobilaceum*, *Sesuvium portulacastrum* (Fig. 164), *Borrichia arborescens* (Fig. 165), *Zygophyllum album*, *Batis maritima* (Fig. 166), *Echinophora spinosa*, *Triglochin maritimum*, *Salicornia*, *Salsola*, and *Haloxylon.*

(e) Tracheids without contact with the conducting tissue located in the palisade tissue: *Salicornia*.

(f) Shorter, more isodiametric, thickened, and swollen tracheids associated with the nerves either with their sides or more frequently with their ends: together with genuine water tissues, in *Batis*; much more common is the mangrove plants (see the subsection with mangroves).

Succulence has been observed in many halophytes vegetating in Romanian saline environments (Grigore 2008; Grigore and Toma 2008a, c, 2010a, b; Grigore et al. 2012a, b; Ivan et al., 2013; Grigore et al. 2014) and in Mediterranean salt marshes (Grigore et al. 2011a, b, 2012b, 2013, 2014).

Grigore et al. (2014) underlined that succulence is a distinctive adaptation found in halophytes; it is built as a water storage tissue; and sometimes a well-developed palisade tissue may contribute to the succulent appearance of halophytes. Succulence is well noticed particularly in *Chenopodiaceae* species.

Grigore et al. (2014) and Grigore and Toma (2017) proposed several groups of succulent halophytes, based on the position of water storage tissue in respect with chlorenchymatic tissues (C_3 and C_4 photosynthetic pathways) and with epidermis.

(a) C_3 halophytes with articulated segments: *Salicornia europaea* (Figs. 11 and 12), *S. ramosissima* (Fig. 13), *Halocnemum strobilaceum*, *Sarcocornia fruticosa* (Fig. 14), and *Arthrocnemum macrostachyum* (Fig. 15). These species are

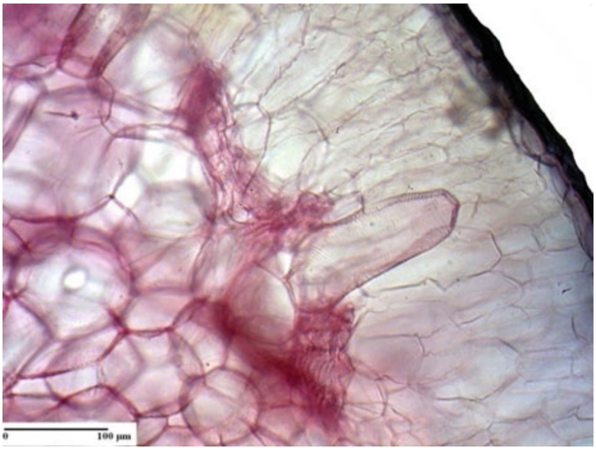


Fig. 11 Cross section through the fleshy segments of *Salicornia europaea* (Grigore and Toma 2017)

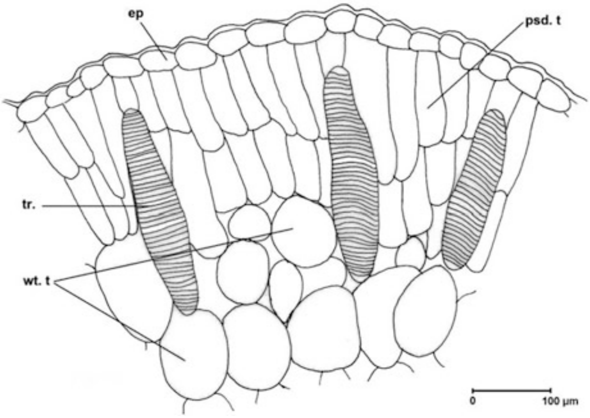


Fig. 12 Cross section through the fleshy segments of *Salicornia europaea* – general aspect; ep, epidermis; psd. t, palisade tissue; tr., tracheid; wt. t, water storage tissue (Grigore and Toma 2017)

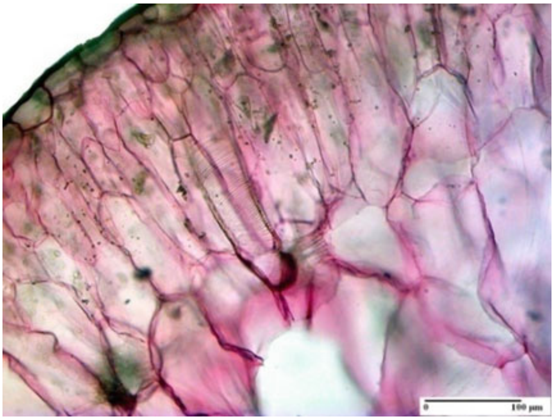


Fig. 13 Cross section through the fleshy segment of *Salicornia ramosissima* (Grigore and Toma 2017)

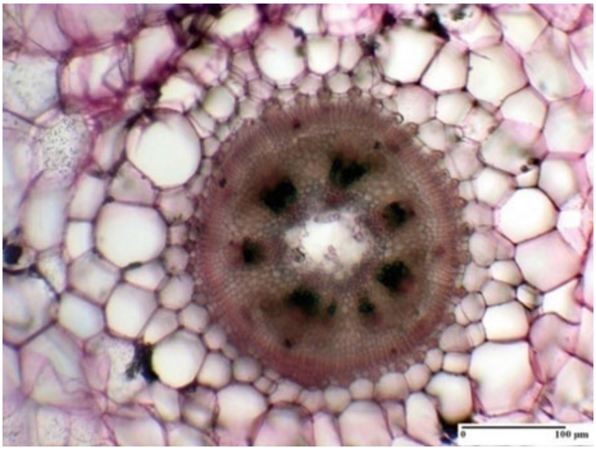


Fig. 14 Cross section through the fleshy segment of *Sarcocornia fruticosa* (Grigore and Toma 2017)

Fig. 15 Cross section through the fleshy segment of *Arthrocnemum macrostachyum* (Grigore and Toma 2017)

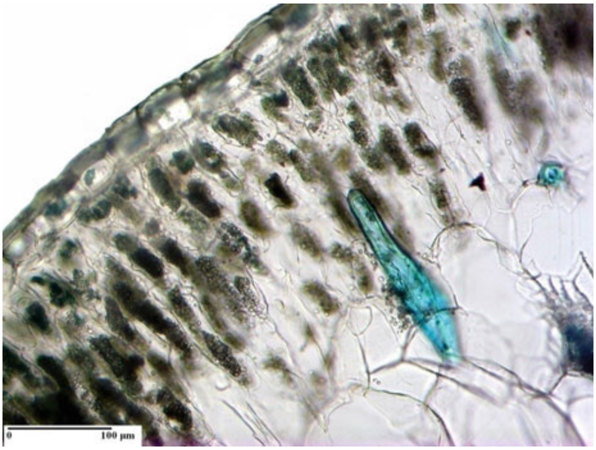
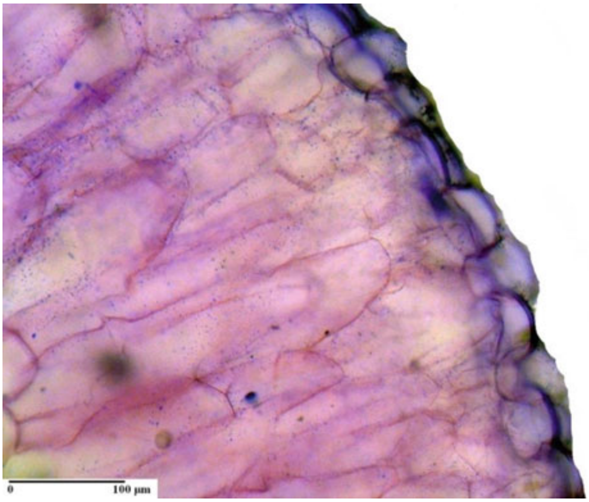


Fig. 16 Cross section through the lamina of *Suaeda maritima* (Grigore and Toma 2017)



apparently leafless, and the developed water tissues contribute to succulent (fleshy) aspect of their habitus.

(b) C_3 species with small, cylindrical, or flattened leaves, where water storage tissue dominates an important volume of leaves: *Suaeda maritima* (Fig. 16), *S. spicata* (Figs. 17 and 18), *Bassia hirsuta* (Fig. 19), *B. sedoides* (Figs. 20 and 21), and *Halimione portulacoides* (Fig. 22). Succulence was also evidenced in *Plantago crassifolia* (Fig. 23) and *P. tenuiflora* (Figs. 24 and 25), *Plantago maritima* (see Fig. 26), in *Inula crithmoides* (Fig. 27), *Spergularia media* (Figs. 28 and 29), *Crithmum maritimum* (Fig. 30).

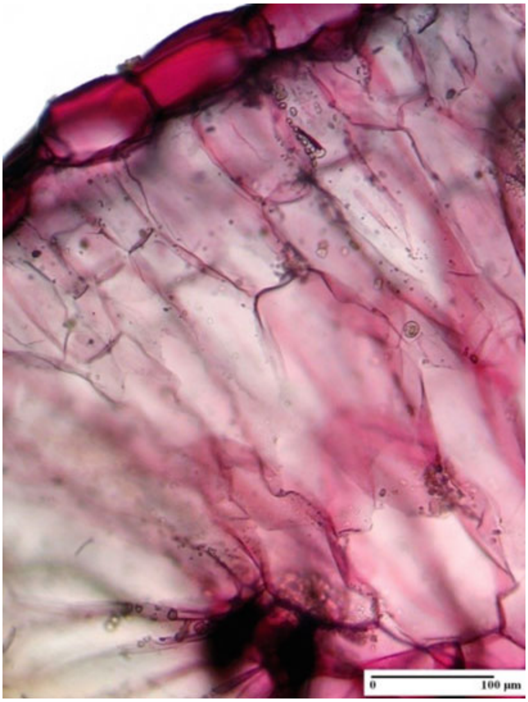


Fig. 17 Cross section through the lamina of *Suaeda spicata* (Grigore and Toma 2017)

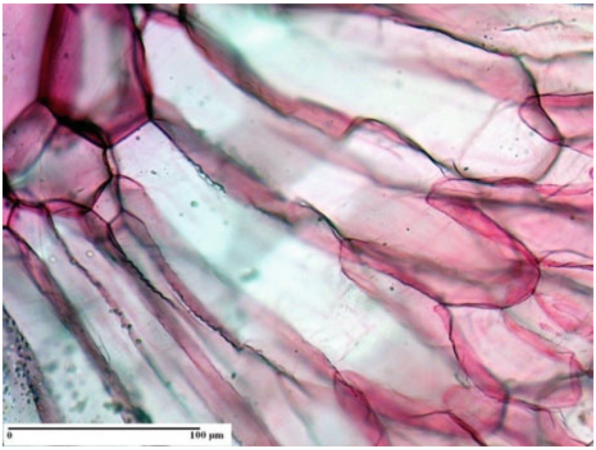


Fig. 18 Cross section through the lamina of *Suaeda spicata* (Grigore and Toma 2017)

(c) C_4 succulent chenopods halophytes: the water storage tissue is confined to the center of the leaf; it is clearly and functionally delimited toward exterior by two typical chlorenchymatic tissues found in C_4 species: *Petrosimonia oppositifolia*

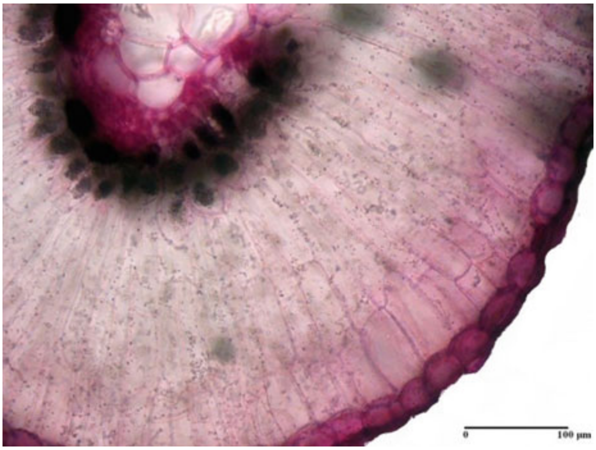


Fig. 19 Cross section through the lamina of *Bassia hirsuta* (Grigore and Toma 2017)

Fig. 20 Cross section through the lamina of *Bassia sedoides* (Grigore and Toma 2017)

(Fig. 31), *P. triandra* (Figs. 32 and 33), *Camphorosma annua* (Figs. 34 and 35), *Salsola oppositifolia* (Figs. 36 and 37), *S. kali* (Fig. 38), *Suaeda splendens* (Fig. 39) and Iranian species of *Bassia turkestanica* (Fig. 40), *B. pilosa* (Fig. 41), and *B. stellaris* (Fig. 42).

(d) C_3 species with massive water storage cells located within mesophyll cells (*Nitraria retusa*) (Fig. 43).

It has been suggested that succulence plays a role in the dilution of accumulated salts in plant organs and may therefore alleviate the toxic effect of ions in cells, thereby allowing plants to cope with large amounts of salts (Waisel 1972; Grigore 2008; Grigore et al. 2014; Grigore and Toma 2017).

Fig. 21 Cross section through the lamina of *Bassia sedoides* (Grigore and Toma 2017)

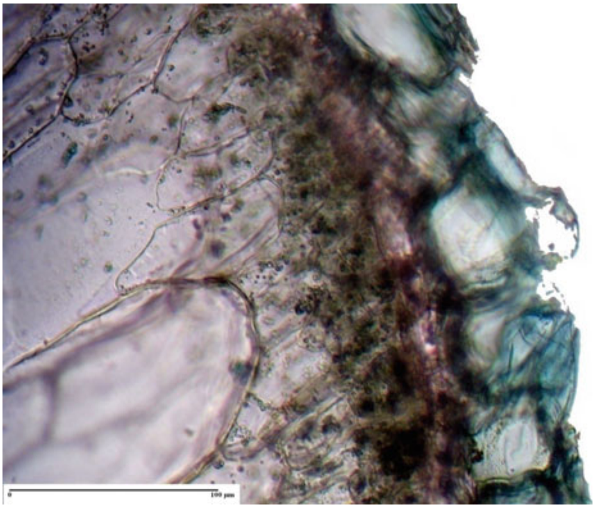


Fig. 22 Cross section through the lamina of *Halimione portulacoides* (Grigore and Toma 2017)

2.2 Mucilage

In some halophytes, mucilage is present within plant cells, as in some xerophytes (Bari et al. 2007). Mucilage is thought to play a role in salinity tolerance in certain halophytic species by regulating water ascent and ion transport (Ghanem et al. 2010). Under salinity exposure, several halophytes increase their mucilage content, such as in *Salicornia brachiata* and *Suaeda maritima* (Jaiswar and Kazi

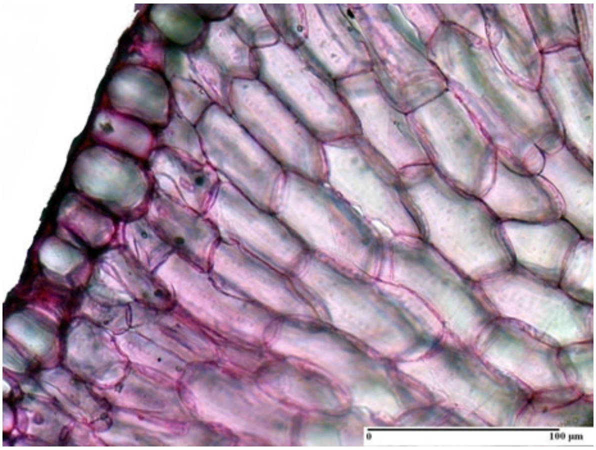


Fig. 23 Cross section through the lamina of *Plantago crassifolia* (Grigore and Toma 2017)

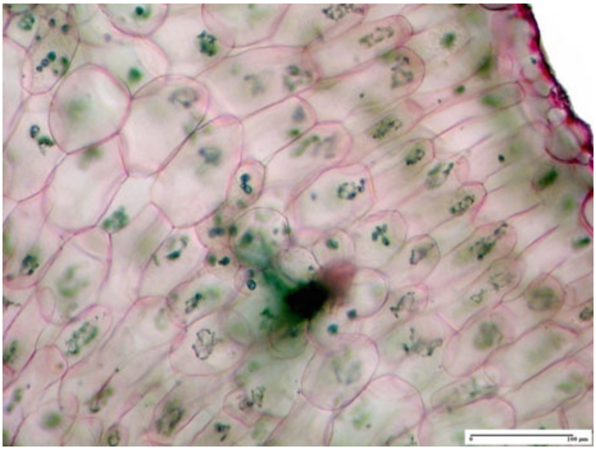


Fig. 24 Cross section through the lamina of *Plantago tenuiflora* (Grigore and Toma 2017)

2016), or mucilage is present in halophytes from natural conditions, such as *Nitraria retusa* (Elhalim et al. 2016). Mucilage cells in many species can increase osmotic pressure, which improve capacity for water retention and water uptake, also providing a relatively wet microenvironment for surrounding photosynthetic cells (Su et al. 2005). In some mangrove species, mucilage cells can occur in leaf hypodermal region of *Bruguiera* and *Rhizophora* (Fig. 199) and beneath the epidermis of *Sonneratia apetala* (Das, 1999).

Fig. 25 Cross section through the lamina of *Plantago tenuiflora* (Grigore and Toma 2017)

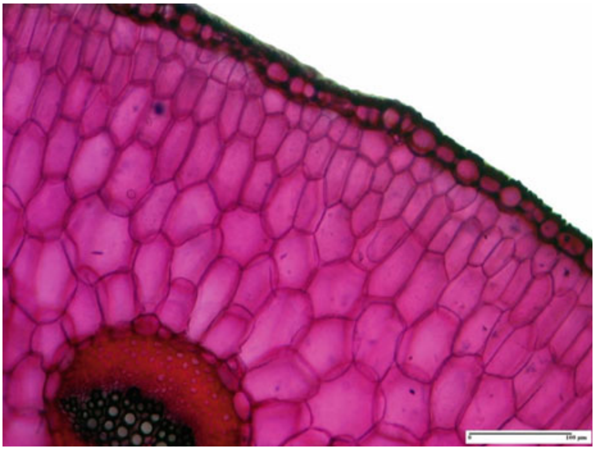


Fig. 26 *Plantago maritima*, cross section through the lamina (Grigore et al., unpublished results)

2.3 Cell Sap

Cell sap of halophytes has to be more concentrated than soil solution, and this can be achieved by accumulation of large quantities of salt (ions) (Grigore et al. 2011c).

2.4 The Palisade Tissue

Palisade tissue in halophytes is often well-developed, as in *Hydrophylax madagascariensis* (leaf of isolateral diplophyll type), *Scaevola plumieri* (leaf isolateral

Fig. 27 Cross section through the lamina of *Inula crithmoides* (Grigore and Toma 2017)

Fig. 28 Cross section through the lamina of *Spergularia media* (Grigore and Toma 2017)

of staurophyll-diplophyll type), *Ipomoea pes-caprae*, *Crambe maritima*, *Honckenya peploides*, *Plantago crassifolia*, *P. coronopus*, and *Beta maritima*, plants that are more or less succulent. In isolateral (cylindrical) leaves, palisade tissue is confined to the leaf periphery, where it forms a variable number of layers; it is clearly delineated from the rest of the leaf, as in *Matricaria maritima*, *Artemisia crithmifolia*, *A. maritima*, *Salsola*, *Traganum nudatum*, *Anabasis*, and *Haloxylon.* In other species, there is subtle transition between palisade tissue and the other tissues within mesophyll, as in *Spergularia*,

Fig. 29 Cross section through the lamina of *Spergularia media* (Grigore and Toma 2017)

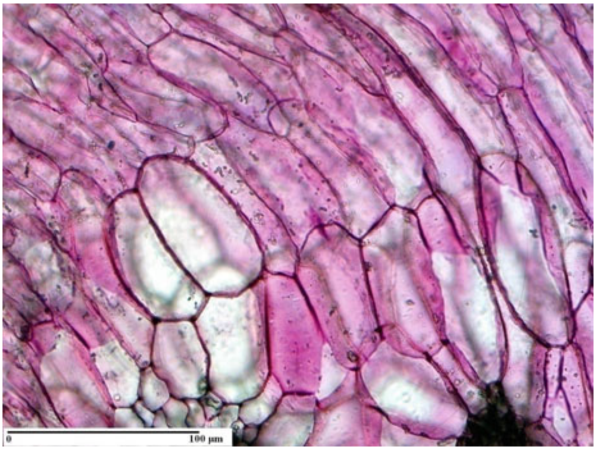


Fig. 30 Cross section through the lamina of *Crithmum maritimum* (Grigore and Toma 2017)

Zygophyllum, *Tetradiclis*, *Atriplex portulacoides*, *Salicornia*, *Arthrocnemum*, and *Suaeda*. According to Schimper (1891), the leaves of plants vegetating in the proximity of the sea in the Barringtonia formation are thicker than those of plants growing in inland areas, because their palisade tissue is more developed.

2.5 The Intercellular Spaces

There are relatively few halophytic species with large intercellular spaces; this is mainly the case of species living in salt marshes (*Triglochin maritima*, *Aster tripolium*,

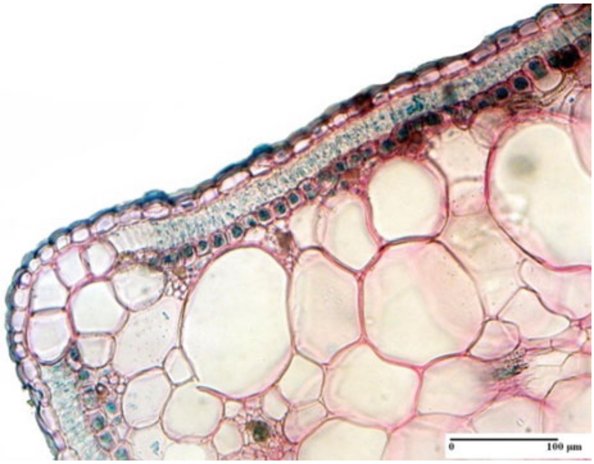


Fig. 31 Cross section through the lamina of *Petrosimonia oppositifolia* (Grigore and Toma 2017)

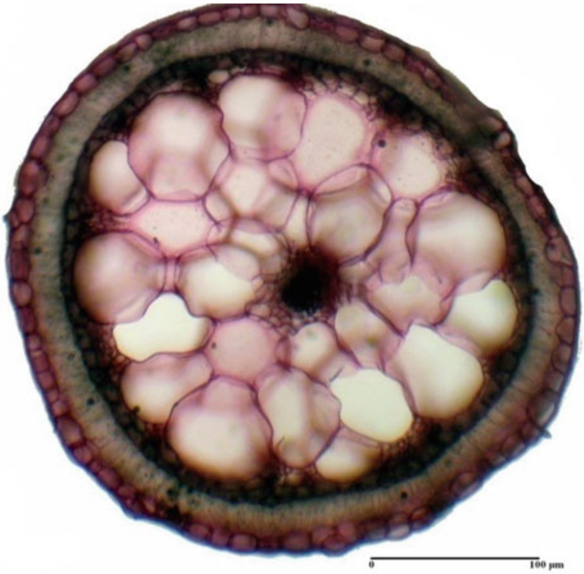


Fig. 32 Cross section through the lamina of *Petrosimonia triandra* (Grigore and Toma 2017)

Glaux maritima), where the cortex is more or less spongy in the stem. In the case of leaf, *Armeria maritima* has in the lower part of mesophyll small-round cells less compact. Chermezon (1910) found that halophyte species with a very compact structure, with very small intercellular spaces, usually vegetate in salt marshes, sea

Fig. 33 Cross section through the lamina of *Petrosimonia triandra* (Grigore and Toma 2017)

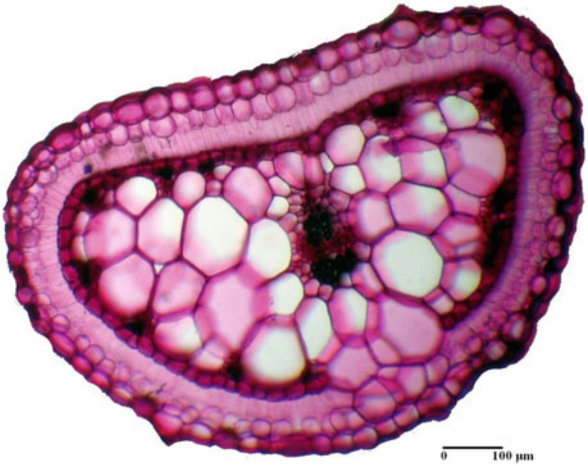


Fig. 34 Cross section through the lamina of *Camphorosma annua* (Grigore and Toma 2017)

rocks, seashores, and saline deserts. He further pointed that inland species have littoral forms with a very compact leaf structure, while littoral plants when cultivated in interior often acquire leaves with less compact internal configuration. It is thought that the reduction of intercellular spaces is a xeromorphous feature and a halophytic adaptation in relation to leaf succulence. In halophytic species from Madagascar, intercellular spaces lack in palisade tissue; sometimes they are absent from lower area of mesophyll (*Tribulus terrestris*, *Hydrophylax madagascariensis*), fairly visible (*Microrhynchus bellidifolius*), or well noticeable (*Ionidium buxifolium*, *Canavalia obtusifolia*, *Dolichos axillaris*, *Vigna lutea*, *Ruellia monanthos*) (Denis 1919).

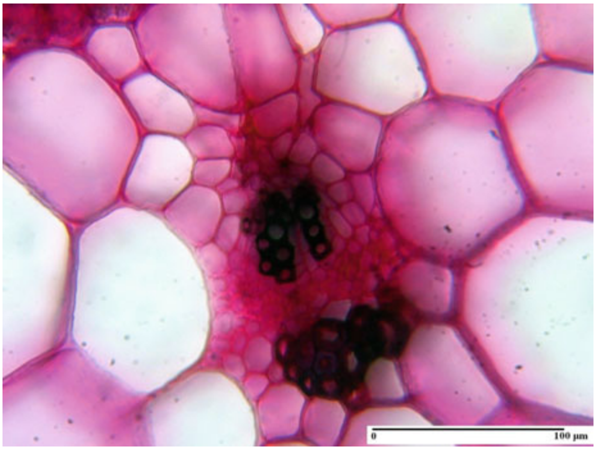


Fig. 35 Cross section through the lamina of *Camphorosma annua* (Grigore and Toma 2017)

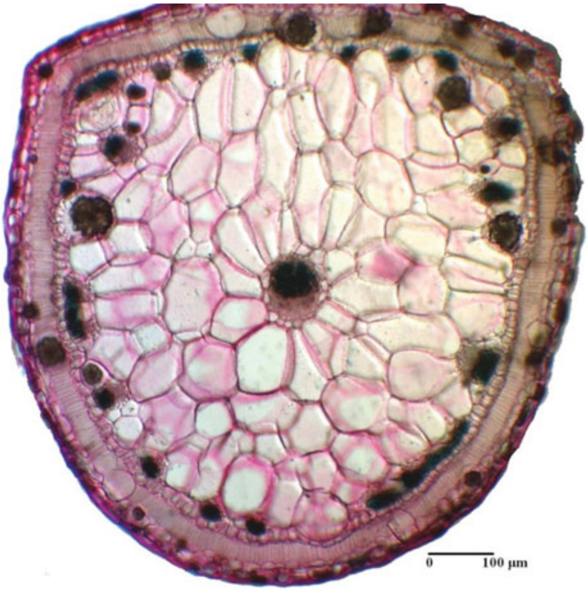


Fig. 36 Cross section through the lamina of *Salsola oppositifolia* (Grigore and Toma 2017)

2.6 Wax

Wax is traditionally considered as an obstacle for limiting the high transpiration by causing a glaucous aspect of leaf surface (Grigore et al. 2014). Wax is found in a rather small number of halophytes, vegetating on maritime rocks (*Crambe maritima*,

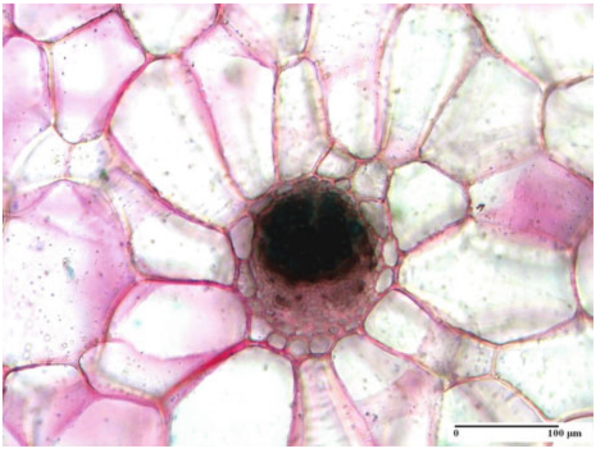


Fig. 37 Cross section through the lamina of *Salsola oppositifolia* (Grigore and Toma 2017)

Fig. 38 Cross section through the lamina of *Salsola kali* (Grigore and Toma 2017)

Silene maritima, *Lathyrus maritimus*), seashores (*Eryngium maritimum*, *Polygonum maritimum*, *Euphorbia paralias*), and maritime dunes (*Dianthus gallicus*, *Linaria thymifolia*, *Ephedra distachya*).

2.7 Tomentum

Generally, most of halophytes are glabrous; some salt-marsh species have a prominent tomentum (*Artemisia gallica*, *A. maritima*), and some *Frankenia* species have short trichomes. In saline deserts there are glabrous species, but also plants enabled with trichomes (*Nitraria tridentata*, *Cressa cretica*, *Salsola tetragona*), but these species are always not as hairy as plants of proper deserts. Halophytic plants from

Fig. 39 Cross section through the lamina of *Suaeda splendens* (Grigore and Toma 2017)

Fig. 40 Cross section through the lamina of *Bassia turkestanica* (Grigore and Toma 2017, photo courtesy of Somayeh Safiallah)

seashores are usually glabrous, but some of them may have short trichomes (*Salsola kali*) or may have a tomentum if they vegetate on sands distant from seashore (*Medicago marina*, *Diotis candidissima*). Developed tomentum is considered to be a xeromorphous adaptation; for this reason is natural that it is found more expressed in plants of dunes.

Fig. 41 Cross section through the lamina of *Bassia pilosa* (Grigore and Toma 2017, photo courtesy of Somayeh Safiallah)

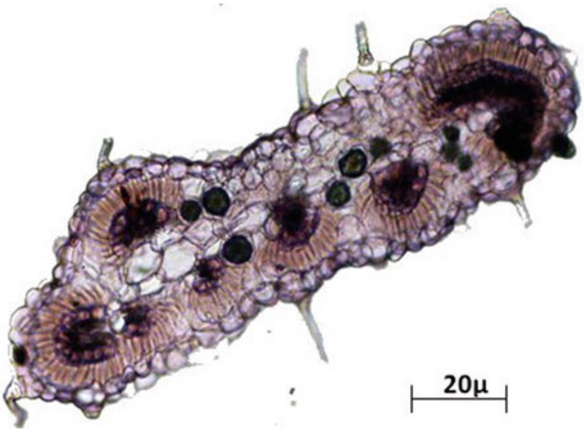


Fig. 42 Cross section through the lamina of *Bassia stellaris* (Grigore and Toma 2017, photo courtesy of Somayeh Safiallah)

Chermezon (1910) made an interesting observation and stated that tomentum and succulence are excluding features: succulent species are almost always glabrous, and hairy species have thin external epidermal walls. Sometimes halophytes have soft or gray hairs, as in *Kochia hirsuta*, *Senecio candicans*, and *Tournefortia gnaphalodes* (Fig. 162). Water-storing hairs (vezicular hairs) are present on leaf surface of several halophytes, such as *Atriplex*, *Halimione (Obione)*, and *Mesembryanthemum*; they have large, spherical, thin-walled

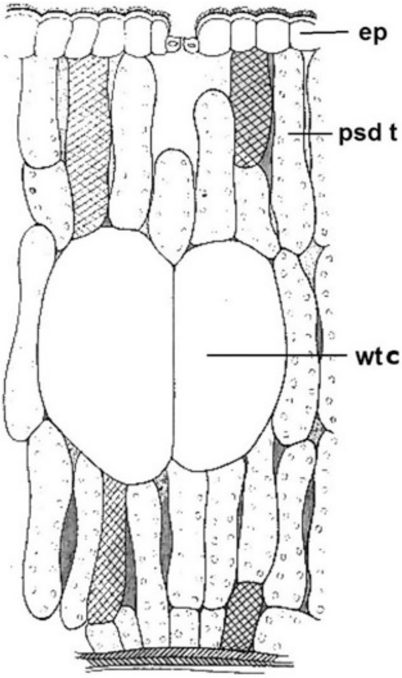


Fig. 43 Cross section through a leaf of *Nitraria retusa* (ep, epidermis; wt c, water storage cells; psd t, palisade tissue) (Volkens 1887)

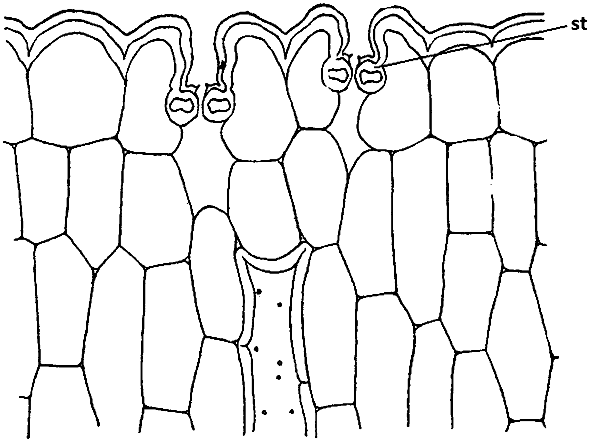


Fig. 44 Sunken stomata (st) in epidermis of fleshy segment of *Arthrocnemum macrostachyum* (Chermezon 1910)

terminal cells (bladders) filled with saline sap. They could be also considered as water reservoirs on leaf surface, apart from their role in removal of salt excess (Grigore and Toma 2017).

2.8 Coriaceous and Glossy Leaves

Coriaceous and glossy leaves can be observed in mangrove trees and shrubs, for instance, in *Rhizophora*, *Bruguiera*, and *Nipa fruticans*, and also in sandy littoral forests. *Limonium gmelini* and *Lepidium crassifolium* also have coriaceous leaves, which can contribute to an increased resistance to harsh environmental conditions such as aridity and salinity (Grigore 2012).

2.9 Stomata

Sunken stomata are generally regarded as a xerophytic mechanism for reducing the transpiration; however, to be effective, this stomatal disposition should be clearly delineated within halophytes leaves.

Chermezon (1910) found sunken stomata in several species of maritime rocks and shingle such as *Crambe maritima*, *Silene maritime*, and *Crithmum maritimum*; from seashore, sunken stomata can be found in *Eryngium maritimum*, *Polygonum maritimum*, and *Euphorbia paralias*. According to Chermezon (1910), sinking of stomata is rather rare in littoral species; this xeromorphic feature is consistent in Mediterranean and desert species. Usually, succulent halophytic species have no sunken stomata. From succulent species, only *Arthrocnemum macrostachyum* (Fig. 44) has stomata clearly sunken; in addition, sinking of stomata seems to be in inverse relation with trichomes development.

Denis (1919) found that halophytes from Madagascar have no completely sunken stomata; several species can be protected by half sunken stomata: *Scaevola plumieri*, *Microrhynchus bellidifolius*, and *Desmodium triflorum*, while others (*Tribulus cistoides*, *Ionidium buxifolium)* have no sunken stomata.

2.10 Tracheoidioblasts (Spiral Cells, Tracheids) and Mangrove Tracheids

In relation to succulence, in several species, tracheids were described: storage tracheids are located in the vicinity of the nervures ends (in mangrove species, *Sonneratia acida* – Fig. 200); in articulated halophytic chenopods (*Salicornia* species), they are isolated in the parenchyma (water storage and palisade tissues) and apparently do not come in contact with nervures (Grigore and Toma 2007a, b; Grigore and Toma 2008a; Grigore et al. 2014; Grigore and Toma 2017).

Their confusing terminology – that sometimes mixed tracheoidioblasts with stereids (see the next section) – has been reviewed and clarified previously (Grigore and Toma 2017), starting from the valuable work of de Fraine (1912). French botanists Duval-Jouve (1868), Mangin (1882), and Dangeard (1888) early observed and described tracheoidioblasts; each of them attributed a specific role to these curious structures. Other botanists tried to add new histological observations and to explain the physiological role of spiral cells (Monteil 1906; Warming 1909; Chermezon 1910; Cooke 1911; Ganong 1903; de Fraine 1912; Grigore et al. 2013, 2014). The spiral-like appearance of spiral cells (see Figs. 45, 46, 47, 48, 49, 50, and 51) convinced many of botanists to use a related ethymological nomenclature: (*les grandes*) *cellules spiralées* (French botanists, Duval-Jouve 1868; Mangin 1882; Dangeard 1888), *spiral cells* (English, de Fraine 1912), *spiral tracheids*, *spicular cells* (translated in English from German, Solereder 1908), *spiraltracheiden*, *spikularzellen* (German, Holterman 1907), *stereïden* (German), and *spiralceller* (Danish, Warming 1891).

Tracheoidioblasts (spiral cells, tracheids) are found especially in halophytic articulated species from *Chenopodiaceae*: *Salicornia europaea* (Figs. 45, 46, and 47), *Salicornia patula* (Fig. 48), *Salicornia australis* (Fig. 49), *Salicornia ramosissima* (Figs. 50 and 51), and *Sarcocornia fruticosa* (Fig. 157) (Grigore et al. 2014; Grigore and Toma 2017).

Different functions have been attributed to tracheoidioblasts (spiral cells, tracheids) in halophytes. Duval-Jouve (1868) suggested an air-storing function (*les cellules aérifères*); Mangin (1882) and van Tieghem (1884) proposed a mechanical role of spiral and underlined that they are not in contact with the stomata. Van Tieghem deals with them as elements of the cortical stereome. De Bary (1884) includes the tracheoidioblasts of *Salicornia* in the category of the scattered tracheids, located outside the vascular bundles; he does not explicitly grant them a particular function, but the simple fact that they are mentioned in this chapter (arrangement of the tracheae and sieve tubes – outside of the vascular bundles) could suggest that their assumed function is in relation to conducting system. Dangéard (1888), who noticed spiral cells in foliar

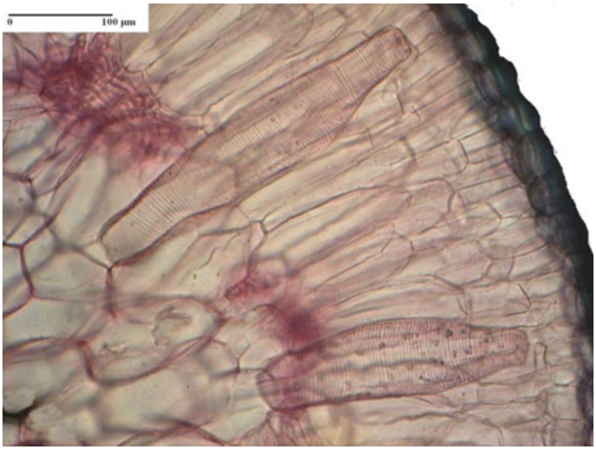


Fig. 45 Tracheoidioblasts in fleshy segments of *Salicornia europaea* (Grigore et al. 2014)

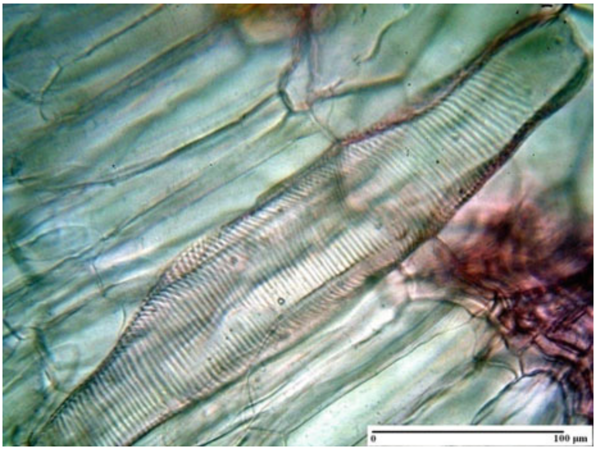


Fig. 46 Tracheoidioblasts in fleshy segments of *Salicornia europaea* (Grigore et al. 2014)

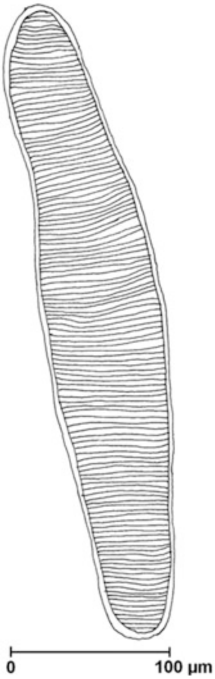


Fig. 47 Tracheoidioblasts in fleshy segments of *Salicornia europaea* (Grigore et al. 2014)

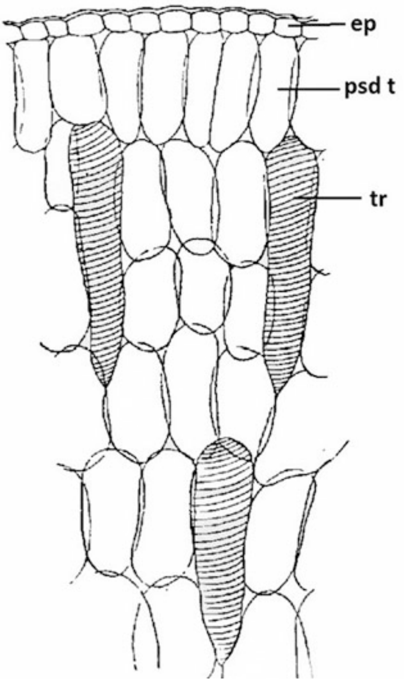


Fig. 48 Tracheoidioblasts (spiral cells) in the fleshy segment of *Salicornia patula* (psd t, palisade tissue; ep, epidermis; tr, tracheoidioblasts) (Monteil 1906)

sheaths of *Salicornia peruviana*, *S. virginica*, and *Arthrocnemum ambiguum*, speculated that they would belong to the cortical stereome.

Ganong (1903) referring on air storage system of *Salicornia herbacea* attributed to tracheoidioblasts an air-storing role, as Cooke (1911) in *Salicornia australis* (Fig. 49).

Holterman (1907) found spiral cells (*spiraltracheiden*) in *Arthrocnemum indicum*, inside the water storage tissue surrounding central cylinder; he ascribed them a role in conducting water toward peripheral regions of the plant.

Monteil (1906) believed that they have an air-storing function (*cellules aérifères*) in *Salicornia patula* (Fig. 48), *S. sarmentosa*, and *S. fruticosa*.

Warming (1909) nominated them water-storing tracheids, as they are filled with water; he considered that they play the same role as the xylem vessels from the vascular bundles. Chermezon (1910) evidenced spiral cells in the succulent articulated segments of *Salicornia fruticosa*; he speculated that these structures have a water storage function.

Several mangrove species (Fig. 201) have terminal tracheids at vein endings: *Sonneratia apetala*, *Sesuvium portulacastrum*, *Avicennia rotundifolia*, *A. corniculatum*, *Bruguiera*, *Ceriops decandra*, and *Excoecaria agallocha* (Das, 1999). They could be regarded as adaptive xerophytic features of the mangroves since tracheids provide mechanical support to the leaves and capillary water storage function.

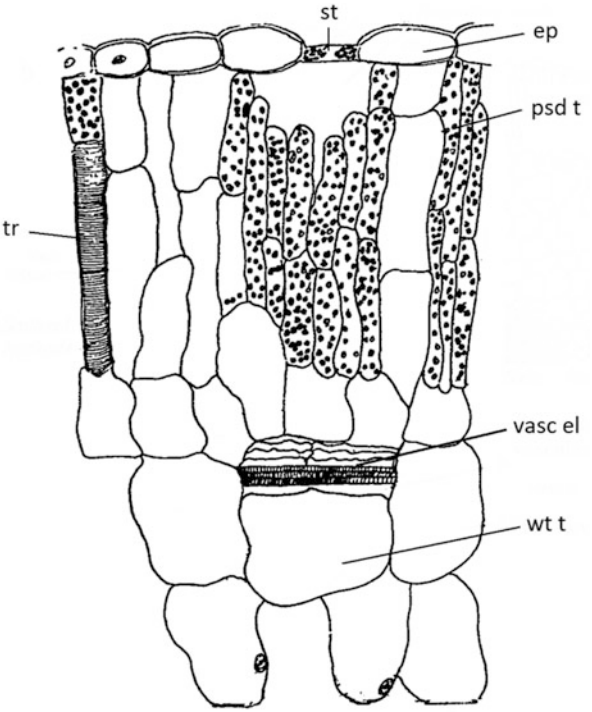


Fig. 49 Tracheoidioblasts (spiral cells) in the fleshy segment of *Salicornia australis* (psd t, palisade tissue; ep, epidermis; tr, tracheoidioblasts; vasc el, vascular elements; wt t, water storage tissue) (Cooke 1911)

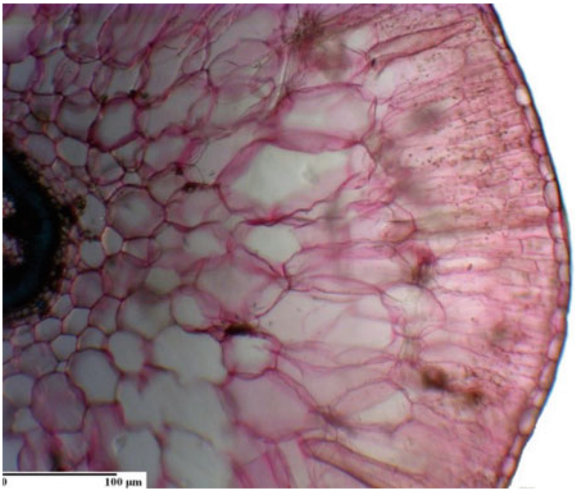


Fig. 50 Tracheoidioblasts in fleshy segments of *Salicornia ramosissima* (Grigore et al. 2014)

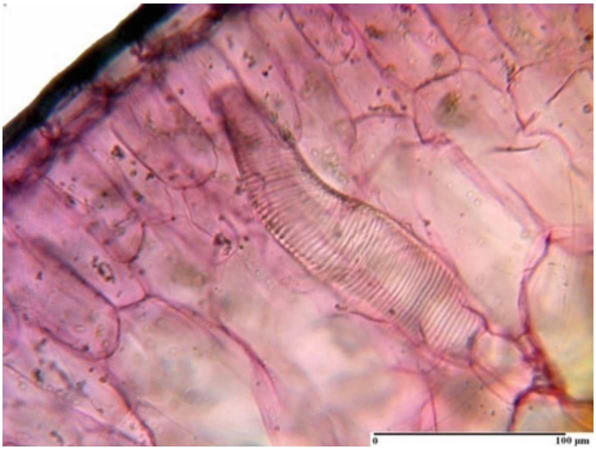


Fig. 51 Tracheoidioblasts in fleshy segments of *Salicornia ramosissima* (Grigore et al. 2014)

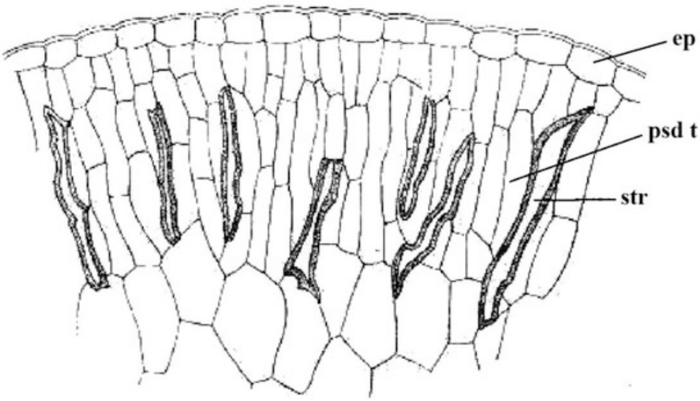


Fig. 52 Stereids (spicular cells) in the fleshy segment of *Salicornia glauca* (psd t, palisade tissue; ep, epidermis; str, stereides) (de Fraine 1912)

2.11 Stereids (Spicular Cells, Sclereids, Idioblasts)

They are found in several chenopods succulent halophytes (*Salicornia glauca*, Fig. 52; *Arthrocnemum macrostachyum*, Figs. 53 and 54; *Sarcocornia fruticosa*, Fig. 55; *Halocnemum strobilaceum*, Fig. 56) and in mangrove species (*Aegialitis rotundifolia*, *Sonneratia*, *Rhizophora*; Fig. 199), which are located in the palisade in water storage tissue. Such elements can be also found in *Limonium* species, in leaf petiole (Fig. 57), leaf sheath (Fig. 58), and lamina (Fig. 59).

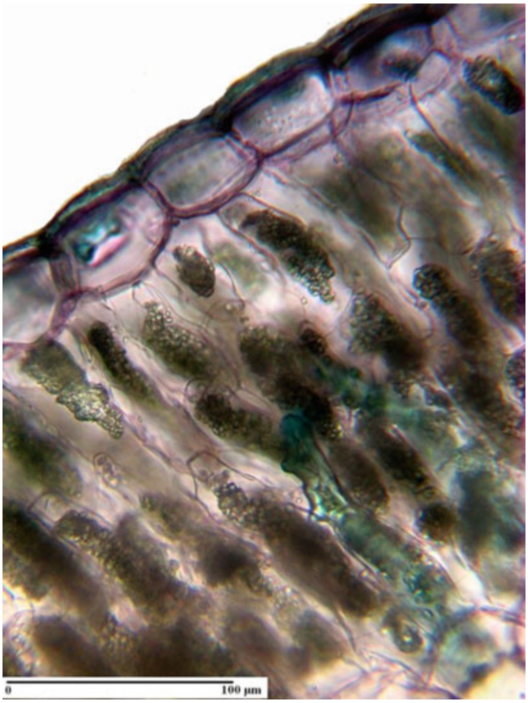


Fig. 53 Spicular cells (stereids) in fleshy segments of *Arthrocnemum macrostachyum* (Grigore et al. 2014)

Fig. 54 Spicular cells (stereids) in fleshy segments of *Arthrocnemum macrostachyum* (Grigore et al. 2014)

They play a mechanical role and might confer the coriaceous aspect of leaves of mangroves and *Limonium* species.

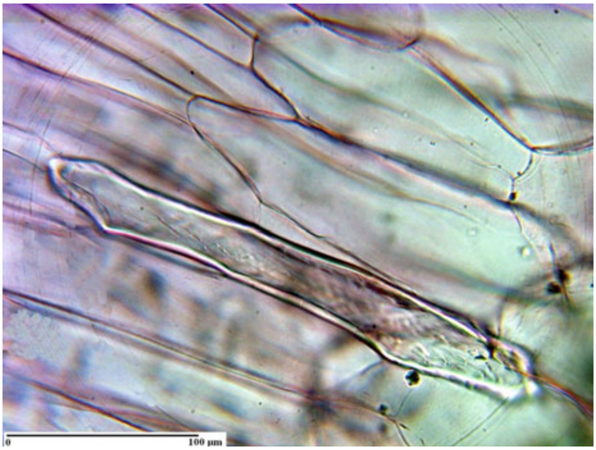


Fig. 55 Spicular cells (stereides) in fleshy segments of *Sarcocornia fruticosa* (Grigore et al. 2014)

2.12 Lignification: The Special Case of Successive (Additional, Supernumerary) Cambia

A general tendency to lignification has been observed earlier especially in xerophytic (desert plants) and halophytic species, and it was correlated with severe climatic conditions in which these species grow (Grigore 2008). This tendency is sometimes correlated to an absence of medullary rays, or, if they exist, they are rare and have thick walls. In some species (*Salsola kali*, *Eryngium maritimum*, *Echinophora spinosa*), there are thorns, especially on leaves, but probably the sand where they vegetate would be involved in the production of the thorns. However, in many halophytes (especially in *Plumbaginaceae*, *Chenopodiaceae*, monocots) there is a significant production of sclerenchyma, at root and stem level (Grigore et al. 2014).

Within these species, halophytic chenopods represent a special case of lignification, as the vegetative organs display successive cambia products. This histological phenomenon that arises in the tertiary structure of these organs produces a huge amount of lignin included in the so-called conjunctive tissue (Grigore and Toma 2005, 2006b, 2007a, b, 2008b, 2017; Grigore et al. 2014).

The phenomenon of successive cambia is primarily known due to successive concentric rings from *Beta vulgaris*. It occurs in many halophytes genera, such as *Atriplex*, *Bassia*, *Chenopodium*, *Petrosimonia*, *Halimione*, *Camphorosma*, *Suaeda*, *Salsola*, *Sarcocornia*, *Salicornia*, (Grigore 2008, 2012; Grigore and Toma 2007a, b, c, 2008a, 2010a, 2017; Grigore et al. 2012a, b, 2014), and *Sesuvium verrucosum* (Abd Elbar 2015).

In short, supernumerary cambia acts as follows: the typical, structure is generated by a normal cambium that produces a few secondary phloemic and xylemic vessels. Afterward an additional (supernumerary) cambium derives from pericycle and generates a ring of fundamental parenchyma, where the vascular bundles are placed

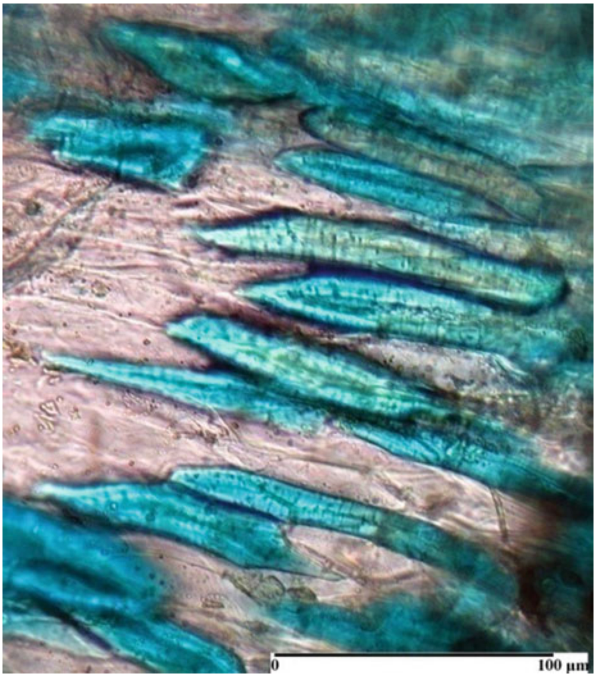


Fig. 56 Spicular cells (stereids) in fleshy segments of *Halocnemum strobilaceum* (Grigore et al. 2014)

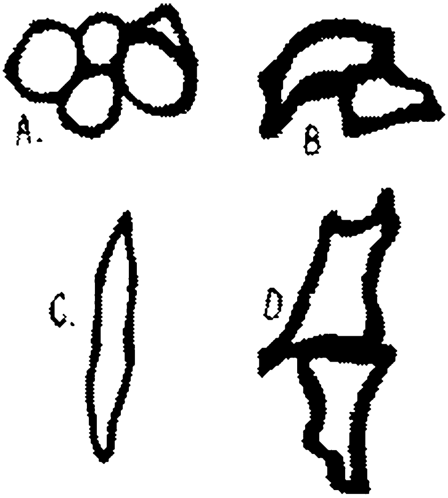


Fig. 57 Spicular cells (stereids) from leaf petiole of *Limonium binervosa*, **A–B**, cross sections; **C–D**, longitudinal sections (de Fraine, 1916)

Fig. 58 Spicular cells (stereids) from leaf sheath of *Limonium binervosa*, **A**, cross sections; **B**, longitudinal sections (de Fraine 1916)

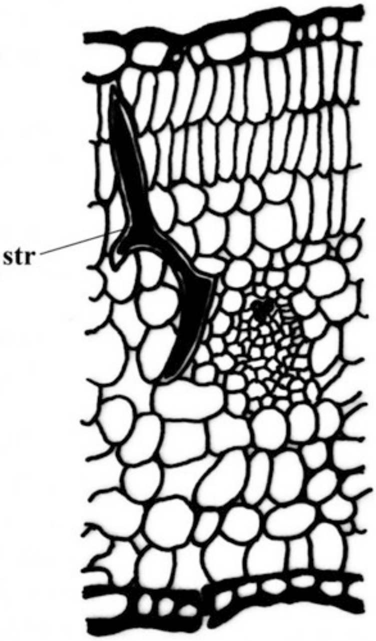


Fig. 59 Spicular cells (stereids, str) from lamina of *Limonium gmelini* – stereid filled with black (Adapted from Moțiu et al. 1987)

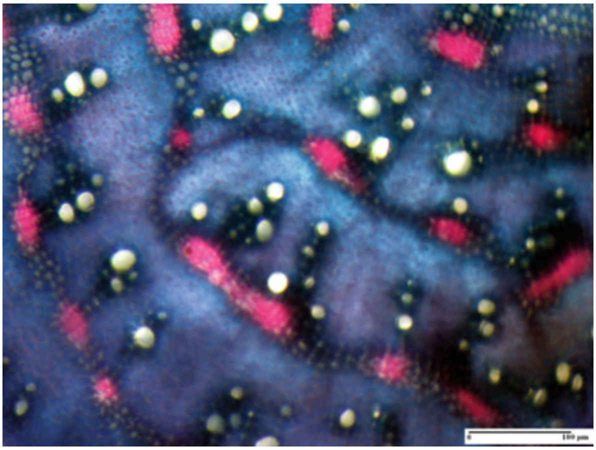


Fig. 60 Successive cambia in root of *Atriplex littoralis* (Grigore and Toma 2017)

usually on a ring, with the phloem outside and the xylem inside. Each cambium is born after that from the phloemic parenchyma produced by the former cambium (Grigore and Toma 2017).

Grigore et al. (2013, 2014) found out that successive (additional) cambia were present in almost all of investigated species from *Chenopodiaceae* in their vegetative organs: *Atriplex littoralis* (Fig. 60), *A. prostrata*, *A. tatarica*, *A. glauca* (Fig. 61), *Bassia sedoides* (Fig. 62), *Camphorosma annua*, *Chenopodium album* (Fig. 63), *Halimione verrucifera* (Fig. 64), *Petrosimonia oppositifolia*, *P. triandra*, *Salicornia europaea*, *S. ramosissima*, *Suaeda maritima*, *S. spicata* (Fig. 65), *S. splendens* (Fig. 66), *Salsola kali* (Fig. 67), and *Sarcocornia fruticosa*.

Despite that there is no consensus on ecological and functional role of successive cambia in halophytes, there is some evidence that lignin deposits are likely to be involved in plant salt tolerance (Liu et al. 2018). Grigore and Toma (2017) suggested that lignin could increase the resistance of the cell walls to the high osmotic pressure found in saline soils.

Grigore and Toma (2006b, 2017) advanced a hypothesis about a possible ecological significance of successive cambia in halophytes. They speculated that the obtained structural configuration could be related to an increased internal surface of the root, considering the increased capacity of retention and “storage” of the saltwater within plant organs. In addition, the cork from periphery of the root could also diminute saltwater uptake. Consequently, salts penetrate slowly in roots, but once arrived there, they would be dispersed in this increased surface, and thus the transport of salts toward upper parts of plant organs (more sensitive to salt) would be delayed. Likely, increasing this surface would inevitably imply a dispersion area for salts, which would be diluted, thus alleviating their harmful effect to the plant. Therefore, successive cambia phenomenon can be considered – based on its effects (numerous vessels, high “internal” surface) as a beneficial “compromise” for the

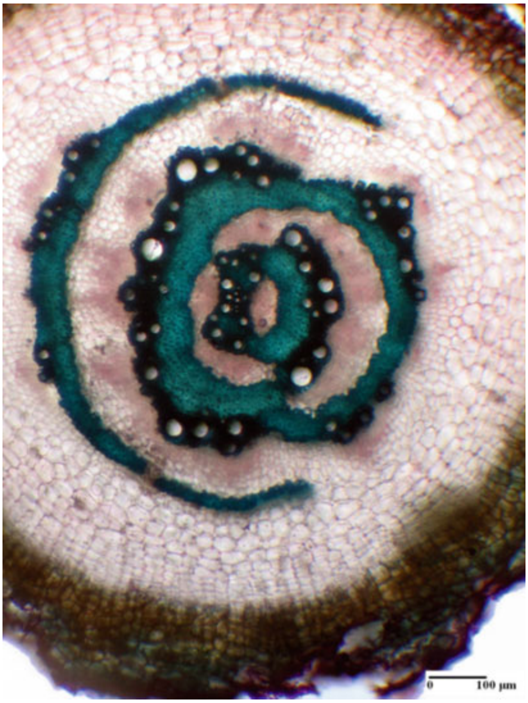


Fig. 61 Successive cambia in root of *Atriplex glauca* (Grigore and Toma 2017)

Fig. 62 Successive cambia in root of *Bassia sedoides* (Grigore and Toma 2017)

Fig. 63 Successive cambia in root of *Chenopodium album* (Grigore and Toma 2017)

Fig. 64 Successive cambia in root of *Halimione verrucifera* (Grigore and Toma 2017)

plant between the growth limitation necessity (controlled by the abscisic acid ABA) and the necessity of imposing dilution strategies of salts in the plant's organ, except perhaps the higher regions of stem (Grigore and Toma 2017).

Fig. 65 Successive cambia in root of *Suaeda spicata* (Grigore and Toma 2017)

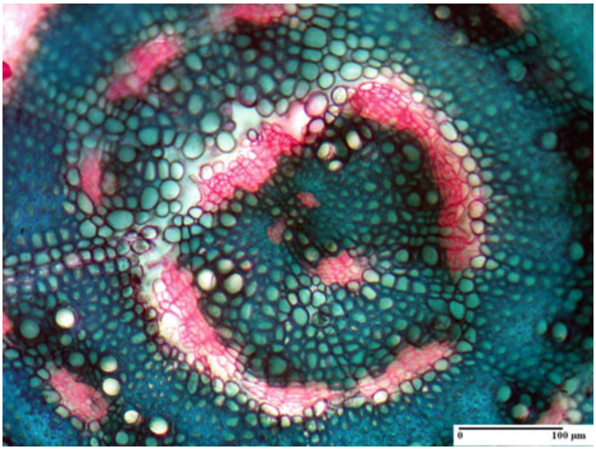


Fig. 66 Successive cambia in root of *Suaeda splendens* (Grigore and Toma 2017)

2.13 Salt-Secreting Structures

Salt-secreting structures (salt hairs and salt glands) are heterogeneously distributed in halophytes (Grigore 2008; Grigore and Toma 2010b), and the halophytes that possess such devices are called crynohalophytes (recretohalophytes). Salt secretion is a complex mechanism in halophytes, involving specialized and often elaborated

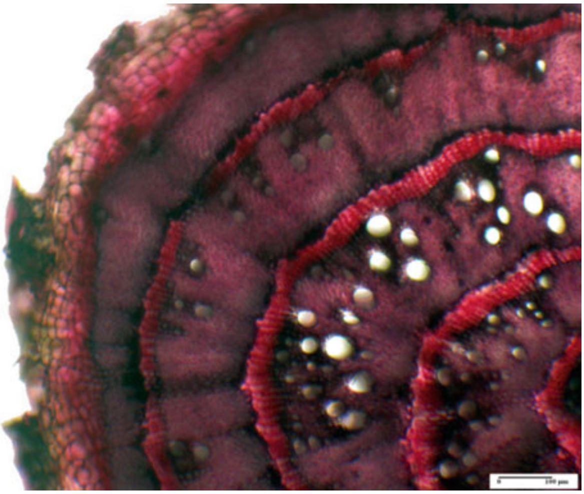


Fig. 67 Successive cambia in root of *Salsola kali* (Grigore and Toma 2017)

structures created during evolution to remove the excess of salts from plants shoots (Grigore and Toma 2010b; Grigore et al. 2012a).

Recretohalophytes can secrete salt from the plant body to the outside through salt glands (as in *Plumbaginaceae*, *Tamaricaceae*, *Primulaceae*, *Frankeniaceae* halophytes) or into salt bladders for temporary storage, and then the salt will scatter from salt bladders when it encounters strong winds or other external stimuli (Chen et al. 2018).

Salt-secreting structures, namely, salt bladders and salt glands, are functional devices that directly secrete ions out of the plant, and they are also notable for their presence in recretohalophytes and absence from other halophytes and all non-halophytes (Shabala et al. 2014; Yuan et al. 2016).

According to Chen et al. (2018), there are 65 halophyte species grouped in 11 families that have salt glands (Table 1). Other halophytes have salt hairs (vezicular, bladders, salt bladders) and belong to *Chenopodiaceae* (*Amaranthaceae*) and single bladder epidermal cells (occurring in *Aizoaceae*).

Grigore and Toma (2010b) have adapted, modified, and completed a previous definition of Fahn (1988) regarding secretory tissues in vascular plants, using an integrated anatomical vision in the salt-secreting structures of halophytes.

Salt-secreting structures of halophytes can be divided as follows (Grigore and Toma 2010b, 2017):

1. Structures (salt hairs) that eliminate (secrete) salts into the vacuole, as in *Atriplex* and *Chenopodium* species. Salt is secreted into a central vacuole of the bladder cell of the leaf hair. Bladders are located on top of a narrow stalk, consisting of one to three cells. Increasing of bladder cell volume is based on formation and expansion of a central vacuole;

Table 1 Distribution of salt-secreting structures in halophytes

Family	Taxa	Observations
Salt glands		
Plumbaginaceae°	*Limonium gmelinii*°, *Limonium furfuraceum*°, *Limonium girardianum*°, *Limonium narbonense*°, *Limonium latifolium*, *Plumbago capensis*, *P. europaea*, *Armeria maritima*, *Aegialitis**, *Limoniastrum*	*Mangrove species °Several *Limonium* species investigated by us
Tamaricaceae	*Tamarix* sp. *(T. nilotica*, *T. passerinoides*, *T. aphylla)*, *Reaumuria palaestina*, *Myricaria**	*Rare on saline soils
Verbenaceae	*Avicennia marina**	*Mangrove species
Primulaceae	*Glaux maritima**, *Samolus littoralis*, *Samolus repens*, *Jacquinia armillaris*°	*Also investigated by us °Recently described (Kuster et al., 2018)
Frankeniaceae	*Frankenia laevis**, *Frankenia pulverulenta*, *Frankenia hirsuta*, *Frankenia reuteri*, *Frankenia grandifolia*, *Frankenia pauciflora*, *Frankenia revoluta*, *Hypericopsis*	*Also investigated by us
Combretaceae	*Laguncularia racemosa**	*Mangrove species, where is debatable if described glands in the upper layer of mesophyll are involved in salt secretion
Acanthaceae	*Acanthus*, *Neuracanthus*	
Sonneratiaceae	*Sonneratia caseolaris*	
Scrophulariaceae	*Cordylanthus*, *Castilleja*	The nature of salt glands needs further clarification
Lamiaceae	*Clerodendrum inerme (Volkameria inermis)*	Saenger (2002)
Convolvulaceae	*Cressa*, *Ipomoea**	*Only in species from saline soils
Myrsinaceae	*Aegiceras**	*Mangrove species
Poaceae	*Aeluropus**, *Distichlis*, *Spartina*, *Bouteloa*, *Buchloe*, *Cynodon*, *Coelochrym*, *Crypsis*, *Dactyloctenium*, *Dinebra*, *Eleusine indica*, *Enteropogon*, *Sporobolus*, *Tetranche*, *Tetrapogon*, *Andropogon*, *Brachiaria*, *Cenchrus*, *Chrysopogon*, *Coix*, *Dichanthium*, *Digitaria*, *Echinochloa*, *Erianthus*, *Hyparrhenia*, *Panicum*, *Paspalum*, *Paspalidium*, *Saccharum*, *Setaria*, *Sorghum*, *Tricholaena*, *Porteresia coarctata*, *Zoysia*	*Several species also investigated by us
Salt hairs (vezicular hairs, bladders, salt bladders)		
Chenopodiaceae	*Atriplex**, *Chenopodium*, *Halimione**, *Salsola*	*Several species also investigated by us

(continued)

Table 1 (continued)

Family	Taxa	Observations
Epidermal bladder cells		
Aizoaceae	*Dorotheanthus**, *Mesembryanthemum**, *Psilocaulon**°	*Only in species from saline soils *°Rare on saline soils

Based on Breckle (1995), Gorham (1996), Breckle (2002), Grigore and Toma (2010b), Grigore et al. (2014), and Grigore and Toma 2017; Chen et al. 2018
For detailed clarifications regarding the nomenclature of salt-secreting structures, see Grigore and Toma's (2010b, 2017) monograph.

2. Structures (glands) that eliminate salts outside of the cells. Here, two types of glands may be included:
   (a) Glands of monocots – they are bicellular and monocellular glands and found mainly on *Poaceae* species.
   (b) Glands of dicotyledons – they are multicellular glands, such as those of *Limonium*, *Tamarix*, *Avicennia*, *Frankenia*, *Cressa cretica*, and *Lavatera arborea*.
3. Epidermal bladder cells from *Aizoaceae* (*Mesembryanthemum* species), which seems to occupy an intermediary position within salt secretory structures. Some authors have included these bladder cells in the group of secretory trichomes, but they look morpho-anatomically as lacking the stalk cell, thus maintaining only the terminal cell (the bladder of salt hairs).

2.13.1 Salt Glands of *Plumbaginaceae*

A typical trait of *Plumbaginaceae* is the presence of glands: chalk glands (Mettenius or Licopoli glands – salt glands) and mucilage glands located on leaves and stems (Grigore and Toma 2010b). The structure of these glands was frequently differently interpreted by some authors, although these controversies are related rather to details than their basic structure. The different reported numbers consisting cells of glands could be rather related to the inconsistent terminology of types of cells than to a real high diversity within recretohalophytes from *Plumbaginaceae*. Grigore and Toma (2016) reviewed the structure of glands in *Plumbaginaceae*, with an emphasis on contribution of Mettenius Licopoli, the two botanists who gave the parallel names of salt glands.

There are two types of glands in halophytic *Plumbaginaceae* (Metcalfe and Chalk 1972).

1. *Chalk (chalk-secreting) glands, also known as Mettenius glands or Licopoli glands ("organs")* (for their nomenclature, see Grigore and Toma 2016), they are located on or in the cavities on the inner side of the leaves and stem and are sometimes surrounded by groups of elongated epidermal cells or by simple trichomes. A typical gland consists of four or eight epidermal cells arranged in palisade surrounded by one or two layers, each made up of four "accessory" cells. These glands have been generally described as chalk glands because they exude

calcium salt and water; calcium salts are sometimes scattered on the leaf or stem surface by rain drops.

2. *Mucilage glands* occur in some species of the *Plumbaginaceae*; they usually comprise a head resting on a head borne on a base consisting of few cells with very thick cuticle-lined walls.

   Chalk glands (Licopoli organs) have been evidenced in *Limonium furfuraceum* (Fig. 68), *Limonium narbonense* (Fig. 69), *Limonium girardianum* (Fig. 70), *Limonium gmelinii* (Figs. 71 and 72), and *Aegialitis annulata* (mangrove species, Fig. 73).

2.13.2 Salt Glands of *Tamaricaceae*

Usually, *Tamarix* species have salt glands with six secretory cells and two collecting cells in a symmetrical structure (Figs. 74 and 75) (Yuan et al. 2016). In *Tamarix aphylla*, salt gland consists of six secreting cells (with dense cytoplasm) and of two extraglandular, collecting cells, intensely vacuolated. Secreting cells have a cuticular "sheath" except for some portions of cellular walls, which are involved in assuring the communication with collecting cells.

Other halophytic species with salt glands include *Reaumuria oxiana* (Fig. 76) (Paulsen 1912), *Reaumuria kermanensis* (Fig. 77) (Brunner 1908), *Reaumuria squarrosa* (Fig. 78) (Brunswik 1920), and *Myricaria germanica* (Fig. 79) (Brunner 1908).

2.13.3 Salt Glands of *Frankeniaceae*

They are glands completely surrounded by cuticular layer, as is the case of *Tamarix* and *Limonium*. They are found in *Frankenia floribunda*, *F. pulverulenta* (Fig. 80), *F. grandiflora*, *F. revoluta*, and *F. laevis* (Fig. 81 and 82).

Fig. 68 Salt glands of *Limonium furfuraceum* (Grigore et al. 2014)

These glands consist of eight cells; six of them are secretory cells and have dense cytoplasm, a high number of small vacuoles, and a large nucleus; the other two cells are collecting cells and have a large central vacuole. The entire complex of cells is covered by a cuticular layer, except for small areas of the walls between secretory and collecting cells (Grigore and Toma 2010b).

2.13.4 Salt Glands of *Mangroves*

Salt extrusion is a very important adaptive strategy of mangroves; it occurs through salt glands in the leaves of *Avicennia officinalis* (Fig. 83), *A. nitida* (Fig. 84), *Acanthus ilicifolius*, *Aegiceras corniculatum* (Fig. 85), *Aegialitis* (see Fig. 73), *Clerodendrum inerme*, and probably *Laguncularia racemosa* (Saenger 2002; Grigore and Toma 2010b) (see Table 1). Salt glands of mangrove species have different numbers of secretory cells: 6–9 cells in *Avicennia officinalis*, 8–12 cells in *A. marina*, 8 in *A. germinans*, and 20–24 in *Aegiceras* (Saenger 2002; Yuan et al. 2016).

2.13.5 Salt Glands of Halophytes from *Primulaceae* Family

Salt glands are found in *Glaux maritima* (Figs. 86, 87, and 88), *Samolus littoralis*, *S. repens*, and likely in *Jacquinia armillaris* (Kuster et al. 2018); they play an

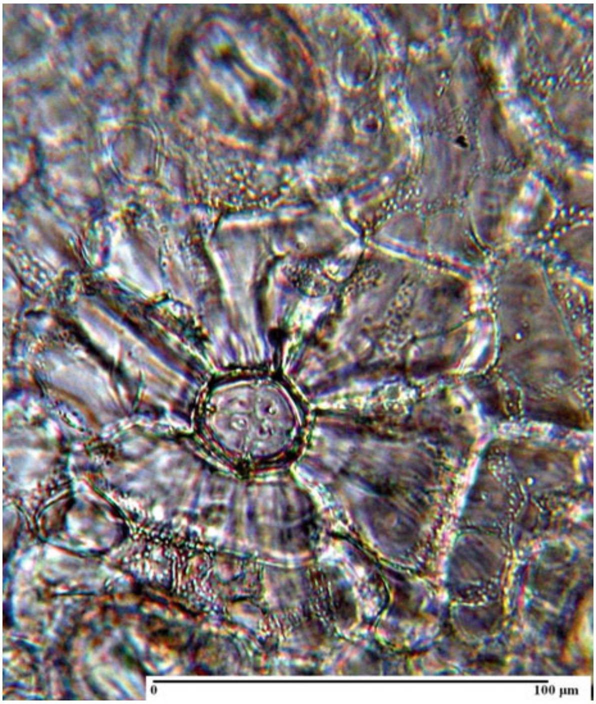


Fig. 69 Salt glands of *Limonium narbonense* (Grigore et al. 2014)

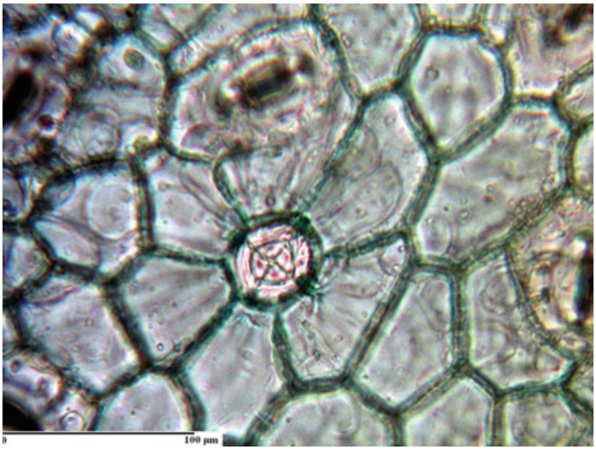


Fig. 70 Salt glands of *Limonium girardianum* (Grigore et al. 2014)

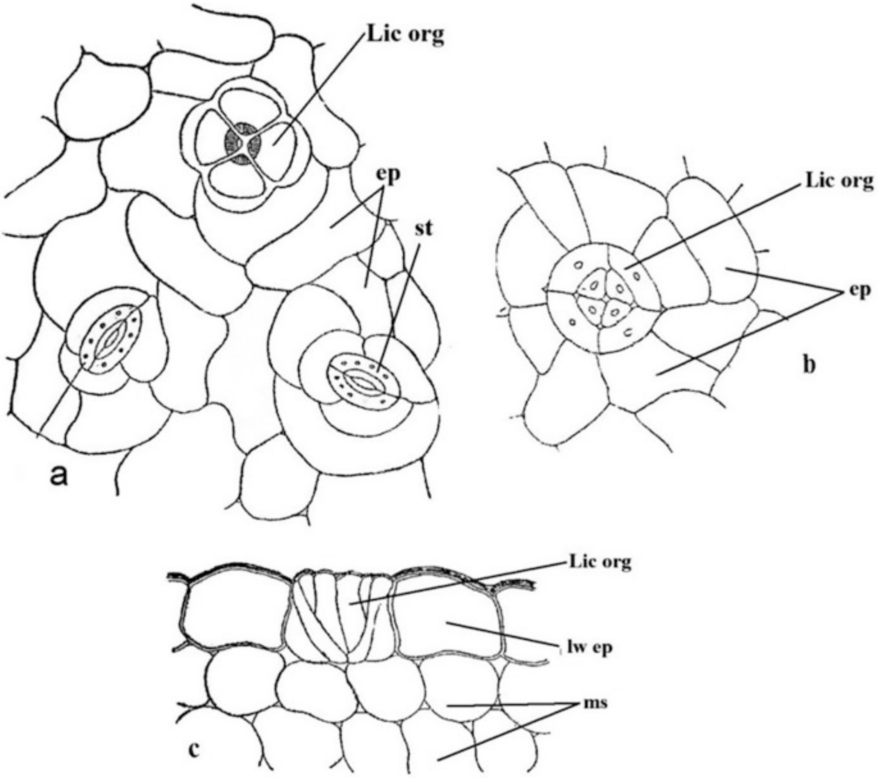


Fig. 71 Salt glands in lamina of *Limonium gmelinii*. (**a**) Lower epidermis, surface view (**b**) Licopoli "organ" (**c**) cross section through the lamina; ep, epidermis cells; Lic org, Licopoli "organ"; ms, mesophyll; lw ep, lower epidermis; st, stomata (Motiu et al. 1987)

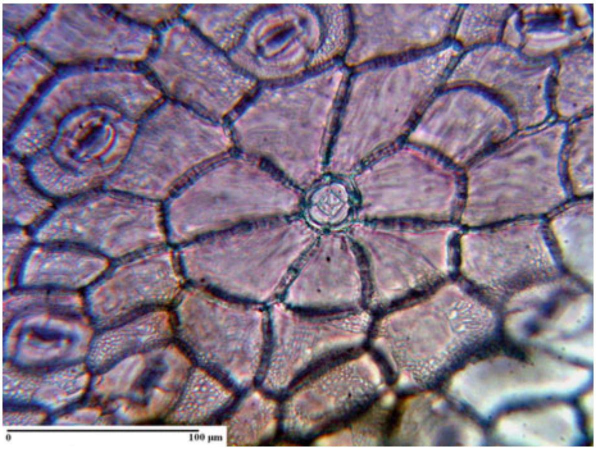


Fig. 72 Salt glands of *Limonium gmelinii*, lower epidermis (Grigore and Toma 2010b)

ecological role within adaptation of these species to maritime habitats (Grigore and Toma 2017).

Glands of *Glaux maritima* appear to be sunk in depressions of the epidermis (Fig. 86). Seen in front view of epidermis, glands appear to be surrounded by six epidermal cells arranged regularly. From the interior to the exterior of the gland, three types of cells can be observed: a large basal cell that corresponds to collecting cell of the gland. Close to it, there is a stalk cell, with a large nucleus. The external part of the gland consists of four to eight gland secretory cells, whose base is in continuation of the upper part of the stalk cell.

2.13.6 Salt Glands of Halophytes from *Poaceae* (*Gramineae*)

Salt glands of *Poaceae* secrete salt outside of the cells and display the simplest anatomy (bicellular or even monocellular-based structure) (Grigore and Toma 2010b). They usually consist of two cells, a basal and a cap cell; their shape, size, and position are highly variable among secreting halophytes.

Bicellular epidermal glands are the most characteristic and occur in more than 30 species of tribes *Chlorideae*, *Eragrosteae*, *Aeluropodeae*, and *Pappophoreae*, the well-studied glands being those from *Aeluropus littoralis*, *Spartina* (Fig. 89), and *Sporobolus.*

2.13.7 Salt Hairs (Vezicular Hairs, Salt Bladders, Bladders) from *Chenopodiaceae*

These salt hairs (also called in the literature vesicular/vezicular hairs, vesiculated hairs, salt bladders, bladder hairs, or simply bladders) are present in many halophytic species of *Chenopodiaceae*, especially in *Atriplex*, *Halimione*, and *Chenopodium* species (Grigore and Toma 2010b, 2017, Grigore et al. 2014).

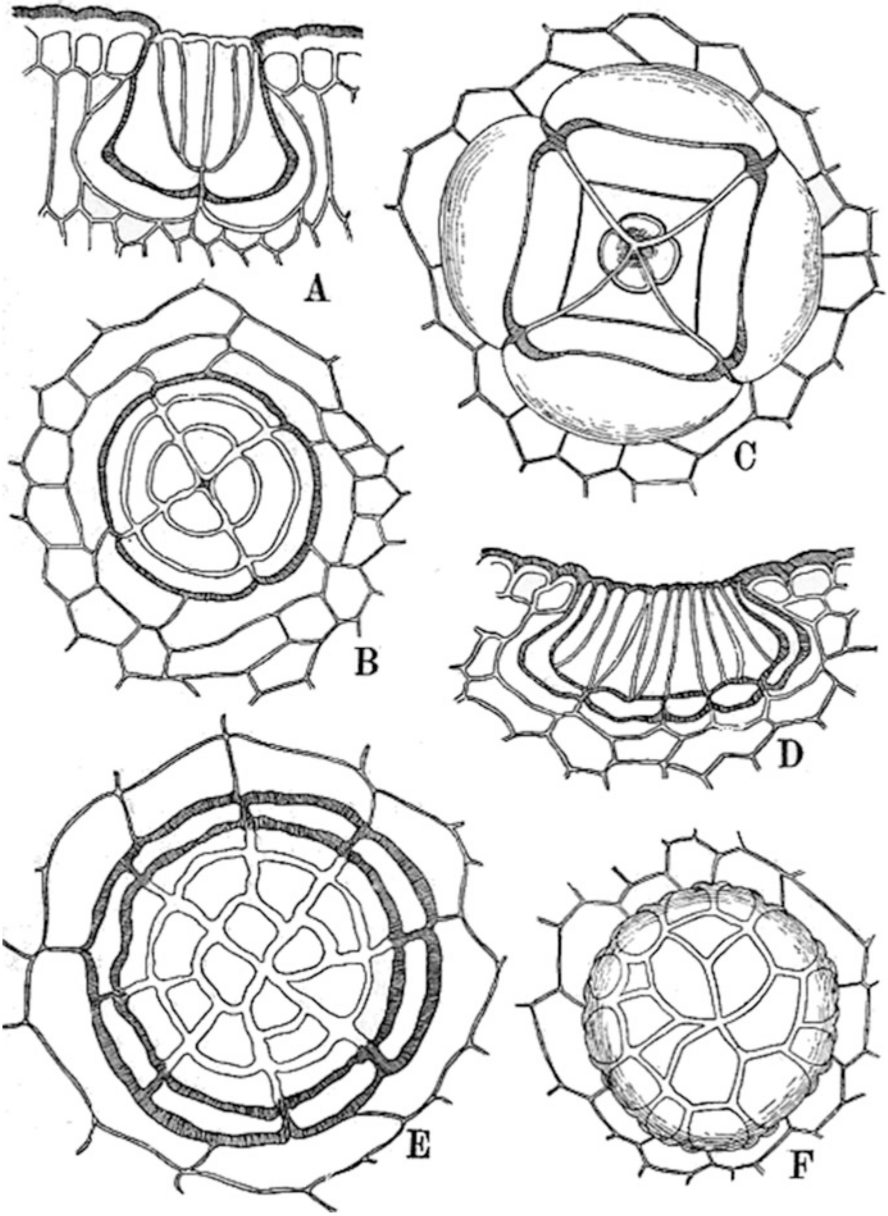


Fig. 73 Structure of the glands of *Aegialitis annulata*. (**A–C**) Chalk glands, (**A**) cross section, (**B**) surface view from outside, (**C**) surface view, from within, (**D–F**) mucilage glands, (**D**) cross section, (**E**) surface view from outside, (**F**) surface view from inside (Solereder 1908)

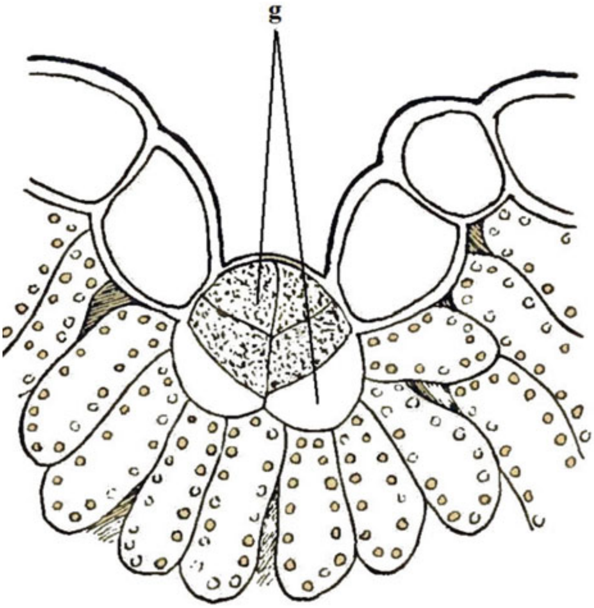


Fig. 74 Salt gland (g) in the leaf of *Tamarix mannifera* (Volkens 1887)

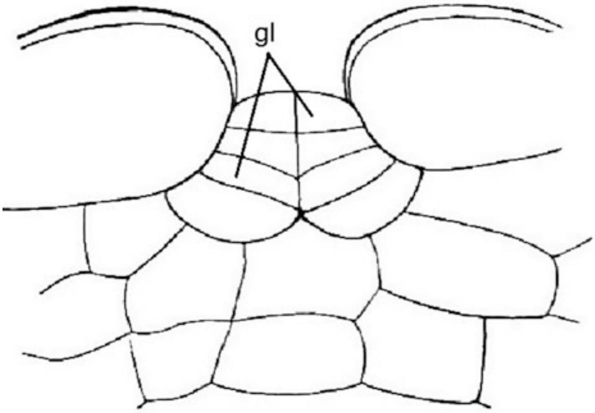


Fig. 75 Salt gland (gl) in the leaf of *Tamarix tetrandra* (Brunner 1908)

Fig. 76 Salt gland (gl) in the leaf of *Reaumuria oxiana* (Paulsen 1912)

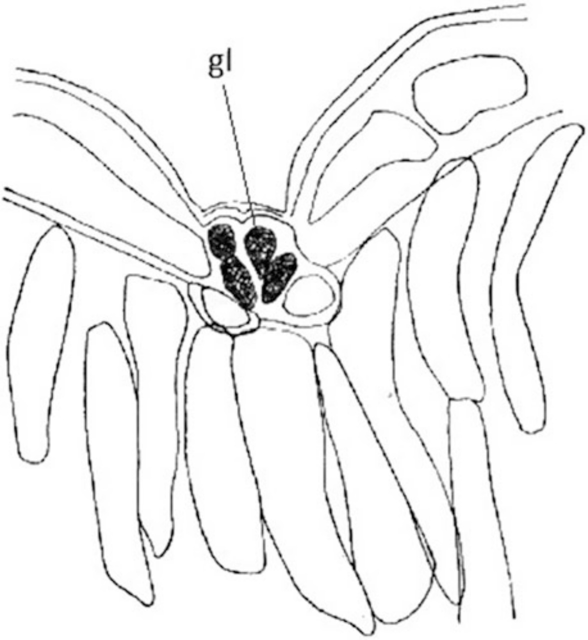
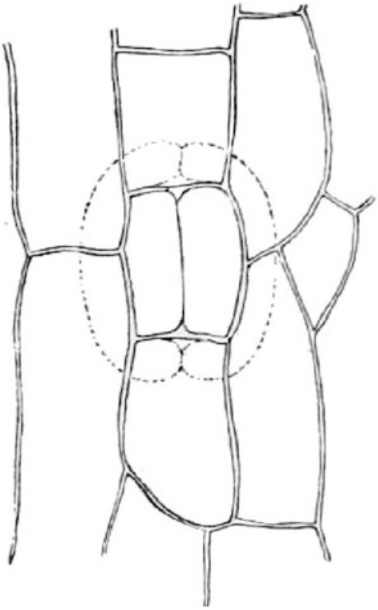


Fig. 77 Salt gland in the leaf of *Reaumuria kermanensis* (Brunner 1908)



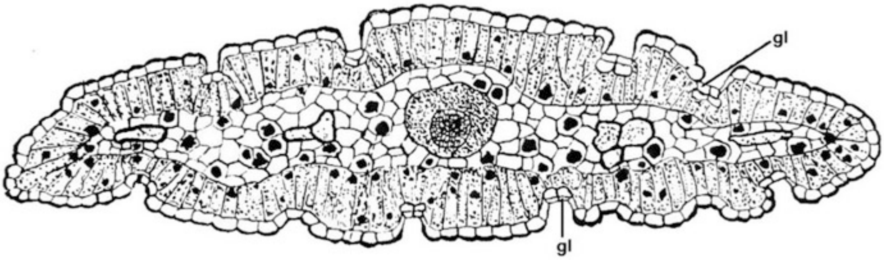
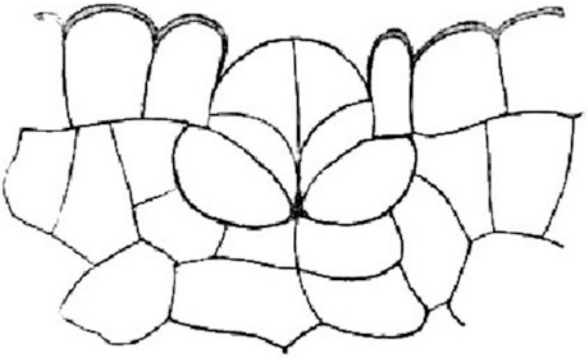


Fig. 78 Salt gland (gl) in the leaf of *Reaumuria kermanensis* (Brunswik 1920)

Fig. 79 Salt gland in the leaf of *Myricaria germanica* (Brunner 1908)



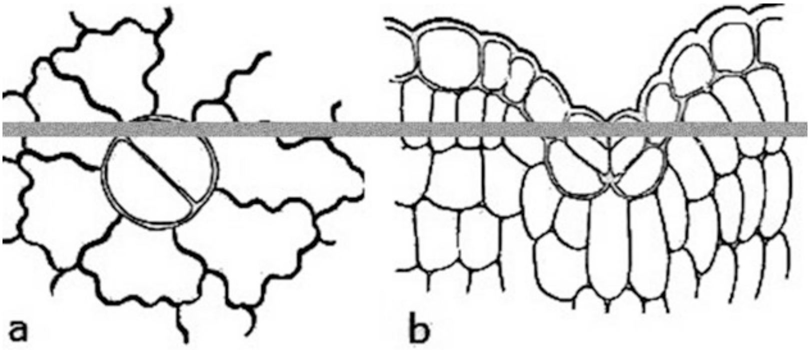


Fig. 80 Salt glands of *Frankenia pulverulenta* (**a**) Surface view and (**b**) cross section (Solereder 1908)

Fig. 81 *Frankenia laevis*. Cross section through the leaf (ep, epidermis; gl, salt gland; st, stomata; tr, trichome) (Chermezon 1910)

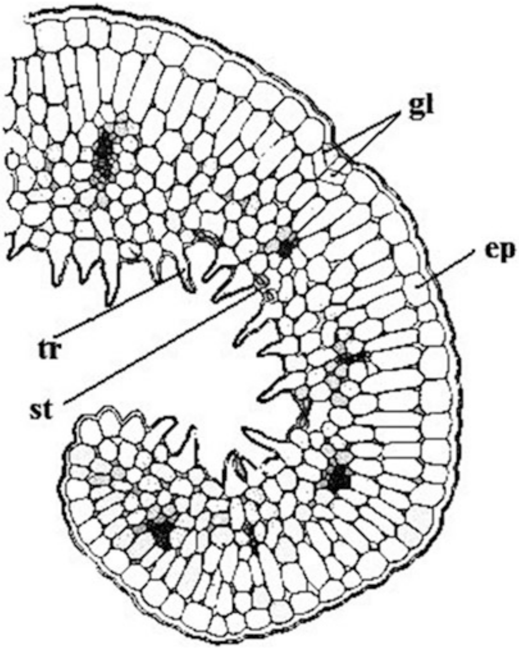


Fig. 82 *Frankenia laevis*. Cross section through the leaf (Grigore et al. 2014)

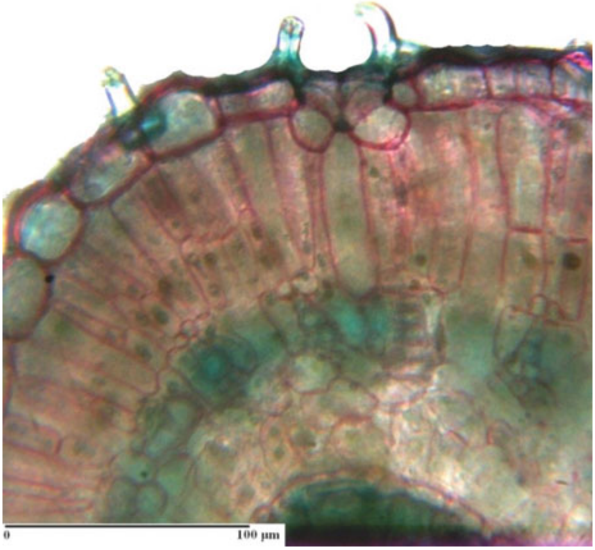


Fig. 83 Salt gland (Sg) of *Avicennia marina*, on the upper side of lamina (photo courtesy of Saikat Naskar)

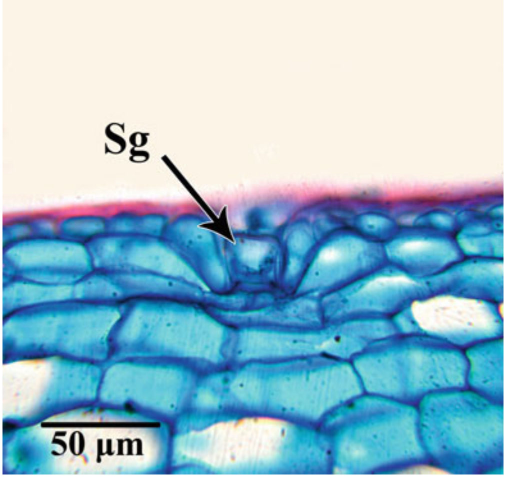
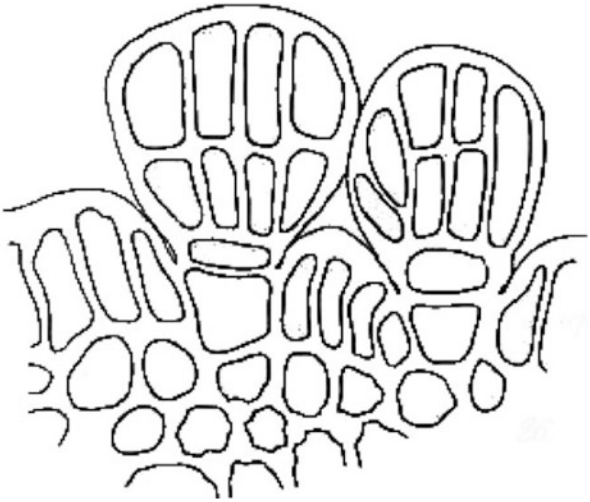


Fig. 84 Salt gland of *Avicennia nitida*, on the upper side of lamina (Wille 1882–1883)



These hairs consist of two cells: a stalk formed of one to three cells and one large cell, intensely vacuolated bladder cell (Fig. 90). Stalk cell contains a dense cytoplasm rich in mitochondria, endoplasmic reticulum, and numerous small vesicles. Inside bladder cells, sodium and chloride concentration is higher than in mesophyll cells and higher than that of the external environment. Salt flow direction is from internal media, through mesophyll, toward these secretory structures.

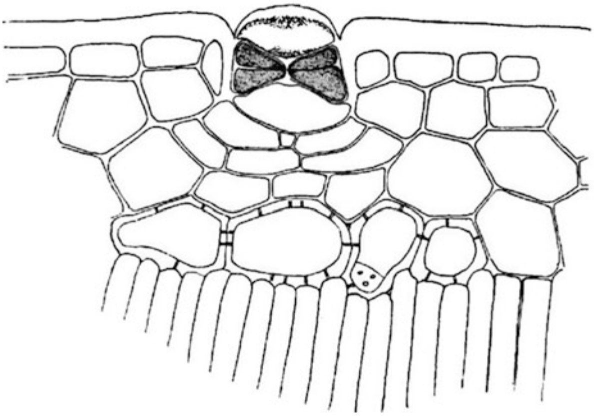


Fig. 85 Salt gland in *Aegiceras corniculata*, cross section through a leaf (Schmidt 1905)

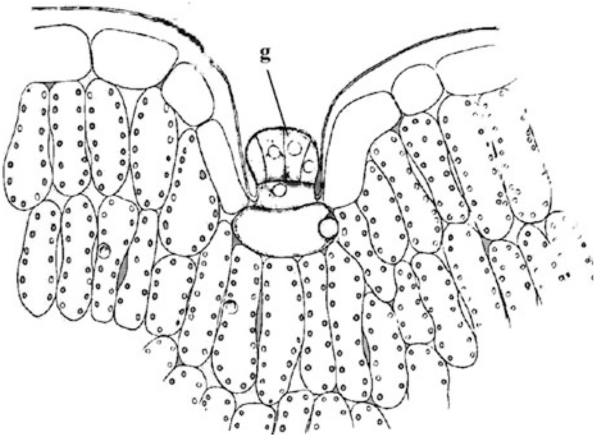


Fig. 86 Salt gland (g) in the lamina of *Glaux maritima* (von Minden 1899)

Salt hairs were observed in *Atriplex leucoclada* (Fig. 90), *A. farinosa* (Fig. 91), *Halimione verrucifera* (Fig. 92), *H. portulacoides* (Fig. 93), *Atriplex tatarica* (Fig. 94), and *A. halimus* (Fig. 95).

2.13.8 Epidermal Bladder Cells from *Aizoaceae* (*Mesembryanthemaceae*)

These cells occur in *Mesembryanthemum* and *Aizoon* species, but the well-known example is *M. crystallinum*, intensely studied also for its special capacity to switch

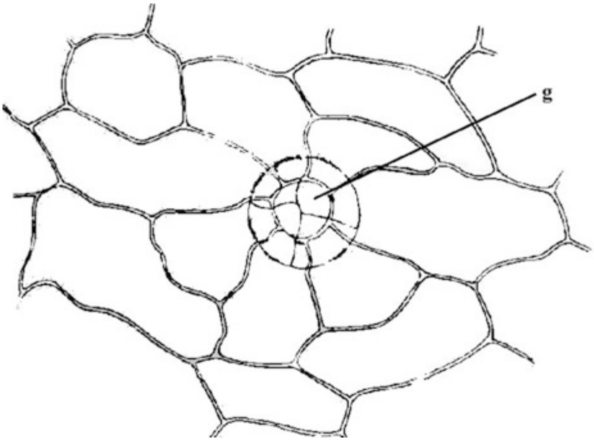


Fig. 87 Salt gland (g) in the lamina of *Glaux maritima*, surface view (von Minden 1899)

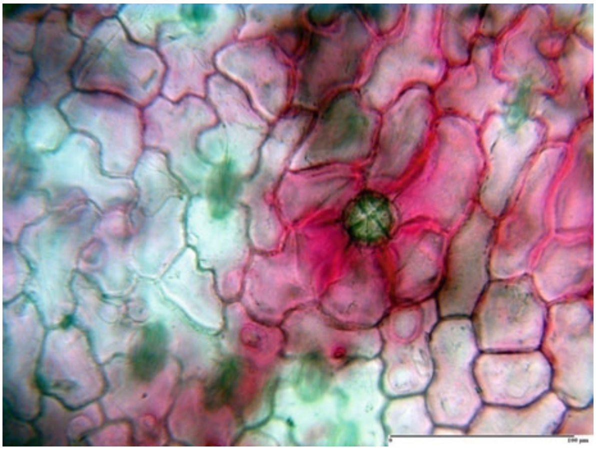


Fig. 88 Salt gland in the lamina of *Glaux maritima*, surface view (Grigore et al. 2014)

from C_3 to CAM photosynthetic pathway (Grigore and Toma 2017). From structural point of view, these epidermal bladder cells would correspond to bladders of vezicular hairs found in *Chenopodiaceae*, since they lack stalk cell.

The epidermal bladder cells from *M. crystallinum* can accumulate large amount of water inside them, thus conferring the typical appearance of "ice plant," the vernacular name of *Mesembryanthemum* (Grigore and Toma 2010b). Thus, they represent a xerophytic adaptation; in parallel, these bladder cells can be regarded as isolated water storage cells, forming a peripheral water storage tissue (Schimper 1903). In fact, some epidermal cells project above epidermis, forming

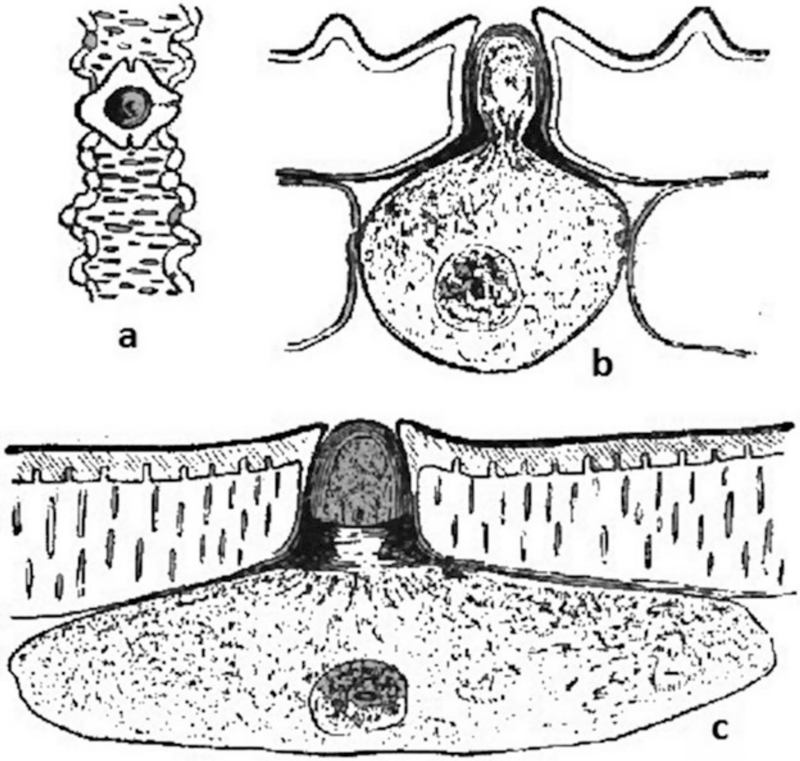
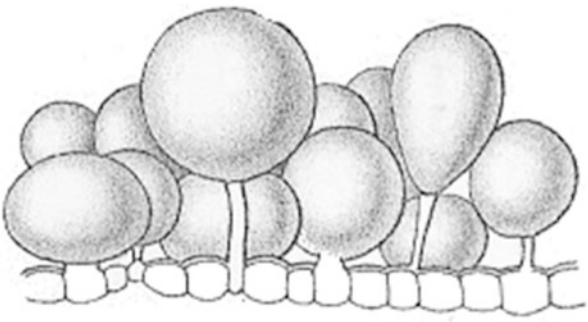


Fig. 89 Salt gland of *Spartina townsendii* (leaf, **a**, surface view; **b**, cross section; **c**, radial longitudinal section) (Sutherland and Eastwood 1916)

Fig. 90 Vezicular hairs of *Atriplex leucoclada* (Volkens 1887)



large water vesicles (Figs. 96 and 97). According to Schimper (1903), when plant transpiration is weak, these vesicles are filled with water during the night or when the sky is cloudy; when transpiration is intense, these vesicles supply assimilating

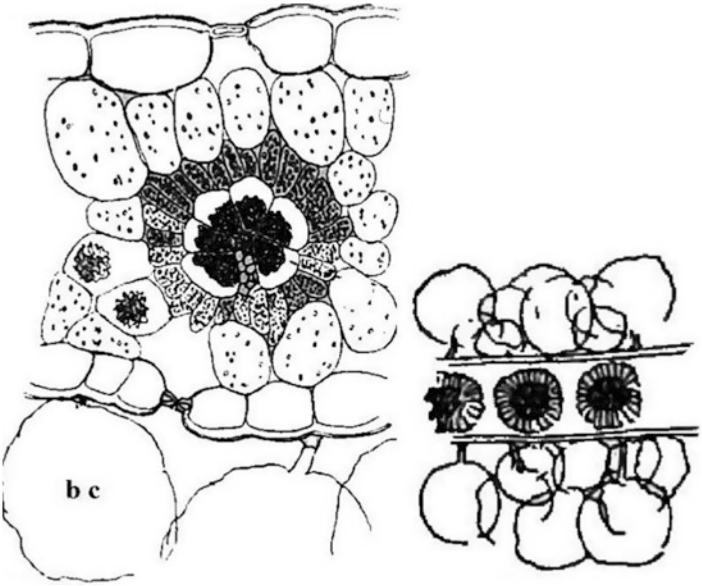


Fig. 91 Vezicular hairs (bladder cells (**b c**) of *Atriplex farinosa* (left, detail; right, general appearance) (Warming 1897)

cells with water and then collapse. Under salt treatments, these cells become larger covering extended parts of aerial organs in *Mesembryanthemum* (Grigore and Toma 2010b).

Haberlandt (1914) attributed to bladder cells of *M. crystallinum* an adaptation typical of xerophytes, whose epidermal cells can sometimes increase their volume, thus acquiring a water storage role.

2.13.9 Other Salt Glands (*Cressa cretica, Ipomoea pes-caprae,* and *Lavatera arborea*)

Ipomoea pes-caprae, *Cressa cretica* (*Convolvulaceae*), and *Lavatera arborea* (*Malvaceae*) have salt glands, which are less studied than those previously discussed (Grigore and Toma 2010b).

Warming described the anatomical structure of *Ipomoea pes-caprae*, designating these glands as either "glandular hairs" or "hydathodes" (Fig. 98). *Lavatera arborea* has a gland consisting of a large basal cell, two intermediary cells, and five apical cells.

2.14 Kranz Anatomy Structures

Despite C_4 photosynthesis is found in many nonhalophytic species, in C_4 halophytes, Kranz anatomy is a good example of connection between structure and specific processes in C_4 photosynthesis. In C_4 plants metabolic processes of C_4

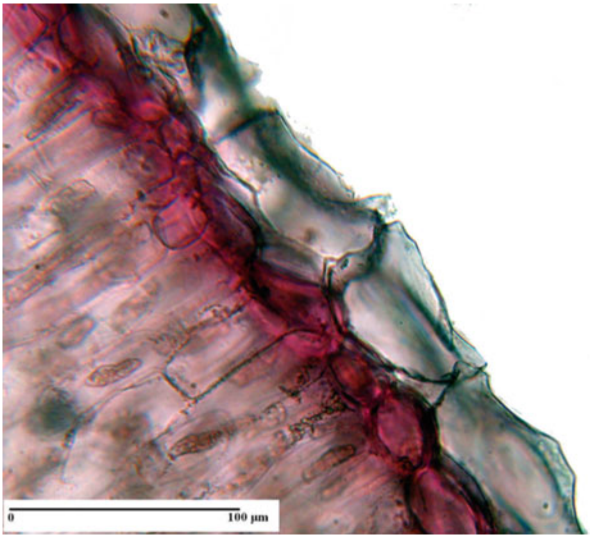


Fig. 92 Vezicular hairs in leaf of *Halimione verrucifera* (Grigore and Toma 2017)

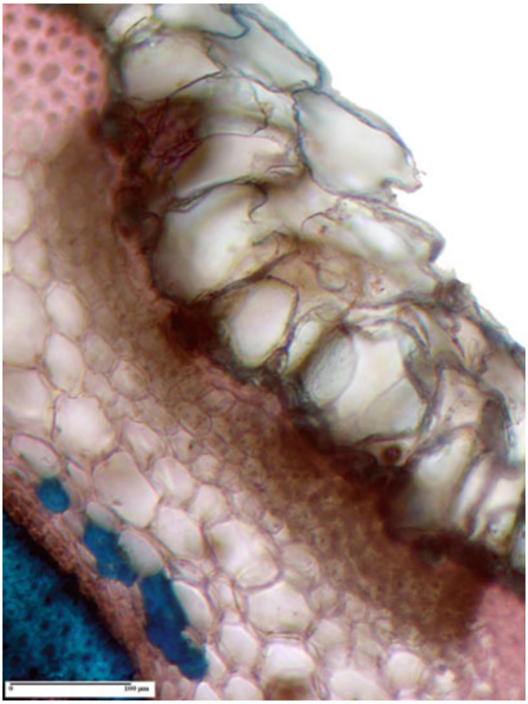


Fig. 93 Vezicular hairs in leaf of *Halimione portulacoides* (Grigore and Toma 2017)

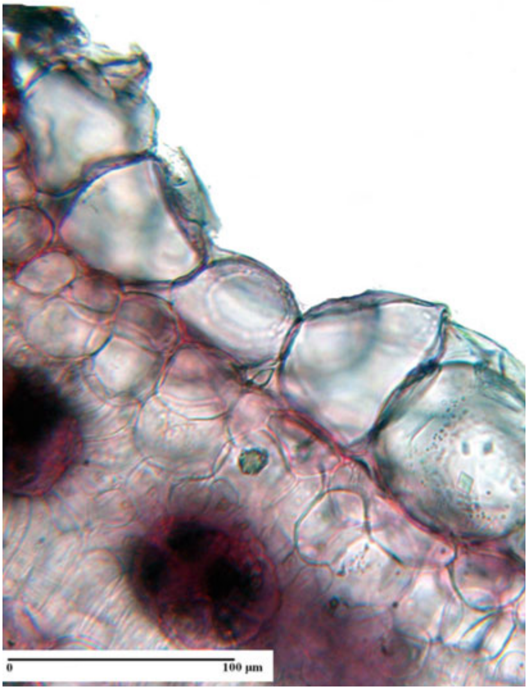


Fig. 94 Vezicular hairs in leaf of *Atriplex tatarica* (Grigore and Toma 2017)

Fig. 95 Vezicular hairs in leaf of *Atriplex halimus* (Grigore and Toma 2017)

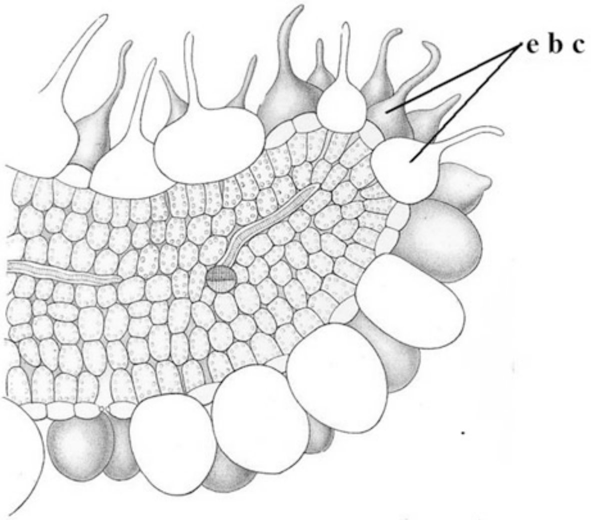


Fig. 96 Epidermal bladder cells (ebc) from the leaf of *Mesembryanthemum crystallinum* (Volkens 1887)

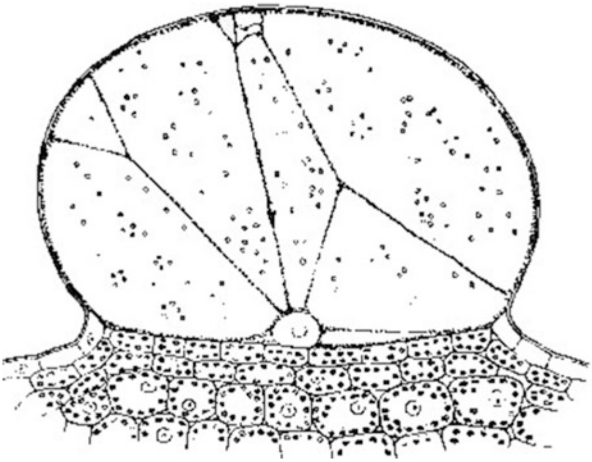


Fig. 97 Epidermal bladder cell, filled with water on leaf surface of *Mesembryanthemum crystallinum* (Haberlandt 1914)

pathway need the cooperation of two distinct chlorenchyma tissues: an external one (or photosynthetic carbon assimilative – PCA) and an inner bundle sheath (or photosynthetic carbon reductive – PCR) tissue. These chlorenchyma tissues are usually arranged concentrically with respect to vascular tissues, forming a structural pattern known as Kranz anatomy (Muhaidat et al. 2007).

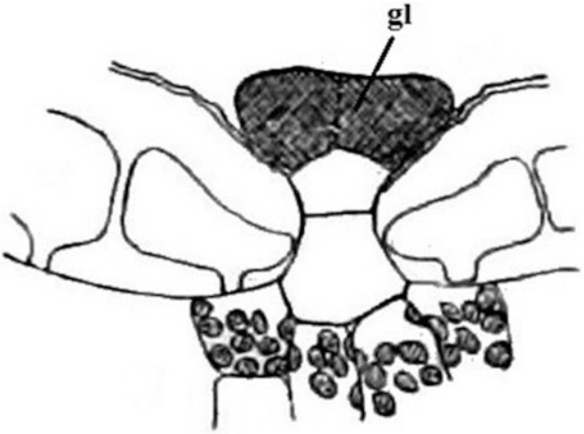


Fig. 98 Salt gland (gl) of *Ipomoea pes-caprae* (Warming 1897)

This internal structure physically partitions the biochemical events of the C_4 pathway into two major phases. In the first step, atmospheric CO_2 is initially assimilated into C_4 acids by PCA tissue-specific phosphoenolpyruvate carboxylase. In the second phase, these acids diffuse into the PCR compartment, where they are decarboxylated, and the released CO_2 is refixed by PCR tissue-specific Rubisco. This biphasic C_4 system enhances CO_2 levels around Rubisco, suppressing photorespiration and improving plant carbon balance (Kanai and Edwards 1999).

Kranz anatomy has been found in several Romanian halophyte species (Grigore and Toma 2007a, b, c, 2008a, 2017; Grigore et al. 2012a, c, 2014), Spanish (Grigore et al. 2011a, b, 2014; Grigore and Toma, 2017), and Iranian halophytes (Safiallah et al. 2017) revealed by Kranz anatomy in many *Chenopodiaceae* species: *Atriplex tatarica* (Fig. 99), *A. glauca* (Fig. 100), *A. halimus* (Figs. 95 and 101), *Petrosimonia oppositifolia* (Figs. 31 and 102), *P. triandra* (Figs. 32 and 103), *Camphorosma annua* (Figs. 34 and 104), *C. monspeliaca* (Fig. 105), *Suaeda splendens* (Figs. 39 and 106), *Salsola kali* (Figs. 38 and 107), *S. oppositifolia* (Figs. 36 and 108), and *Bassia hyssopifolia* (Fig. 109). Kranz anatomy has been also evidenced in several halophytic Iranian species of *Bassia*: *B. prostrata* (Fig. 110), *B. pilosa* (Fig. 111), and *B. turkestanica* (Fig. 112) (photo courtesy of Somayeh Safiallah).

2.15 Bulliform Cells

Bulliform cells (motor cells, "hinge cells") have been evidenced in several Romanian salt-tolerant plants, nominated as "amphibious halophytes": *Juncus gerardii*, *Bolboschoenus maritimus*, *Carex distans*, *C. vulpina*, *Agrostis stolonifera*, *Alopecurus arundinaceus*, *and Puccinellia distans* (Grigore et al. 2014; Grigore and Toma 2017). These cells ensure the rolling up of leaves under drought conditions and reopening again under favorable conditions of rehydration. Thus, they

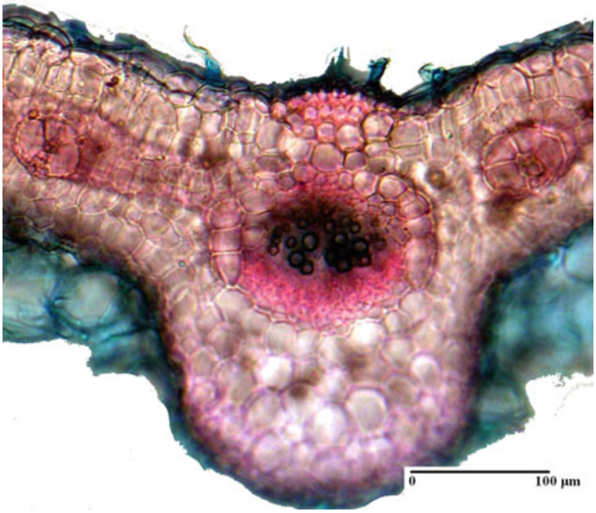


Fig. 99 Cross section through the lamina of *Atriplex tatarica* (Grigore et al. 2014)

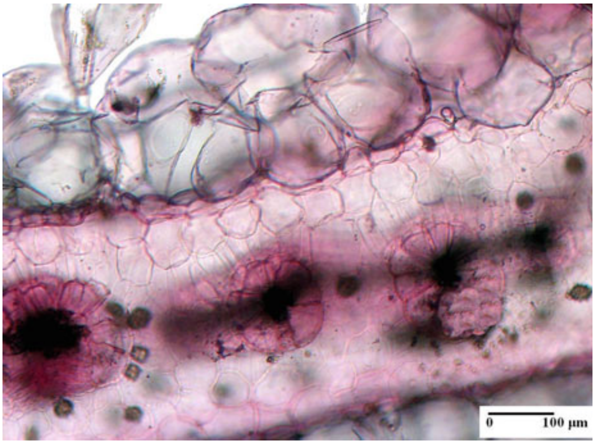


Fig. 100 Cross section through the lamina of *Atriplex glauca* (Grigore et al. 2014)

could be regarded as a xeromorphic adaptation in this group of halophytes; the abovementioned species are usually hygrophilous, vegetating in salt marshes that sometimes can be flooded but often are exposed to prolonged droughts. The temporary characters of soil moisture and atmosphere humidity induce anyway the necessity of some xeromorphic adaptations, as a response to both water stress and salt stress (Grigore 2012; Grigore and Toma 2014; Grigore et al. 2014).

Grigore and Toma (2010c) included halophytes with bulliform cells that vegetate in wet, salinized environments but also subjected to seasonal droughts in the category of *amphibious halophytes*: *Bolboschoenus maritimus*, *Carex distans*

Fig. 101 Cross section through the lamina of *Atriplex halimus* (Grigore et al. 2014)

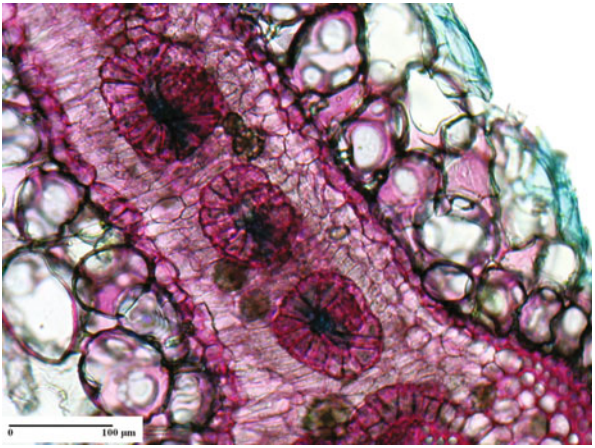


Fig. 102 Cross section through the lamina of *Petrosimonia oppositifolia* (Grigore et al. 2014)

(Fig. 113), *Carex vulpina* (Fig. 114), *Juncus gerardii* (Fig. 115), *Agrostis stolonifera* (Fig. 116), *Alopecurus arundinaceus* (Fig. 117), and *Puccinellia distans* (Fig. 118).

3 Morphological and Anatomical Adaptations of Halophytes from (Nontropical) Salt-Marsh Formations

A typical example of adaptations of halophytes belonging to maritime formations (salt-marsh formation): *Spartina stricta*, *Juncus roemerianus*, *Typha*, *Spartina patens*, and *Baccharis-Hibiscus* associations will be provided (Kearney 1900, 1901).

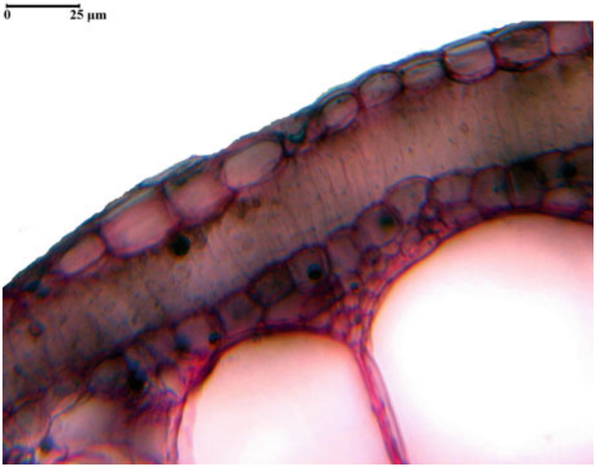


Fig. 103 Cross section through the lamina of *Petrosimonia triandra* (Grigore et al. 2014)

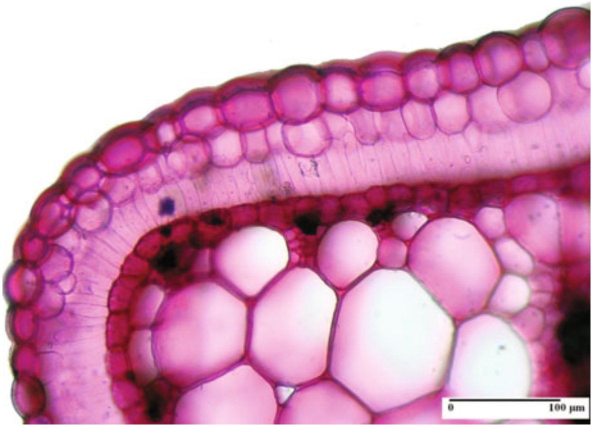


Fig. 104 Cross section through the lamina of *Camphorosma annua* (Grigore et al. 2014)

These are the conditions of the physical environment that most probably affect the structure and habit of salt-marsh plants vegetating in various salt-marsh ("creek-marsh") formations, often subjected to tidal influence (Kearney 1901):

1. Liability to partial submersion at high tide
2. A soft, more or less mobile substratum
3. *The presence of a relatively high percentage of common salt (sodium chloride) in soil and water*

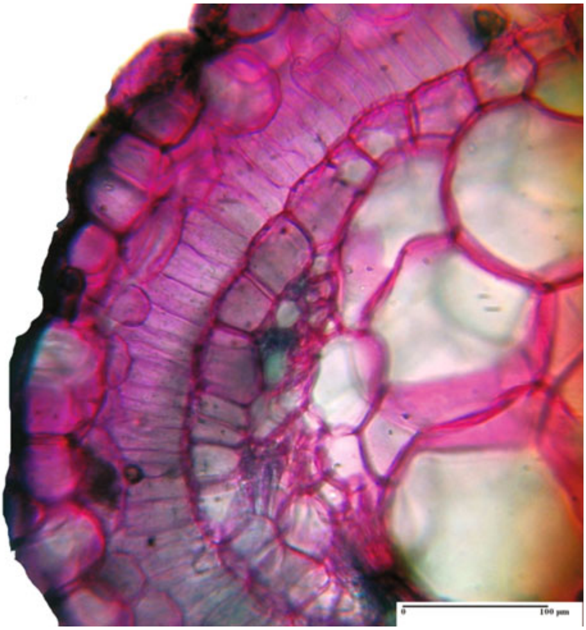


Fig. 105 Cross section through the lamina of *Camphorosma monspeliaca* (Grigore et al. 2014)

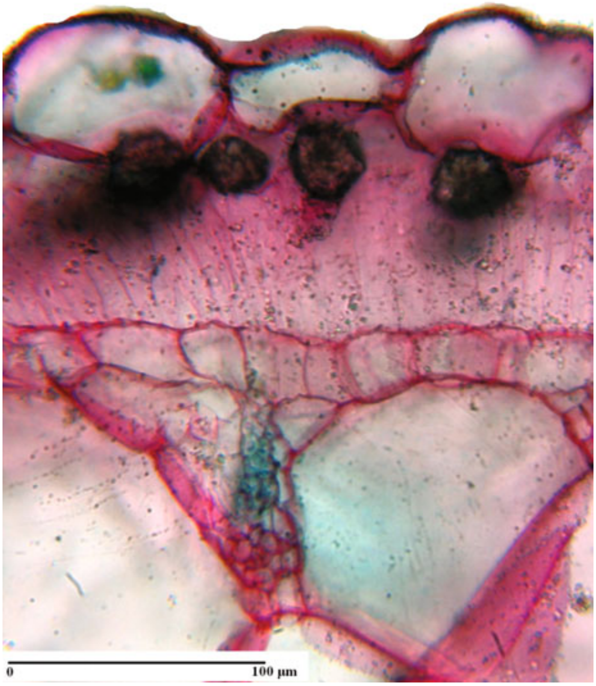


Fig. 106 Cross section through the lamina of *Suaeda splendens* (Grigore et al. 2014)

Fig. 107 Cross section through the lamina of *Salsola kali* (Grigore et al. 2014)

Fig. 108 Cross section through the lamina of *Salsola oppositifolia* (Grigore et al. 2014)

In respect to abovementioned and discussed ecological conditions that induce general and particular adaptations in halophytes, it is easily noticeable that it is important to take into account the substratum, the tidal influence, and the mechanical action of the wind.

Fig. 109 Cross section through the lamina of *Bassia hyssopifolia* (Grigore et al. 2014)

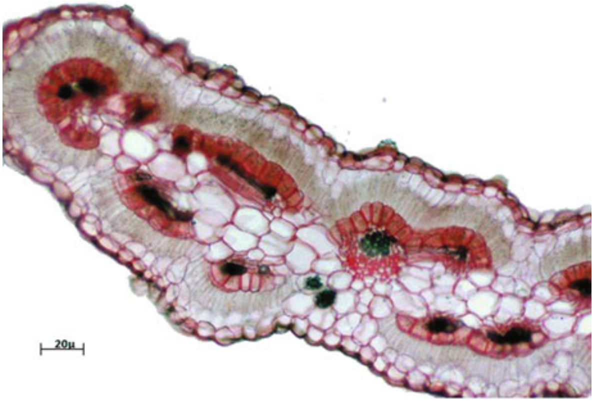


Fig. 110 Cross section through the lamina of *Bassia prostrata* (Grigore et al. 2014, photo courtesy of Somayeh Safiallah)

The modifications of structure that can be attributed to the influence of these three factors may be included in several principal categories:

(A) *Structures preventing free access of water to submerged parts.* The most obvious adaptation of this class is the persistence of the basal sheaths in grasses and grass-like plants. This is well exemplified in *Spartina stricta maritima*, where the bases of culms are tightly enveloped by the closely imbricated, large papery sheaths (Fig. 119).

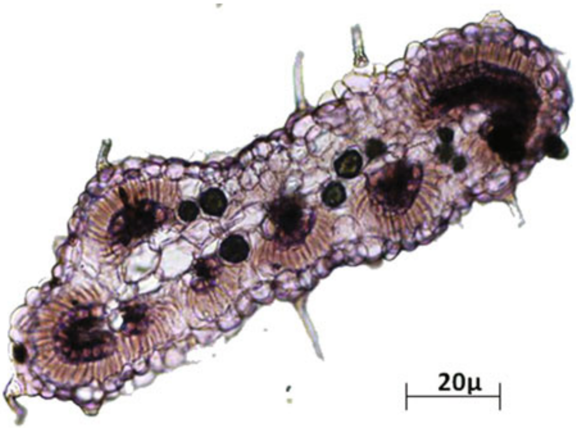


Fig. 111 Cross section through the lamina of *Bassia pilosa* (Grigore et al. 2014, photo courtesy of Somayeh Safiallah)

Fig. 112 Cross section through the lamina of *Bassia turkestanica* (Grigore et al. 2014. Photo courtesy of Somayeh Safiallah)

(B) *Structures serving to hold the plant fast in the watery, incoherent soil*. These take the form in most cases of long rootstocks, creeping through the mud and sending up erect leafy and flowering branches at frequent intervals (Fig. 120). This feature is found in the underground parts of the great majority of salt-marsh plants. Often, as in *Typha*, *Spartina polystachya*, *Phragmites*, and other large plants with a considerable weight to be supported, the rhizomes are very long and large. Annual plants, which are few in the salt marshes (*Aster subulatus* and *Salicornia herbacea* being the only common species), have less need of firm anchorage in the soil.

(C) *Structures serving to reduce the loss of water from the leaves*, which would otherwise be excessive, as the chiefly herbaceous salt-marsh vegetation, unsheltered by large, woody plants, are directly exposed to the drying effect

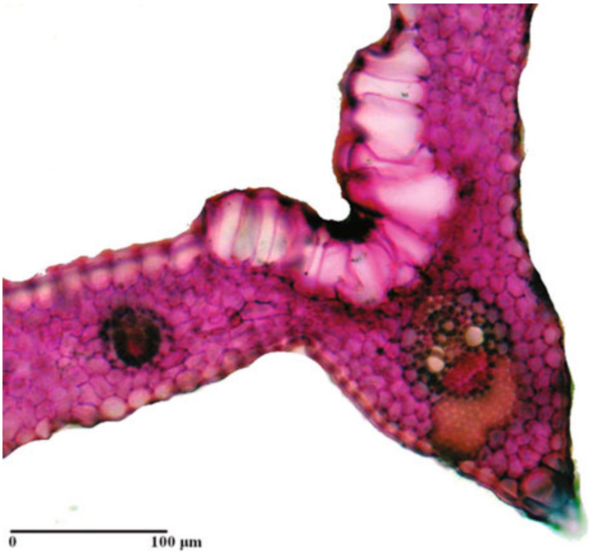


Fig. 113 Bulliform cells in Romanian “amphibious” halophyte *Carex distans* (Grigore et al. 2014)

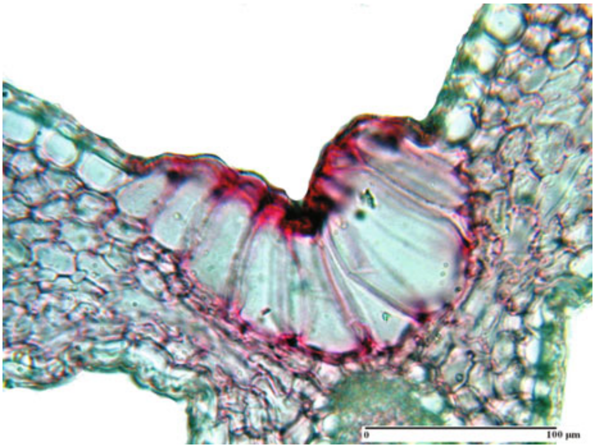


Fig. 114 Bulliform cells in Romanian “amphibious” halophyte *Carex vulpina* (Grigore et al. 2014)

of the wind and to the strong light and heat of the sun. The necessity for such protection is greater because, as is well-known, roots absorb water with difficulty when it contains any considerable percentage of salts in solution, owing to the decreasing force of endosmosis when the degree of concentration of the external water approaches that of the cell sap. In order to compensate the reduced absorbing activity of the roots, it is obvious that the escape of water from the upper part of the plant, especially from the leaves, where it is normally

Fig. 115 Bulliform cells in Romanian "amphibious" halophyte *Juncus gerardii* (Grigore et al. 2014)

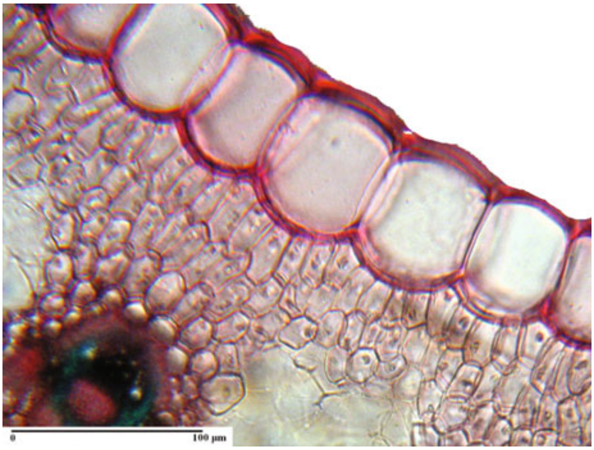
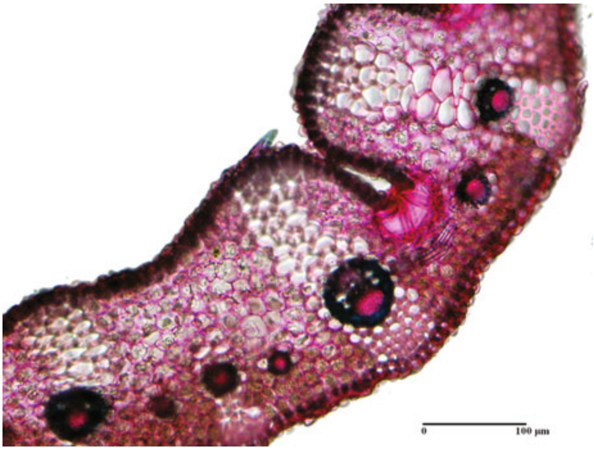


Fig. 116 Bulliform cells in Romanian "amphibious" halophyte *Agrostis stolonifera* (Grigore et al. 2014)



greatest, must be correspondingly checked. To the plants of the salt marshes, growing in a soil that is impregnated with salt (in solution) and subject to partial or total inundation twice a day by brackish water, it is very important that the supply of water so scarce provided to their substratum should be carefully kept. However, even it is not easy for salt-marsh plants to absorb water, it would not be to their benefit to take it up in great quantities, because it would lead in an increased accumulation in the cells of sodium chloride, which would turn into a harmful effect (Grigore et al. 2014; Grigore and Toma 2017 and reference therein).

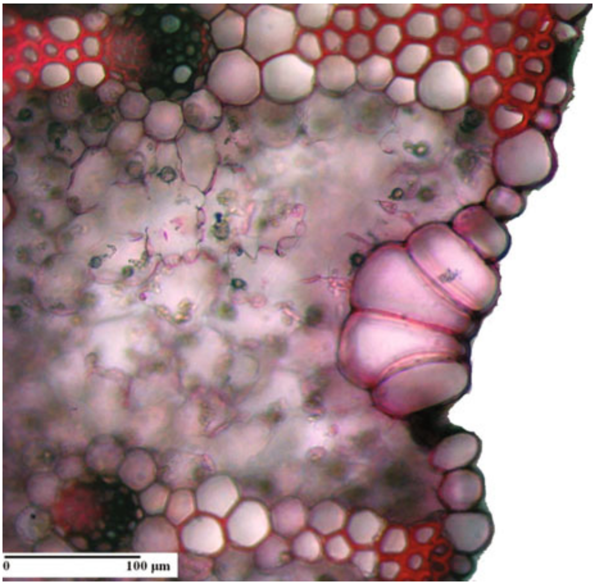


Fig. 117 Bulliform cells in Romanian "amphibious" halophyte *Alopecurus arundinaceus* (Grigore et al., 2014)

Fig. 118 Bulliform cells in Romanian "amphibious" halophyte *Puccinellia distans* (Grigore et al. 2014)

There are several morphological-anatomical modifications that may be involved in diminishing transpiration (Warming 1897, 1909; Henslow 1895; Kearney 1901; Schimper 1903; Coulter 1900; Børgesen and Paulsen 1900; Grigore and Toma 2017):

(a) *Thickening of the cuticle and epidermis walls*, which is exhibited, often to a high degree, by nearly all plants of the salt marsh (Fig. 121). This thickening

Fig. 119 *Spartina stricta* (Fitch and Smith 1880)

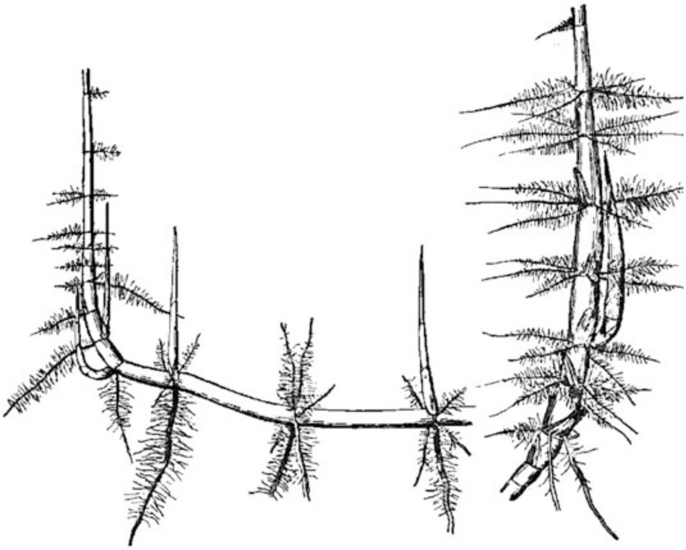


Fig. 120 *Phragmites communis* (Warming 1906)

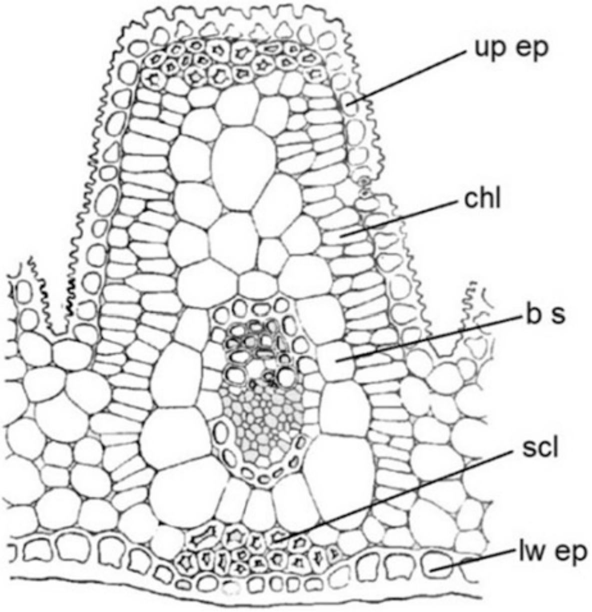


Fig. 121 *Spartina stricta*, cross section through lamina, showing the thickening of epidermis (up ep, upper epidermis; lw ep, lower epidermis; chl, chlorenchyma; b s, bundle sheath; scl, sclerenchyma (Chermezon 1910)

(sometimes forming papillae) is often evident when species of the salt marsh are compared with nearly related species from other localities or even when individuals of the same species, vegetating in salt marsh and some in inland habitat, are compared.

(b) *Hairy covering* sufficiently dense to act as a protection against excessive transpiration occurs only in *Borrichia frutescens*, which has both leaf surfaces very densely covered with two- to four-celled hairs (each epidermis cell being thus extended by tangential division) (Fig. 122a, b). Hairs located on both leaf surfaces are also found in *Kosteletzkya virginica*, *Lippia nodiflora* (Fig. 123), *Monniera monniera*, *Iva frutescens* (Fig. 124), and *Solidago sempervirens.*

(c) *Waxy covering* in *Panicum amarum*, *Uniola paniculata*, and *Euphorbia polygonifolia*.

(d) *Stomata*, *protected by being located in furrows of the leaf surface*, where all or at least most of the stomata lie, especially in *Spartina* species and several sedges.

(e) *Leaf conduplicate or involute* (Fig. 125), thus concealing the ventral surface, where all or most of the stomata are located, especially in the species of *Spartina* and in certain sedges.

(f) Leaf vertical in *Juncus roemerianus*, *Fimbristylis spadicea* (Fig. 126), and *Typha latifolia* (Fig. 127), nearly vertical in species of *Spartina* and other grasses and in *Baccharis*, *Aster* spp., *Iva frutescens*, and other dicots with isolateral leaves.

(g) Transfer of the normal functions of leaves in large part to the (erect) stems, in *Juncus roemerianus*, *Scirpus* species (Fig. 128), and *Salicornia herbacea*

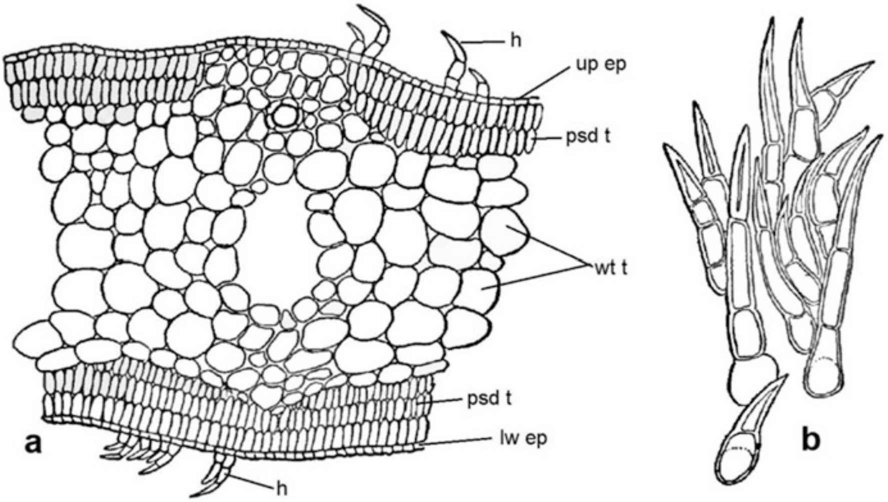


Fig. 122 *Borrichia frutescens* – (**a**), cross section through the lamina showing the location of hairs on both sides of the leaf (up ep, upper epidermis; lw ep, lower epidermis; psd t, palisade tissue; wt t, water storage tissue; h, hairs); (**b**), hairs (Kearney 1900)

(Fig. 129). It refers mainly to photosynthetic function, transferred to stem by the important development of chlorenchyma.

(h) Small size of the leaves, and thus of the transpiring surface, without transfer of function to the stems, in *Aster subulatus* (Fig. 130), *Aster tenuifolius* (Fig. 131), *Sabbatia gracilis* (Fig. 132), *Lythrum lineare* (Fig. 133), *Lippia nodiflora* (Fig. 134), *Monniera (Herpestis) monniera* (Fig. 135), and many other species.

(i) *Succulence*: of stem (accompanied by reduction of the leaves to mere scales) in *Salicornia herbacea* (see Figs. 45 and 129) and other halophytic chenopods with articulated stems and of leaves (moderate) in *Borrichia* (Fig. 122), *Solidago sempervirens*, and *Aster subulatus* (Fig. 136) (where the stems are also somewhat succulent). Succulent plants lose their water much more slowly than do others, since the water storage tissue, the strong development of which causes the thickening of the succulent parts, gives up its supply reluctantly. This is in some cases due to the presence of mucilage in the cells of water storage tissue, which contribute to a better retaining of water (Volkens 1887; Grigore 2008; Grigore et al. 2014; Grigore and Toma 2017).

(j) *Presence of a considerable amount of mineral salts*, especially sodium chloride, in solution in the cell sap. A plant organ which holds in its cells more than the ordinary quantity of dissolved mineral substances loses through transpiration less than the ordinary amount of vapor of water.

(k) *Development of compact palisade* tissue (Fig. 122), usually on both surfaces of the (in such cases) isolateral leaf. Nearly all the species, of both sand strand and salt marsh, are characterized by the development of palisade, a compact

Fig. 123 *Lippia nodiflora* – (**a**), stomata; (**b**), stomata and hair, ventral leaf surface; (**c**), stomata and hair, dorsal leaf surface (Kearney 1900)

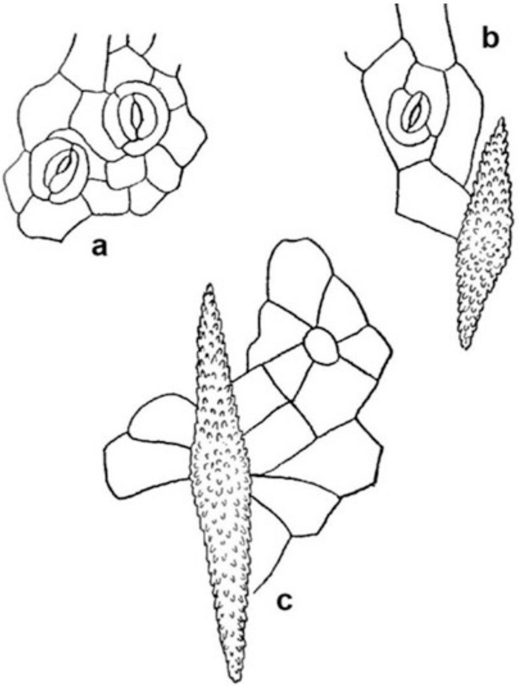
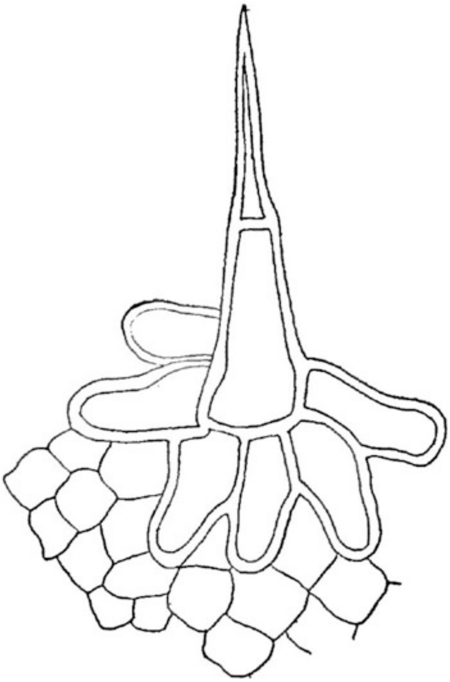


Fig. 124 Iva frutescens, hair from ventral leaf surface (Kearney 1900)



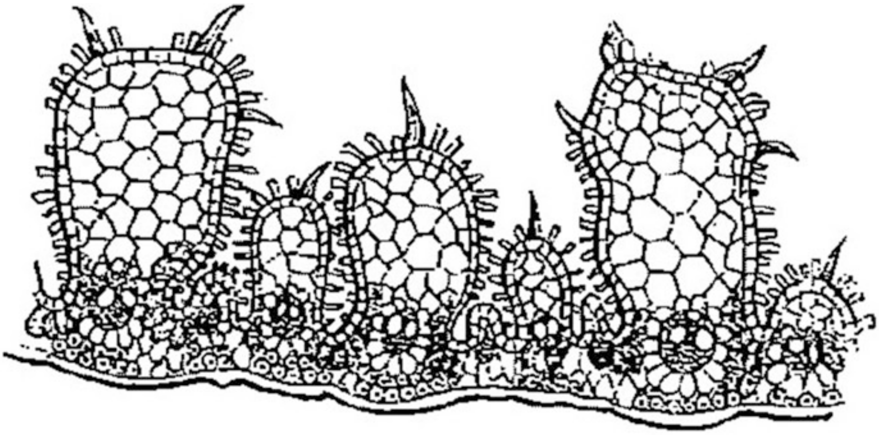
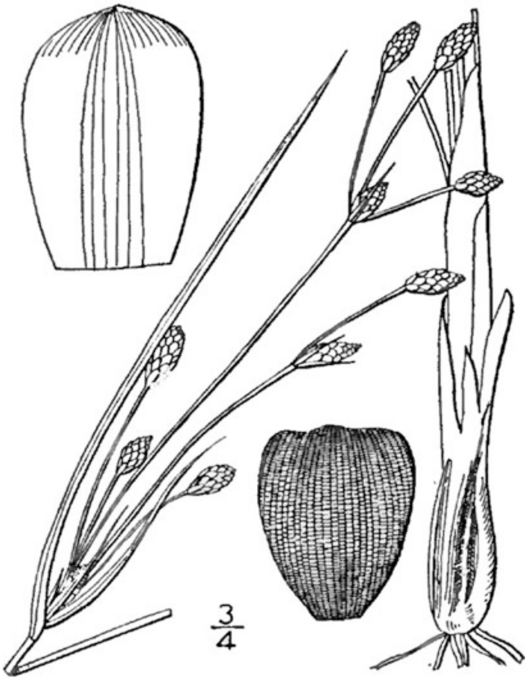


Fig. 125 *Spartina versicolor* (Duval-Jouve 1870)

Fig. 126 *Fimbristylis spadicea* – general aspect (Britton and Brown 1896)



chlorophyll tissue with cells more or less elongated at a right angle to the surface and occupying the exposed face or faces, i.e., the ventral face in bifacial leaves, both faces in such as are isolateral. Such tissue is believed to have, among other functions, that of protecting against excessive loss of water the remainder of the

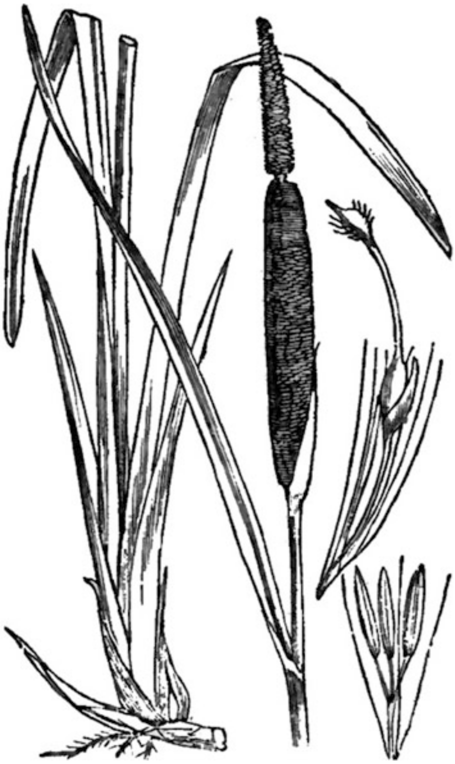


Fig. 127 *Typha latifolia* – general aspect (Fitch and Smith 1880)

leaf (the interior or the lower face, as the case may be), which is usually occupied by less compact tissue (Kearney 1900).

(l) *Aromatic (volatile) oil* – secreted by *Myrica* species, it has been suggested that volatile oils enable a protection against excessive loss of water by formation around the plant in an envelope (Henslow 1895; Kearney 1900;Volkens 1887).

(D) *Adaptations to exposure to the mechanical action of the wind* A notable characteristic of the vegetation is the prevalence of low forms. Tall stems (more than 1 meter high) among herbaceous species which are not grass-like are almost lacking. Often the stems creep above or below the surface of the ground and root at intervals. *Lippia nodiflora*, *Monniera monniera*, *Capriola dactylon*, and *Paspalum distichum* have stems creeping upon the surface. These may be regarded as correspondent representatives of the *Ipomoea pes-caprae* form, which is also characteristic of tropical strands (Warming, 1897, 1906). Some salt-marsh species have creeping subterranean stems, from which arise subaerial leafy and flowering branches, such as *Panicum amarum minus* and

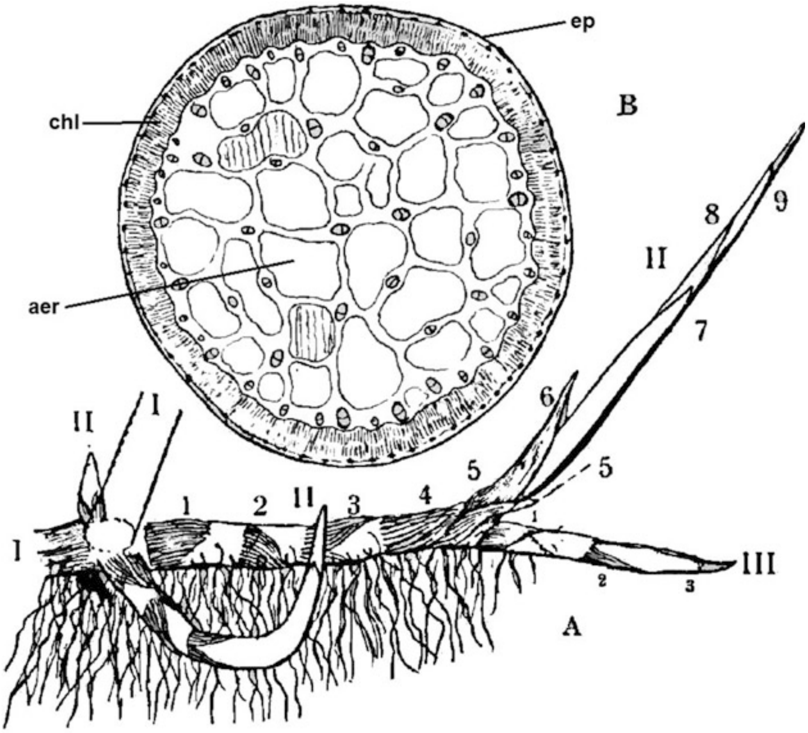


Fig. 128 *Scirpus tabernaemontani*. (**A**), terminal part of a rhizome; I–III, shoots of different generations; 1–9, leaves; (**B**), cross section through a stem; ep, epidermis; chl, chlorenchyma; aer, aerenchyma (Warming 1906)

Uniola paniculata; other species such as *Juncus roemerianus*, *Typha latifolia*, and *Spartina stricta* possess strong, creeping rhizomes that form a dense network in the marshy soil. In *Uniola paniculata* the rhizome is strong and descends obliquely or almost vertically deep into the sand. *Physalis viscosa* has a long, slender, branching root, which creeps horizontally often a distance of a meter or more near the surface and originates at intervals erect, leafy, and flowering branches. *Teucrium nashii* possesses thick stolons, which arise in the axils of the scale-like, lowest leaves (Kearney 1900).

Another adaptation against the coast winds, whose harmful effect upon plants is greatly increased by the quantity of carried sand, is the great development of mechanical tissue (Kearney 1900, 1901) in the leaves of many species: *Uniola paniculata*, *Juncus roemerianus*, *Quercus virginiana* – and the strong thickening of the outer cell walls of the epidermis, in grasses, and in the evergreen leaves of *Quercus virginiana* and *Ilex*.

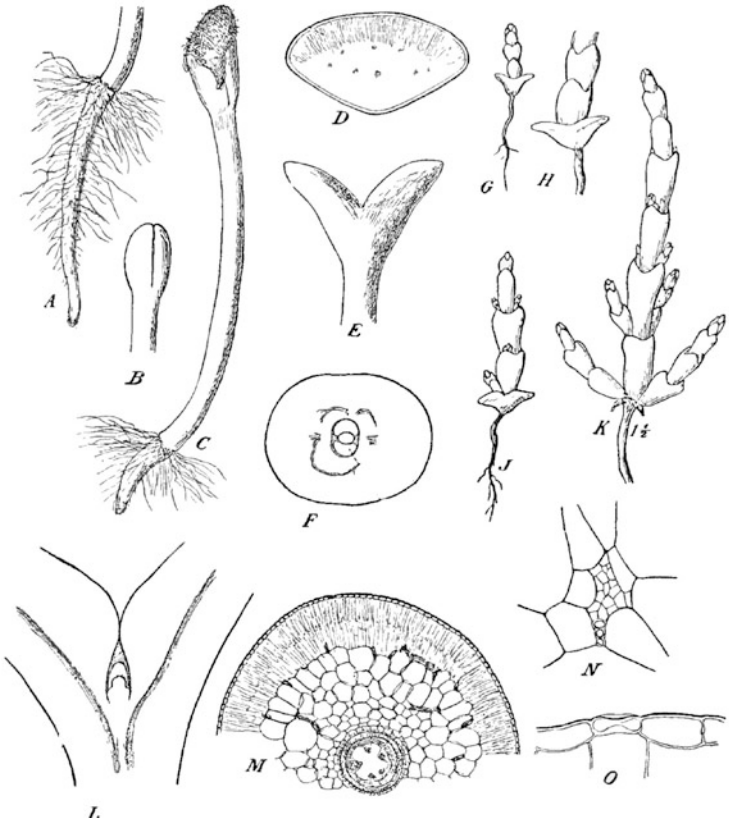


Fig. 129 *Salicornia herbacea*. (**A–C**), fragments of the seedling; (**D**, cross section through a cotyledon; **E**), unfolded cotyledons; (**F**), cross section through a cotyledon; (**G**–**K**), seedlings of different ages; (**L**), longitudinal section through a node; (**M**), cross section through a stem, through an articulation (**N**); (**O**), stomata (Warming 1906)

A synthesis of leaf anatomical features of salt-marsh species is presented in Tables 2, 3, 4, and 5 (Kearney 1900).

4 Morphological and Anatomical Adaptations of Littoral (Tropical, Nontropical) Halophytes (Seashore Plants, Sea-Coastal Plants, Strand Plants, Psammohalophytes)

As already underlined, diverse ecological conditions where halophytes vegetate delineate different contexts in which adaptations of halophytes can be discussed and approached. The terminology of halophytes may be difficult, tricky, and

Fig. 130 *Aster subulatus* – general aspect (Britton and Brown 1898)

sometimes confusing – different terms that are not perfectly interchangeable describe slightly different halophytic plants – but it covers a large spectrum of salt-ecological realities (Grigore 2008, 2014; 2019; Grigore and Toma 2010a, b, 2017; Grigore et al. 2014).

While not all littoral (seashore) plants are true halophytes, *stricto sensu* (see Grigore and Toma 2017, and references therein), the halophytes from littoral areas must be particularly approached; moving forward, halophytes from tropical and nontropical seashores should be differently approached.

There is a large list with classic papers dealing with morphological and anatomical adaptations of halophytes from littoral, being nontropical (Harshberger 1909; Chermezon 1910) or tropical (Warming 1897; Børgesen and Paulsen 1900; Warming 1906; Børgesen 1909; Denis 1919).

Børgesen and Paulsen (1898) divided the halophytic vegetation of the Danish islands (former Danish West Indies) in:

(a) The seagrass vegetation
(b) The sand strand vegetation
(c) The rocky coast vegetation
(d) The mangrove vegetation
(e) The marsh land vegetation near lagoons and salt ponds

Fig. 131 *Aster tenuifolius* – general aspect (Britton and Brown 1898)

Fig. 132 *Sabatia gracilis* – general aspect (Britton and Brown 1897)

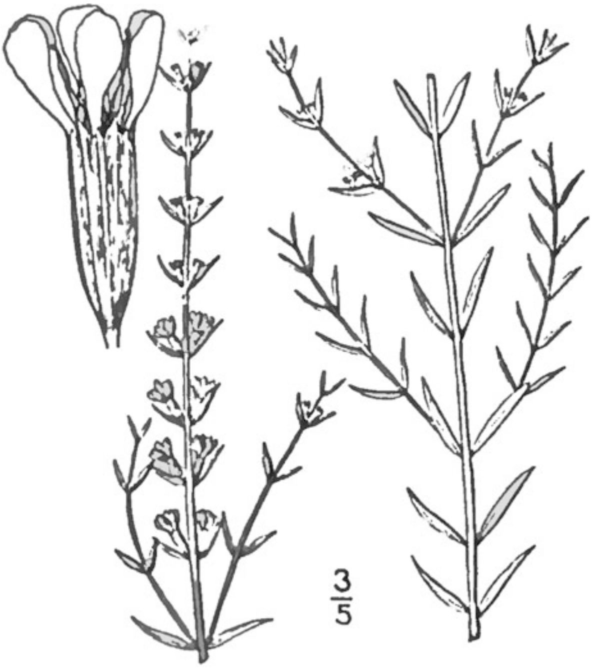


Fig. 133 *Lythrum lineare* – general aspect (Britton and Brown 1897)

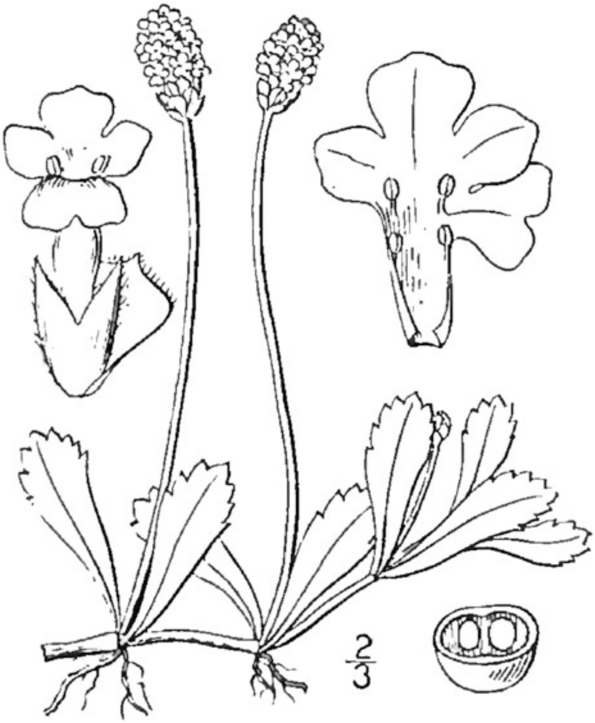


Fig. 134 *Lippia nodiflora* – general aspect (Britton and Brown 1898)

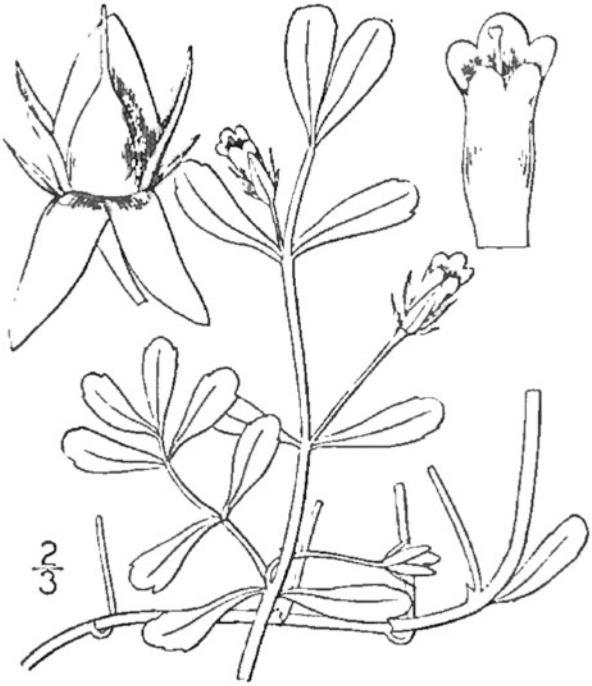


Fig. 135 *Monniera monniera* – general aspect (Britton and Brown 1898)

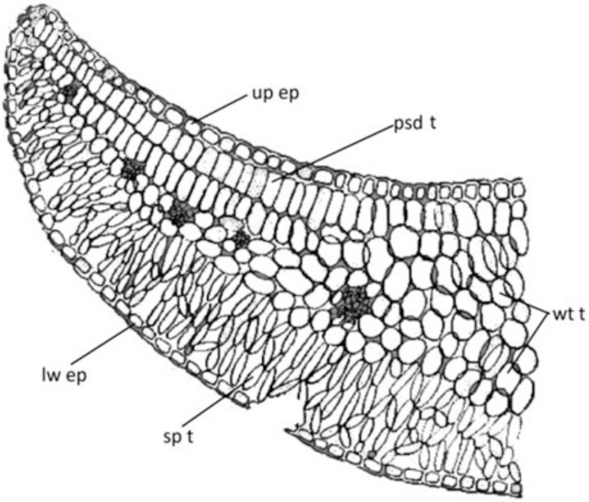


Fig. 136 *Aster subulatus*. Cross section through the leaf (up ep, upper epidermis; lw ep, lower epidermis; sp t, spongy tissue; psd t, palisade tissue; wt t, water storage tissue) (Harshberger 1909)

In a later study on the halophytic vegetation from the Danish West Indies, Børgesen (1909) added new material and consequently divided the coastal halophytic vegetation in:

A. The Hydrophyte Vegetation
I. The muddy and sandy soil vegetation
1. The seagrass (and algae) formation
B. The Halophyte Vegetation
I. The muddy soil vegetation

1. The mangrove formation
2. The *Salicornia* formation
3. The *Conocarpus* formation

II. The sand strand vegetation

1. The *Pes caprae* formation
2. The *Tournefortia* formation
3. The *Coccoloba*-Manchineel formation

III. The rocky coast vegetation

This chapter does not intend to deal with halophytic flora and vegetation, but this unique example of complexity of classifying halophytes clearly illustrates the heterogeneous nature of morphological and anatomical adaptations in halophytes that vegetate in different ecological conditions.

The vast majority of the Caribbean plants of the West Indies are shrubs, either larger as *Suriana maritima*, *Scaevola plumieri*, *Tournefortia gnaphalodes*, *Borrichia arborescens*, *Conocarpus erectus*, *Salicornia ambigua* (Fig. 137), *Batis maritima* (Fig. 138), *Heliotropium fruticosum* or *curassavicum*, *Ernodea littoralis*, and *Erithalis fruticosa* or smaller shrubs as *Cakile aequalis* and *Euphorbia buxifolia* (Warming 1897).

This salt-bush vegetation, which has been mentioned in direct connection with the mangrove vegetation and included under the *Salicornia* formation (Børgesen (1909)), occurs partly and especially on the wide marsh-like flats, which lie in the interior of lagoons, partly it also encircles the lagoons and salt ponds, where the mangrove vegetation is absent (Børgesen and Paulsen 1898, 1900). The West Indian *Salicornia* formation closely corresponds to the *Salicornia* formation of the Danish shores, and the West Indian species and *Salicornia herbacea* are also nearly related even perhaps the same species (Raunkier 1907). *Salicornia ambigua* has almost evenly thick, cylindrical branches, and they are sometimes erect, sometimes lying, rooting, and from the latter numerous side branches merge in such great number that compact bush arise (Fig. 137); this is an adaptation to wet, coastal, saline conditions.

Batis maritima has long, prostrate, rooting main branches often almost straight as a line, from which at each internode two opposite branches, the one more vigorous than the other, emerge upward; and a similar number of roots descend toward the salt

Table 2 Leaf anatomy of salt-marsh species from Ocracoke Island, general characters (Kearney 1900) (+, character present; /, imperfect development of the character)

	Leaf				*Epidermis*			
					Cuticle			
Species	Bifacial	Isolateral	Terete	Relatively thick	Thick	Wrinkled	Warty or granular	Radial walls undulate
Triglochin striata		+		+	+		+	
Spartina stricta								
Juncus roemerianus			+		+			
Sesuvium maritimum		+		+	+			
Tissa marina		+		+				+
Kosteletzkya virginica	+							
Ammannia koehnei		/						+
Vincetoxicum palustre		/			+	+		
Lippia nodiflora	/				+	+		
Monniera monniera		+				+		+
Iva frutescens		+		+	+	+		
Solidago sempervirens		/		+	+	+		
Aster tenuifolius		+		+	+	+		
Aster subulatus		+			+	+		
Baccharis halimifolia		+		+	+		+	
Borrichia frutescens		/		+				

Table 3 Leaf anatomy of salt-marsh species from Ocracoke Island, stomata in respect to epidermis (Kearney 1900) (+, character present; /, imperfect development of the character)

	Epidermis								
	Stomata								
Species	Both surfaces	Ventral surface only	Dorsal surface only	Prominent	Level with surface	Sunken	Parallel to leaf axis	Irregularly disposed	Subsidiary cells present
Triglochin striata	+				+		+		+
Spartina stricta					+				
Juncus roemerianus					+		+		
Sesuvium maritimum	+				+			+	
Tissa marina				+	+		+		
Kosteletzkya virginica	+			+			+		
Ammannia koehnei	+			+			/		
Vincetoxicum palustre	+				+				
Lippia nodiflora	+				+	/		+	+
Monniera monniera	+				+				

(continued)

Table 3 (continued)

	Epidermis								
	Stomata								
Species	Both surfaces	Ventral surface only	Dorsal surface only	Prominent	Level with surface	Sunken	Parallel to leaf axis	Irregularly disposed	Subsidiary cells present
Iva frutescens	+				+	+		+	
Solidago sempervirens	+				+				
Aster tenuifolius	+				+	+	/		
Aster subulatus	+				+		+		
Baccharis halimifolia	+			+	+		/		
Borrichia frutescens						/			

Table 4 Leaf anatomy of salt-marsh species from Ocracoke Island, hairs in respect to epidermis and collenchyma (Kearney 1900) (+, character present; /, imperfect development of the character)

	Epidermis										*Hypodermal collenchyma or collenchymatic tissue*	
	Hairs											
Species	Both surfaces	Ventral surface only	Dorsal surface only	Forming dense covering	Unicellular	Pluricellular	Simple	Branching	Stellate	Glandular hairs or scales	Only opposite veins	Elsewhere
Triglochin striata	+				+		+		+			
Spartina stricta					+							
Juncus roemerianus					+		+					
Sesuvium maritimum	+				+			+				
Tissa marina				+	+		+			+		
Kosteletzkya virginica	+			+			+				+	
Ammannia koehnei	+			+			/					
Vincetoxicum palustre	+				+							
Lippia nodiflora	+				+	/		+	+		+	

(continued)

Table 4 (continued)

	Epidermis										*Hypodermal collenchyma or collenchymatic tissue*	
	Hairs											
Species	Both surfaces	Ventral surface only	Dorsal surface only	Forming dense covering	Unicellular	Pluricellular	Simple	Branching	Stellate	Glandular hairs or scales	Only opposite veins	Elsewhere
Monniera monniera	+				+							
Iva frutescens	+				+	+		+		+	+	
Solidago sempervirens	+				+						+	
Aster tenuifolius	+				+	+	/				+	
Aster subulatus	+				+		+					+
Baccharis halimifolia	+			+	+		/				+	
Borrichia frutescens						/					+	

Table 5 Leaf anatomy of salt-marsh species from Ocracoke Island, stereome, chlorenchyma, water storage tissue, and vascular bundles (Kearney 1900) (+, character present; /, imperfect development of the character)

	Stereome			*Chlorenchyma*					*Water storage tissue*		*Vascular bundles*	
Species	Subepidermal	In leaf margins	Adjoining mestome bundles	Homogeneous	Differentiated	Palisade compact	Palisade interrupted by water tissue	Palisade converging toward midrib	Filling the interior of the leaf	Chiefly opposite the mestome bundles	With mestome sheath	With parenchyma sheath
Triglochin striata				+							+	+
Spartina stricta												
Juncus roemerianus	+		+	+		+					+	+
Sesuvium maritimum				+								
Tissa marina				+					+			
Kosteletzkya virginica			+		+	+						
Ammannia koehnei				+								
Vincetoxicum palustre				+								
Lippia nodiflora			+		/	+						

(continued)

Table 5 (continued)

Species	*Stereome*			*Chlorenchyma*					*Water storage tissue*		*Vascular bundles*	
	Subepidermal	In leaf margins	Adjoining mestome bundles	Homogeneous	Differentiated	Palisade compact	Palisade interrupted by water tissue	Palisade converging toward midrib	Filling the interior of the leaf	Chiefly opposite the mestome bundles	With mestome sheath	With parenchyma sheath
Monniera monniera				+								
Iva frutescens			+	+			+	+		+		
Solidago sempervirens			+	+			+			+		
Aster tenuifolius				+		+		+	+			
Aster subulatus				+		+				+		
Baccharis halimifolia			+	+				+		+		
Borrichia frutescens			+	+		+	+		+			

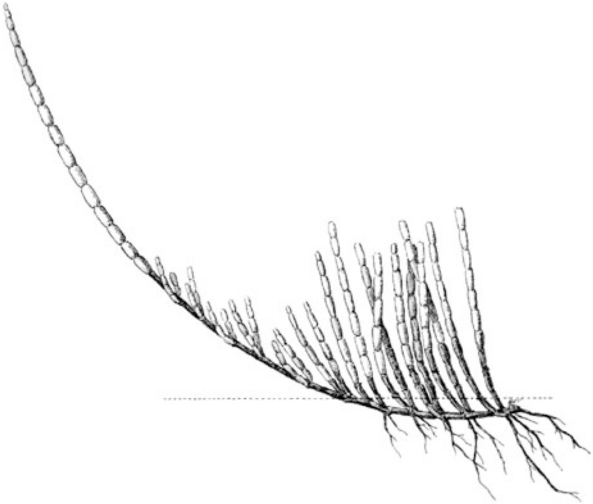


Fig. 137 *Salicornia ambigua*. A rooting branch from the outside of a larger bush. The dotted line indicates the surface of the ground (Børgesen 1909)

marshy soil (Fig. 138). The plant is commonly fresh green and has thick, fleshy, glossy, erect leaves. *Sesuvium portulacastrum* is also a typical halophyte with prostrate, rooting branch (Fig. 139).

Warming in his consistent study referring to structural characteristics of tropical halophytes from West Indies seashore (1897) described succulent or narrow-reduced leaves (Fig. 140), which is a xeromorphic adaptation (Grigore et al. 2014).

Based on his extensive results on anatomical adaptations of tropical halophytes, but also reported to those collected from Denmark, Norway, Greenland, Warming (1897) tried to cluster them in different groups. This consistent data are very important because they bring data about epidermis, chlorenchymatic tissues, water storage tissue, bundle sheaths, and hypodermis and relation between them in the context of saline conditions.

Thus, Warming described:

A. *Dorsiventral leaf – differs little or nothing from usual leaves. No water tissue, all leaf cells are green tissue cells. No real bundle (veins) sheaths.* The leaves are distinctly dorsiventral, reminding of the common profile of mesophilic leaves. This foliar type also occurs in halophytic species from moderate and cold climates, but there are also Mediterranean and tropical plants among them. Vascular sheaths could be found, but they are weakly pronounced. In this group can be included *Glaux maritima* (Figs. 141 and 142), *Erythraea vulgaris*, *Plantago major f. scopulorum*, *Cochlearia officinalis*, *C. anglica*, *Teucrium polium*, *Canavalia obtusifolia*, *Acanthospermum xanthioides*, and *Diodia radicans*.

B. *Dorsiventral leaf of the ericoid type (Frankenia laevis)* (see Figs. 81 and 82).

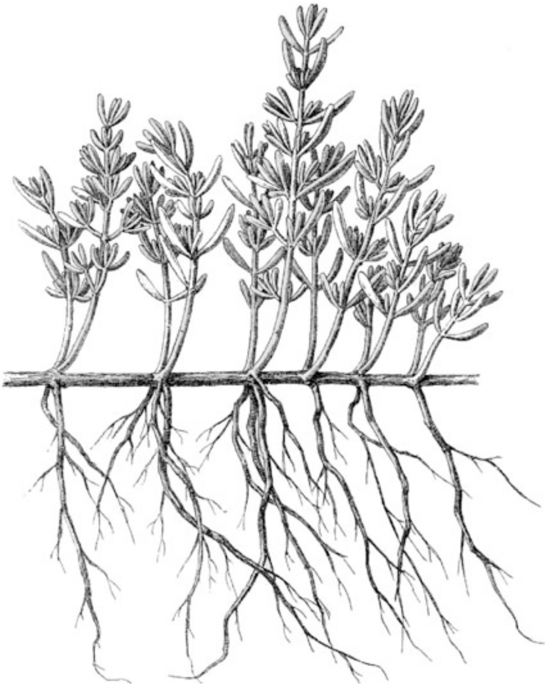


Fig. 138 *Batis maritima* – a part of a prostrate, rooting branch (Børgesen 1909)

C. *Intermediate forms between dorsiventral and isolateral leaves. In most, there are chlorophyll-containing bundle sheaths.* After the aspect of the epidermis, it must be referred to the dorsiventral type, but after the succulence of the leaf, to the isolateral. The group is close to that described at the point "A" and contains, like this, species that vegetate in moderate climates: *Mertensia maritima* (Fig. 143), *Silene maritima*, *Chenopodium ambrosioides*, *Euphorbia paralias*, *Armeria vulgaris*, and *Juncus gerardi.*
D. *Isolateral leaves with chlorophyll-containing interlayer*, clear sheaths around bundles. The leaves are isolateral. Mesophyll is a palisade tissue with a thinner or thicker intermediate layer, which has less chlorophyll content than the palisade tissue, but is not yet a genuine pure water tissue. The nervures lie in the middle layer and have clear sheaths (at least on the larger nerves). In the latter species, there is more than one layer of clear cells that connect to the nerves: *Plantago maritima* (Fig. 144), *Plantago coronopus*, *Plantago crassifolia* (Figs. 23 and 145), *Silene inflata*, *Statice monopetala*, *Tetragonolobus siliquosus*, *Matricaria inodora*, *Glyceria maritima*, *Ipomoea pes-caprae* (Fig. 146), *I. acetosaefolia*, *Baccharis dioica*, and *Ernodea littoralis* (Fig. 147).
E. *Isolateral leaves with more or less developed chlorophyll-containing interlayer*, chlorophyll-containing bundle sheaths (but not starch sheaths) in some species, indistinct or no sheaths in others. The leaves are in this group

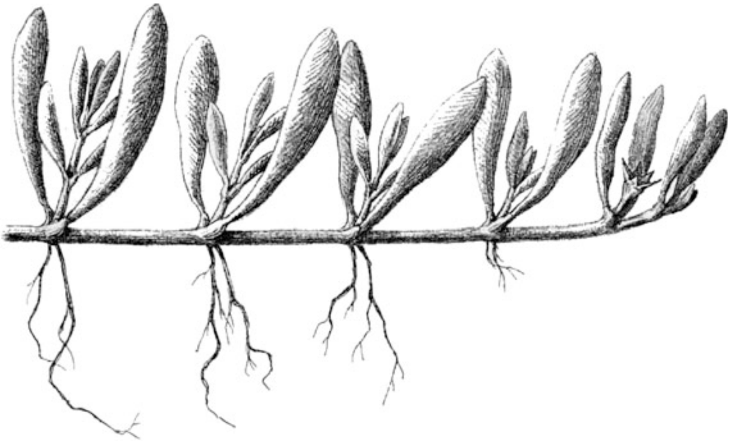


Fig. 139 *Sesuvium portulacastrum*, prostrate, rooting branch (Børgesen 1909)

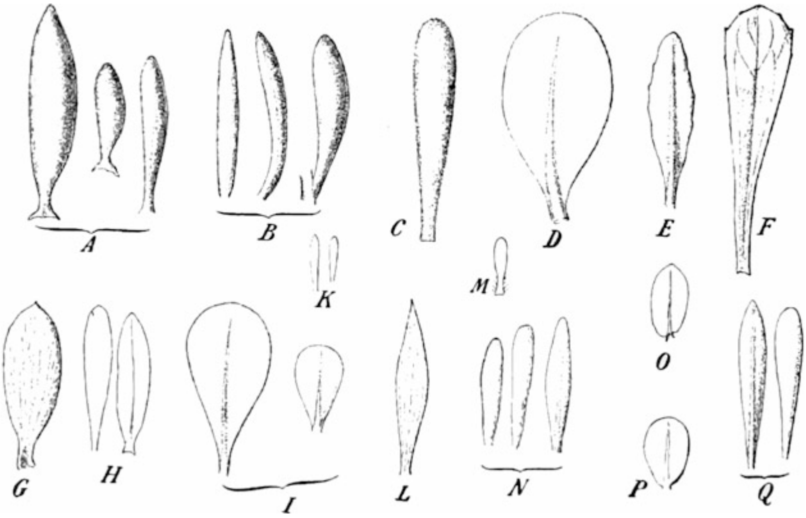


Fig. 140 General form of leaves of tropical halophyte species: *Sesuvium portulacastrum* (**A**), *Batis maritima* (**B**), *Tournefortia gnaphalodes* (**C**), *Scaevola plumieri* (**D**), *Cakile aequalis* (**E**), *Acicarpha spathulata* (**F**), *Borrichia arborescens* (**G**), *Philoxerus vermiculatus* (**H**), *Baccharis dioica* (**I**), *Alternanthera muscoides* (**K**), *Ernodea littoralis* (**L**), *Pectis humifusa* (**M**), *Heliotropium curassavicum* (**N**), *Euphorbia buxifolia* (**O**), *Portulaca oleracea* (**P**), *Suriana maritima* (**Q**) (Warming 1897)

isolateral. The leaf mesophyll is formed by palisade tissue and a thin intermediate layer, which may be more or less chlorenchymatic, but cannot yet be called water tissue and is not sharply distinct from palisade tissue. The nervures are confined to this middle layer: *Acicarpha spathulata* (Fig. 148), *Atriplex*

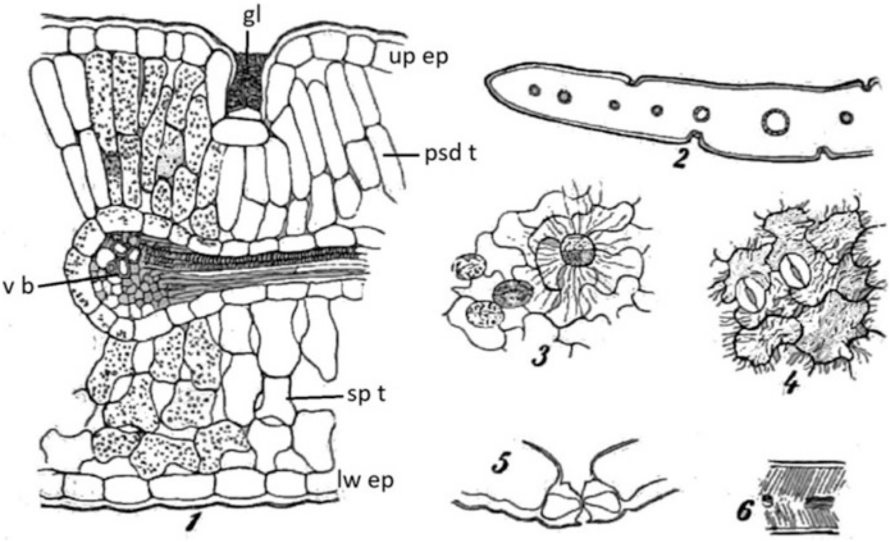


Fig. 141 *Glaux maritima* (1, cross section through the leaf; 2, general contour of the leaf cross section; 3, upper epidermis, stomata, and gland; 4, lower epidermis, stomata; 5, stomata; 6, general aspect of cross section through the leaf; gl, gland; up ep, upper epidermis; lw ep, lower epidermis; v b, vascular bundle; sp t, spongy tissue) (Warming 1897)

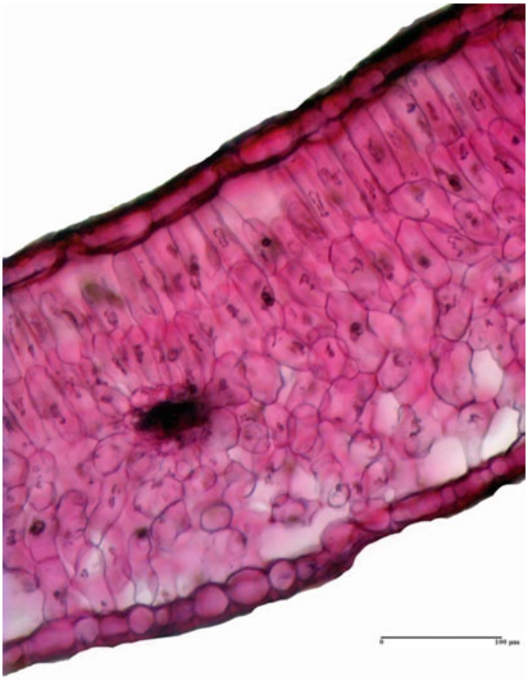


Fig. 142 *Glaux maritima*. Cross section through the leaf (Grigore et al. 2014)

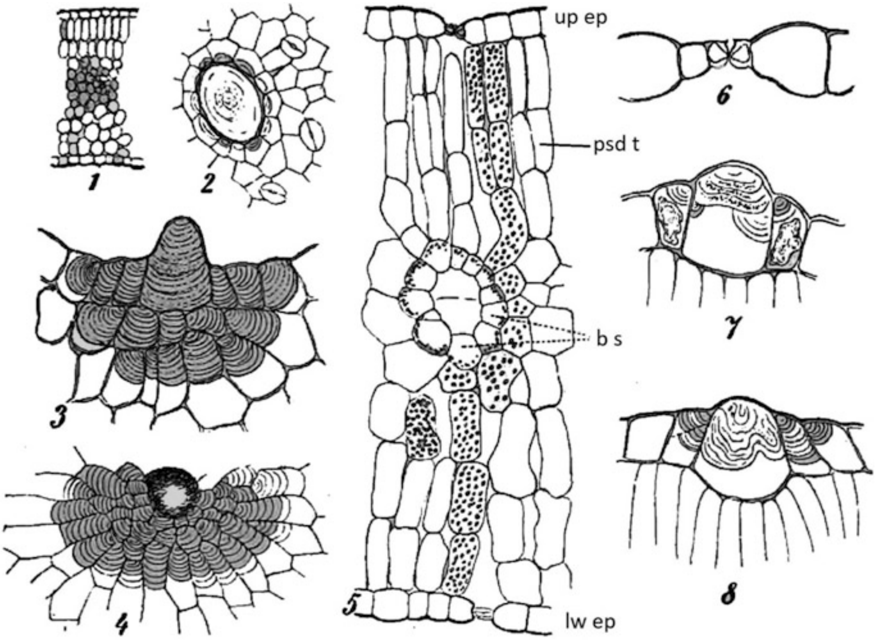


Fig. 143 *Mertensia maritima* (1–4, collected from Jyllands Vestkyst; 5–7, from Tromso; 8, Iceland); 1, dorsiventral leaf; 2–4, cystolith cells; 5, cross section through the lamina; 6, stomata; 7–8, cystolith cells; up ep, upper epidermis; psd t, palisade tissue; b s, bundle sheath; lw ep, lower epidermis) (Warming 1897)

hastata, *Alisne (Halianthus) peploides*, *Silene nicaeensis*, *Conocarpus erecta* (Fig. 149), *Inula crithmoides* (see Fig. 27), *Aster tripolium* (Figs. 150, 151, and 152 – where the isolateral character of the leaf may vary depending on the level of cross section through the leaf), *Suriana maritima* (Fig. 153), *Beta vulgaris*, *Cakile aequalis* (Fig. 154), *Cakile maritima* (Fig. 155), *Crambe maritima*, *Heliotropium currasavicum*, *Polygonum maritimum*, *Bupleurum tenuissimum*, *Silene otites*, *Crucianella maritima*, *Statice limonium*, *Statice rariflora*, *Medicago marina* (Fig. 156), *Malcolmia littorea*, *Polygala cyparissias*, *Convolvulus soldanella*, *Sedum anglicum*, and *Halocnemum strobilaceum*.

F. *Isolateral leaves, the intermediate layer is sharply delimited from the palisade tissue and is more related to a water tissue*. No special sheaths around vascular bundles. The leaves are isolateral, and the leaf succulence is mainly due to palisade tissue: *Suaeda maritima* (Figs. 16 and 157), *Suaeda (Sarcocornia) fruticosa* (see Figs. 13, 14, and 158), *Spergularia marina* (Fig. 159), *S. media* (see Figs. 28 and 29), *Obione (Halimione) portulacoides* (Fig. 160), and *Halimus* sp.

G. *As group F but with hypodermic water tissue*. In *Eryngium maritimum* (Fig. 161 – Toma 1979), its water tissue may still have a little chlorophyll, so it is not quite clear if it has a hypodermic genuine water tissue.

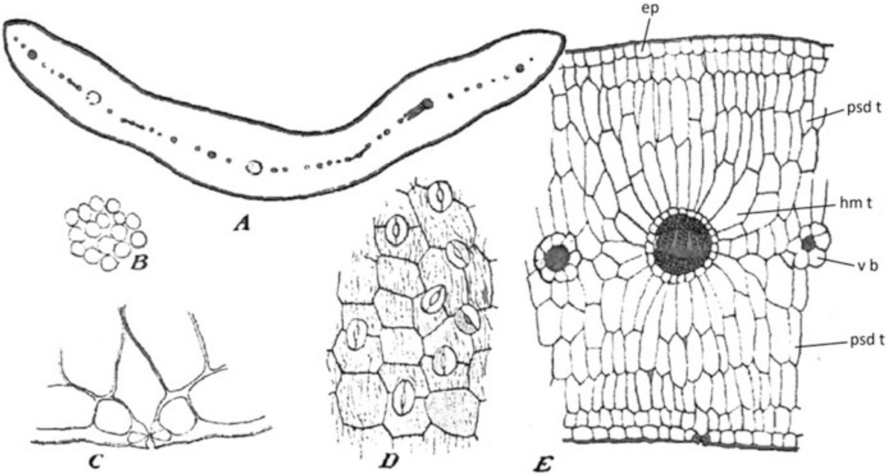


Fig. 144 *Plantago maritima* (A, general aspect of lamina; B, cross section through palisade cells; C, stomata; D, epidermis; E, cross section through the leaf; ep, epidermis; psd t, palisade tissue; v b, vascular hm t, homogeneous tissue) (Warming 1891)

H. *Isolateral leaves with an intermediate layer that is genuine water tissue.* The vascular bundles lie in one plane and have no contact with the chlorenchyma. No vascular sheaths: *Tournefortia gnaphalodes* (Fig. 162) and *Scaevola plumieri* (Fig. 163).

I. *Isolateral leaves with central water tissue in which the main nervures lie*. A net of thin nervures start from them to all sides, but does not enter into contact with palisade tissue. There are no bundle sheaths. The leaves, which are very thick, have a large, colorless layer (water tissue), surrounded by chlorenchyma tissue for all sides: *Sesuvium portulacastrum* (Fig. 164), *Borrichia arborescens* (Fig. 165), *Zygophyllum album*, *Batis maritima* (Fig. 166), *Echinophora spinosa*, and *Triglochin maritimum.*

J. *Similar to the type I, but the morpho-anatomical conditions indicate the "leafless" stems (Salicornia type)*: *Salicornia herbacea* (Fig. 129; see Figs. 45 and 48, *Salicornia patula*; 49, *Salicornia australis*; 50 and 51, *Salicornia ramosissima*; 52, *Salicornia glauca*)*, Ephedra distachya, and Tamarix gallica.*

K. *Isolateral leaves with large central water tissue, surrounded by a starch sheath (internal chlorenchyma), which is again surrounded by a palisade tissue (external chlorenchyma).* There are fine nerves in contact with internal chlorenchyma (*Salsola* type): *Salsola kali* (Fig. 167; see Figs. 38 and 107). This corresponds to a C_4 photosynthetic type (Grigore 2008; Grigore et al. 2014; Grigore and Toma 2017).

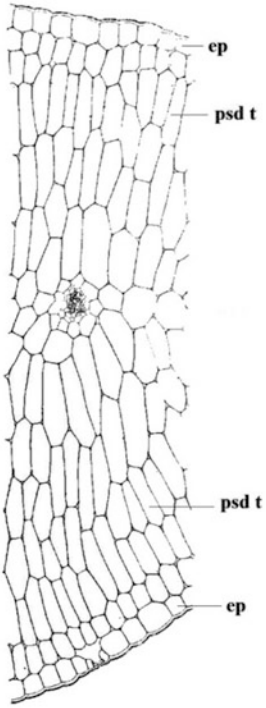


Fig. 145 *Plantago crassifolia*, cross section through the lamina; ep, epidermis; psd t, palisade tissue (Chermezon 1910)

L. *Like "L" type, but the morphological and anatomical features suggest a "leafless" stem (Haloxylon type): Haloxylon ammodendron* (Fig. 168 and 169).

M. *More or less dorsiventral or isolateral leaves with complete starch bundle sheaths*, wreath palisades in many species. Water storage tissue is present in smaller or larger extent: *Heliotropium fruticosum* (Fig. 170), *Pectis humifusa* (Fig. 171), *Euphorbia bahiensis*, *E. buxifolia* (Fig. 172), *Portulaca oleracea*, *Philoxerus vermiculatus* (Fig. 173), *Sporobolus virginicus*, *Stenotaphrum americanum*, and *Cynodon dactylon.*

N. *As previous type, but the starch bundle sheath is opened on the phloem side. E*ven around the smallest nerves, the sheath is interrupted: *Atriplex farinosa* (Fig. 174), *Atriplex cristata*, *Atriplex halimus* (Fig. 175), and *Atriplex laciniata.* It is also a C_4 photosynthetic type (Grigore and Toma 2017).

O. *As N type, but a mechanical sheath is inserted between the starch bundle sheath (internal chlorenchyma) and the external chlorenchyma tissue, which is more or less a typical Kranz palisade*: *Remirea maritima* (Fig. 176) *and Galilea mucronata.*

P. *Dorsiventral leaf with hypodermic water storage tissue, which has different disposition: Lippia nodiflora* (Fig. 177), *Erithalis fruticosa, and Sophora littoralis.*

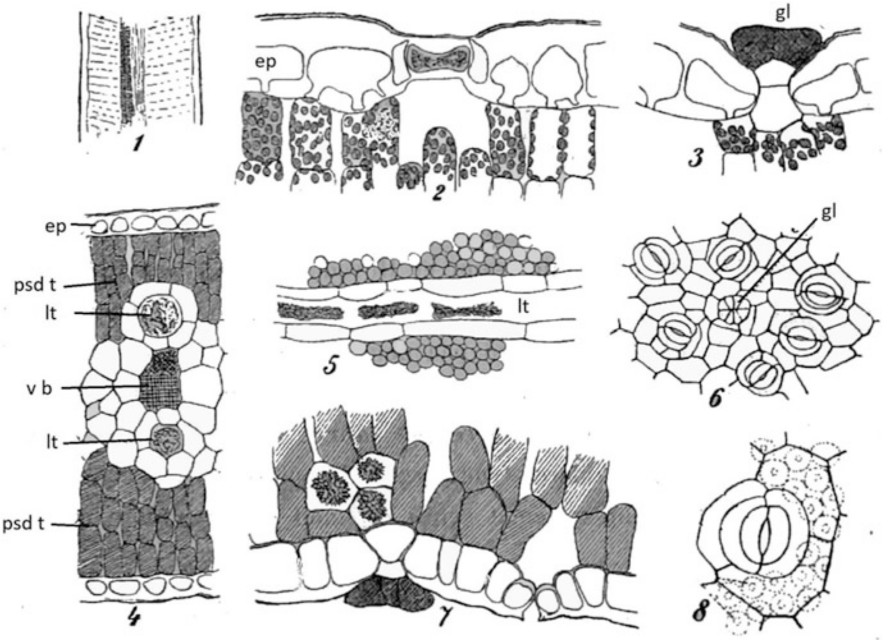


Fig. 146 *Ipomoea pes-caprae* (1, general aspect of a cross section through a leaf; 2, aspect of upper epidermis level; 3, salt gland (gl); 4, cross section through lamina; 5, laticifer (lt) surrounded by nervures; 6, epidermis (ep), with stomata and salt gland (gl); 7, lower epidermis aspect; 8, stomata; psd t, palisade tissue; v b, vascular bundle) (Warming 1897)

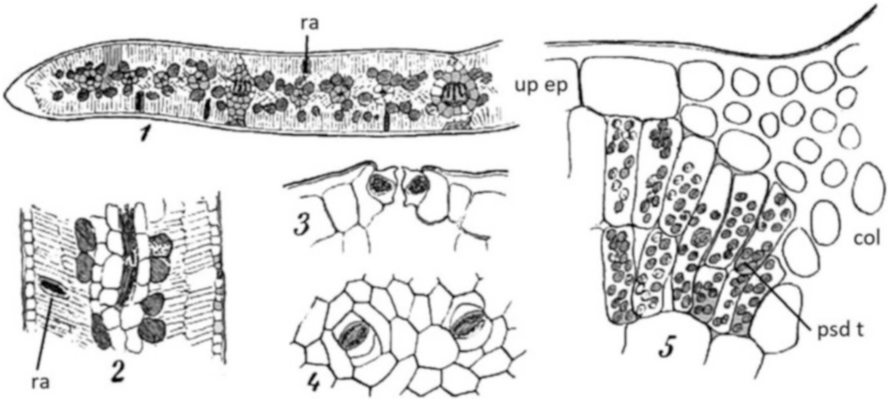


Fig. 147 *Ernodea littoralis* (1–2, general aspect of a cross section through a leaf; 3, stomata; 4, epidermis, front view; 5, cross section through lamina, detail; up ep, upper epidermis; ra, raphid; col, collenchyma; psd t, palisade tissue) (Warming 1897)

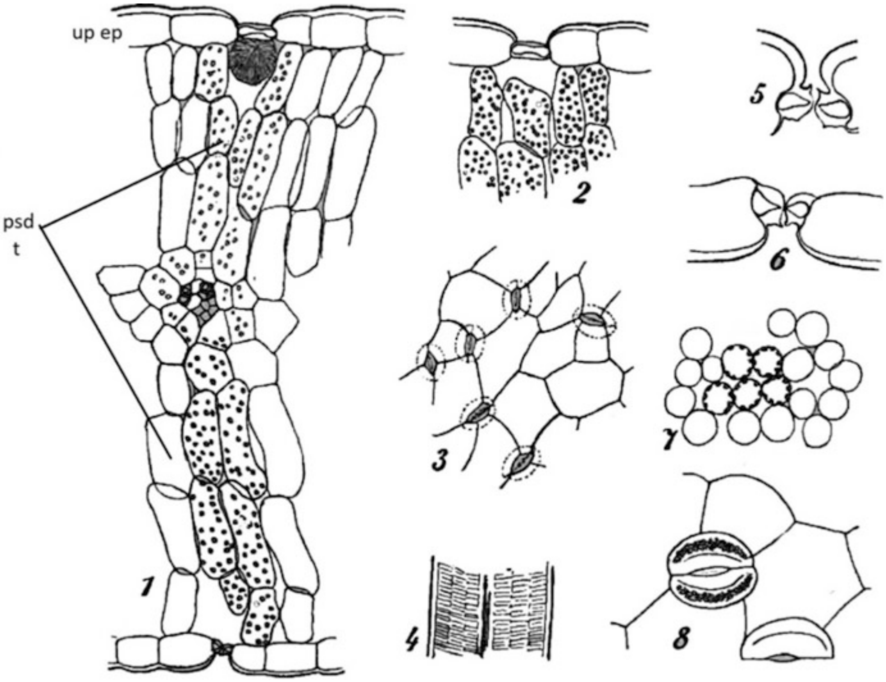


Fig. 148 *Acicarpha spathulata* (1, cross section through a leaf; 2, stomata, cross section; 3, epidermis, front view; 4, cross section through lamina, general view; 5,6, up ep stomata; 7, palisade cells, observed from upper side; 8, stomata, detail, front view; up ep, upper epidermis; psd t, palisade tissue) (Warming 1897)

5 Mangroves (Tropical Coastal Halophytes, Littoral Swamp Forest, Tidal Forest)

The term mangrove is manifold; in this subsection, the morphological and anatomical adaptations of mangrove species are discussed in general terms, without following the classification of halophytic coast vegetation above mentioned (Børgesen and Paulsen 1898, 1900; Børgesen 1909).

Davis (1940) refers to mangrove as a general term applied to plants, which live in muddy, loose, wet soils in tropical tide waters. According to Macnae (1968), mangroves are trees or shrubs that grow between the high water mark of spring tides and a level close to but above mean sea level. They are circumtropical on sheltered shores and often grow along the banks of rivers as far inland as the tide penetrates (Walsh 1974).

Børgesen (1909) dealt with mangroves from Danish West Indies as a formation of tree-like evergreen plants growing on the sheltered shores, partly in shallow, salt, or

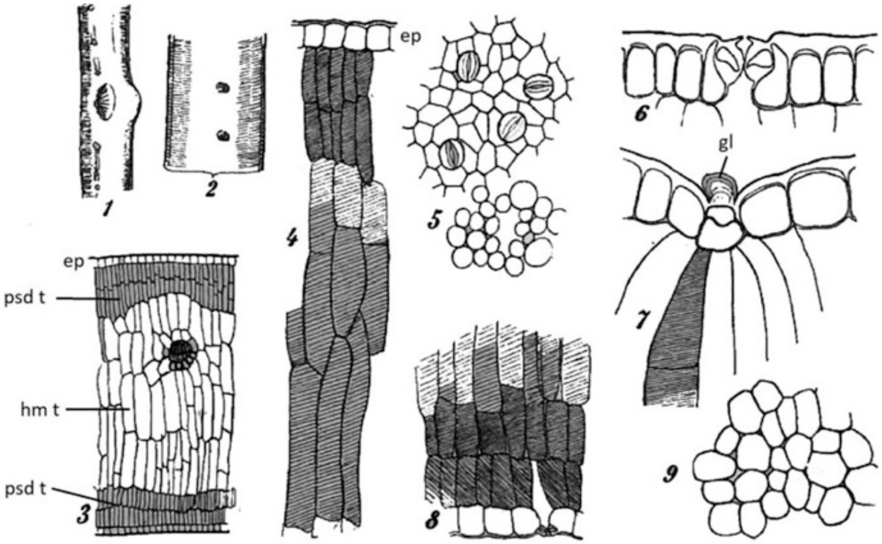
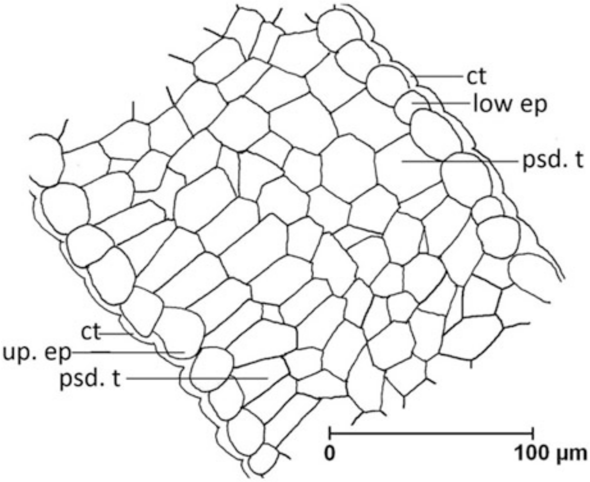


Fig. 149 *Conocarpus erecta* (1,2, cross section through a leaf, general view; 3,4, cross section through a leaf, details; 5, epidermis and palisade cells, front view; 6, stomata, detail; 7, gland (probably salt gland); 8, lower epidermis and palisade tissue, details; 9, cells of homogeneous tissue, front view; ep, epidermis; psd t, palisade tissue; hm t, homogeneous tissue) (Warming 1897)

Fig. 150 *Aster tripolium*, cross section through a leaf, upper level; low ep, lower epidermis; ct, cuticle; up ep, upper epidermis; psd t, palisade tissue (Grigore and Toma 2010a; Grigore et al. 2014)



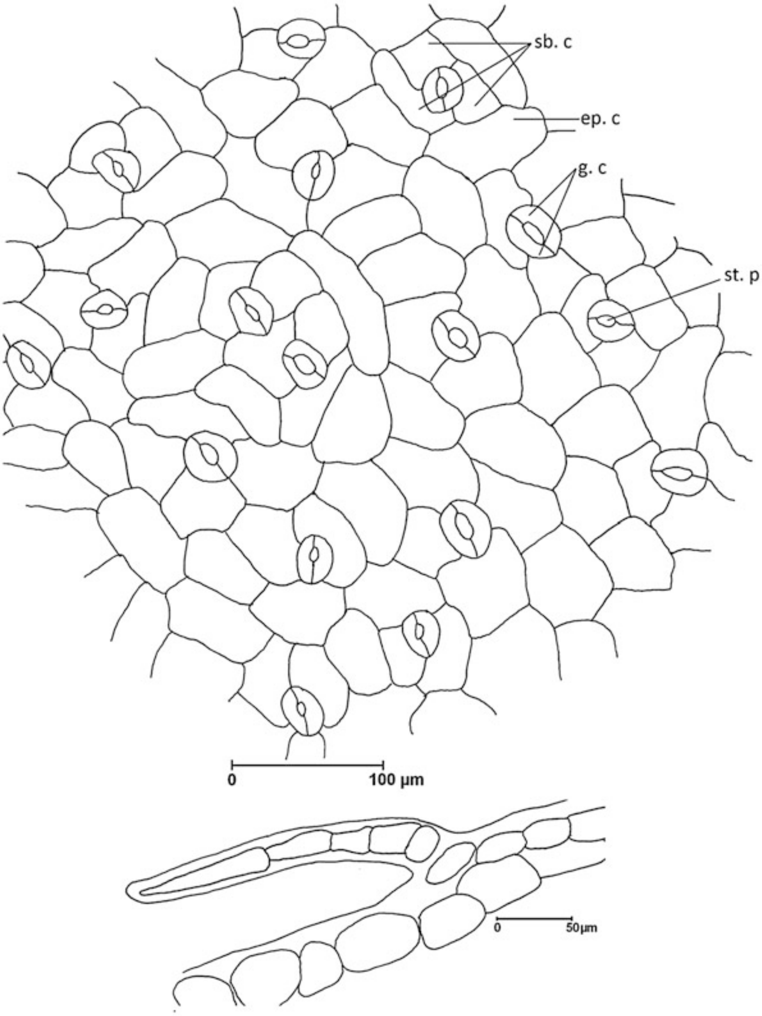


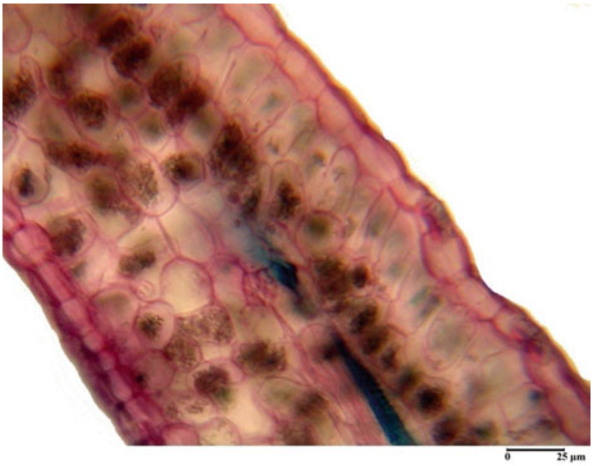
Fig. 151 *Aster tripolium*, lower epidermis, front view (above) and a protecting hair (below); sb c, subsidiary cells; ep c, epidermal cells; g c, guard cells; st p, stomatal pore (Grigore and Toma 2010a; Grigore et al. 2014)

brackish water, partly on low-lying soil that is comparatively rarely, and sometimes perhaps never covered by salt or brackish water.

In very general terms, there seem to be five basic requirements for extensive mangal development: tropical temperatures, fine-grained alluvium, shores free of strong wave and tidal action, salt water, and large tidal range (Walsh 1974).

Warming (1877, 1883, 1909) described very well the environmental conditions where mangrove species vegetate. They occur by all tropical seas, especially on flat,

Fig. 152 *Aster tripolium*, cross section through a leaf, upper level (Grigore and Toma 2010a; Grigore et al. 2014)



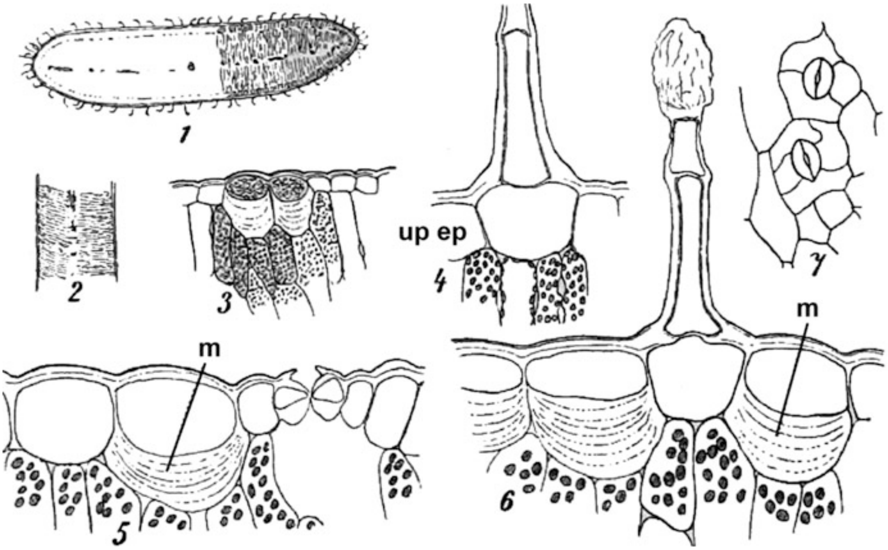


Fig. 153 *Suriana maritima;* 1–2, general aspect of the cross section through a leaf; 3,5, details of epidermis and palisade cells; 4, trichome; 6, epidermis with a trichome; 7, epidermis, front view; m, mucilage (Warming, 1897)

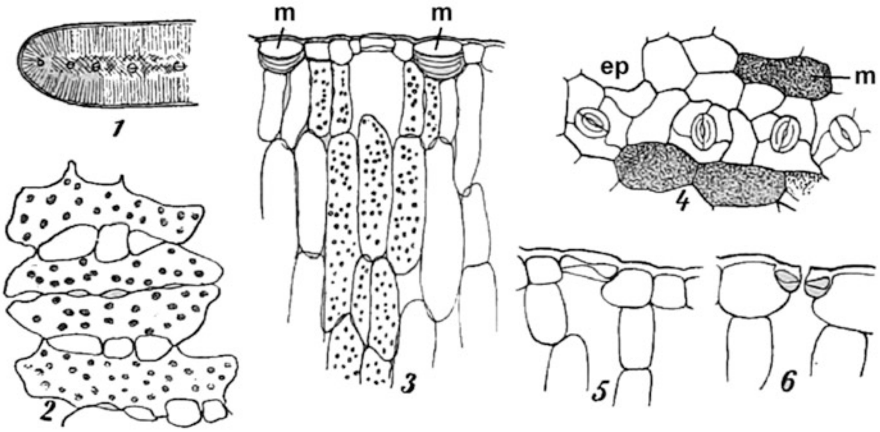
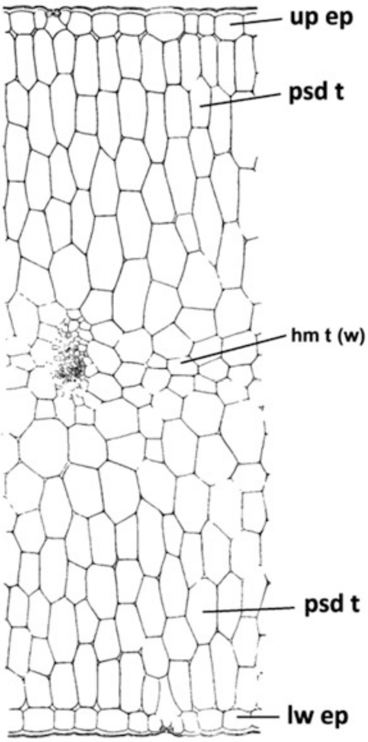


Fig. 154 *Cakile aequalis*; 1, general aspect of the cross section through a leaf; 2, chlorenchymatic parenchyma cells from median layer, with nervures; 3, details of epidermis and palisade cells; 4, epidermis, front view; 5, 6, stomata, cross section; ep, epidermis; m, mucilage (Warming 1897)

Fig. 155 *Cakile maritima*, cross section through a leaf; up ep, upper epidermis; lw ep, lower epidermis; psd t, palisade tissue; hm t (w), homogeneous tissue, resembling of a water tissue (Warming 1897)



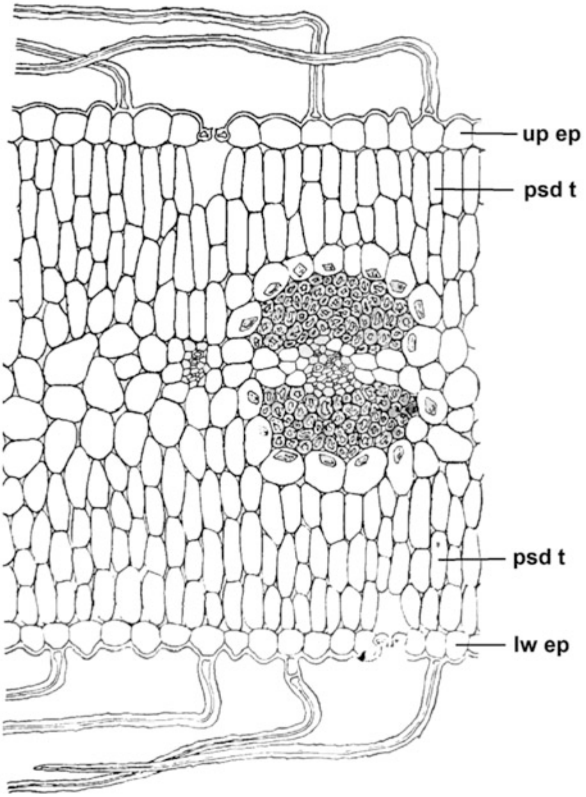


Fig. 156 *Medicago marina*, cross section through a leaf; up ep, upper epidermis; lw ep, lower epidermis; psd t, palisade tissue (Chermezon 1910)

muddy shores, where the water is relatively calm, as in lagoons, inlets, estuaries, but not where rocky soil and breakers prevail. The soil is flooded with water either permanently or at high tide. In many places mangrove vegetation extends far inland along the banks of large rivers. The water is usually more or less brackish, as far as the tide extends.

The soil, which in places is not covered with water at low tide, is soft, deep, black mud, and full of rotting, organic bodies in which bacteria abound. The water between the trees may be covered with dirty film and bubbles of gas rising from the bottom burst at the surface.

The morphological and anatomical adaptations of mangrove species are well-documented (Warming 1877, 1909; Liebau 1914; Bowman 1917; Schimper 1891, 1898, 1903; Børgesen and Paulsen 1898, 1900; Børgesen 1909).

Warming (1909) reveals the adaptations of mangroves.

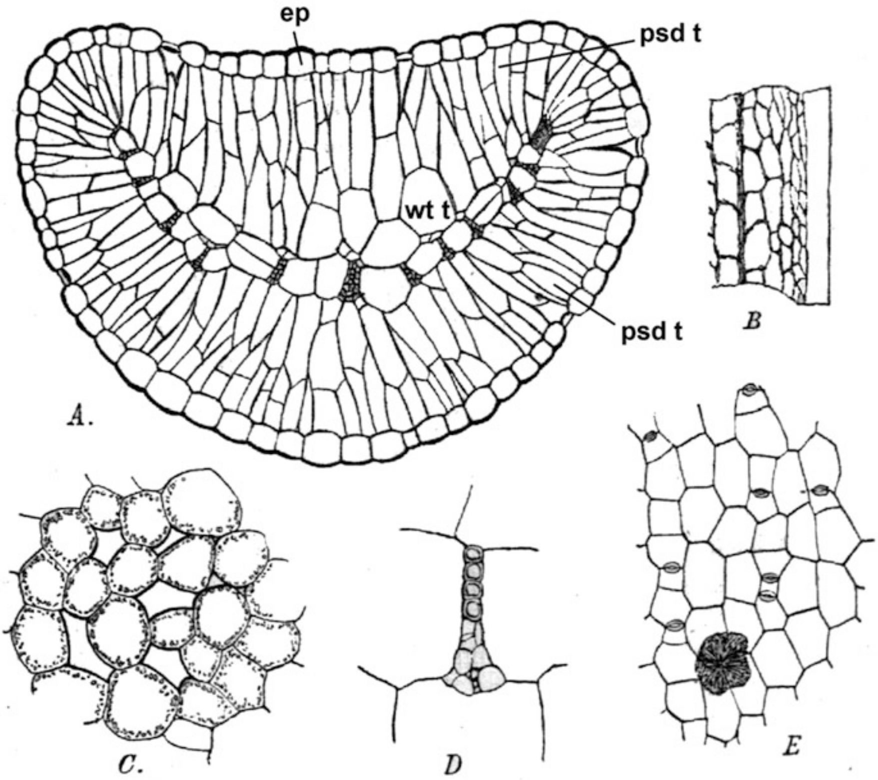


Fig. 157 *Suaeda maritima*; **A**, cross section through a leaf; **B**, longitudinal section through a leaf, showing the nervure network; **C**, cross section through palisade tissue and vascular bundle (**D**); **E**, epidermis, front view; ep, epidermis; psd t, palisade tissue; wt t, water storage tissue (Warming 1891)

a. Fixation in the Substratum with Aerial Prop Roots

The degree of softness of the soil and the variety in depth of water evoke differences and cause the species to assume a zonal distribution into associations. On the landward side, mangrove plants vanish and are replaced by other shrubs and trees. Furthest out toward the sea are those that are best capable of fixing themselves in deep water, namely, species of *Rhizophora*; within these, in shallower water or on drier ground, succeed those species that have smaller capabilities in this respect, species of *Avicennia*, *Bruguiera*, *Aegiceras*, *Carapa*, and others. The species of *Rhizophora* are fixed by prop roots that are aerial roots, which spring from the main trunk and form arched stilts which penetrate the ground. Sometimes, the aerial roots arise adventitiously from the lower branches of the tree; they curve down to the ground in an arching fashion. These bow-like

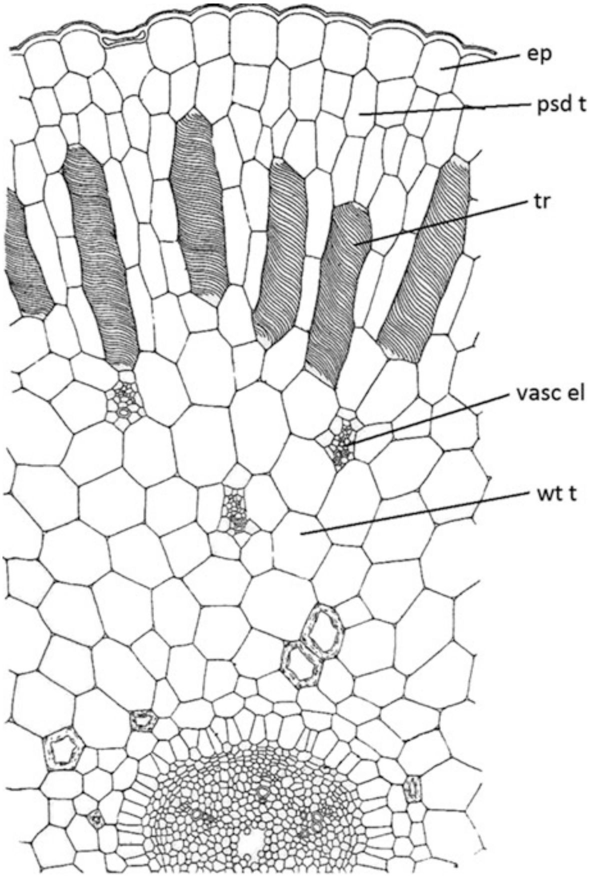


Fig. 158 *Sarcocornia fruticosa*, cross section through a succulent segment; ep, epidermis; psd t, palisade tissue; tr, tracheoidioblasts; vasc el, vascular elements; wt t, water storage tissue (Chermezon 1910)

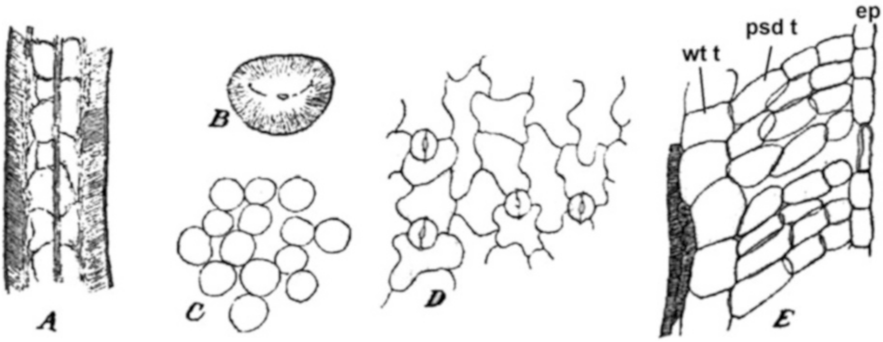


Fig. 159 *Spergularia marina*; **A**, longitudinal section through a leaf, general aspect; **B**, cross section through a leaf, general aspect; **C**, palisade cells in cross section; **D**, epidermis with stomata, front view; **E**, cross section through a leaf, detail; ep, epidermis; psd t, palisade tissue; wt t, water storage tissue (Warming 1891)

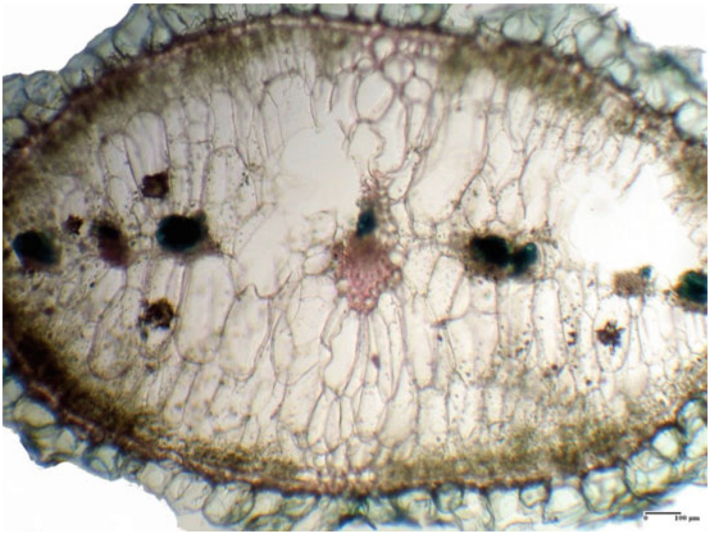


Fig. 160 *Halimione portulacoides*, cross section through a leaf (Grigore et al. 2014)

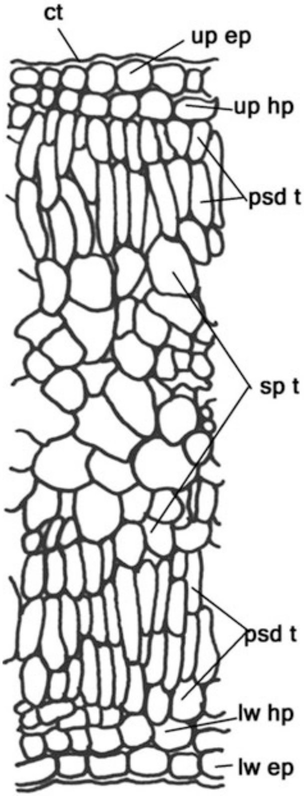


Fig. 161 *Eryngium maritimum*, cross section through the leaf; ct, cuticle; up ep, upper epidermis; up hp, upper hypodermis; psd t, palisade tissue; sp t, spongy tissue; lw ep, lower epidermis; lw hp, lower hypodermis (Toma et al. 1979)

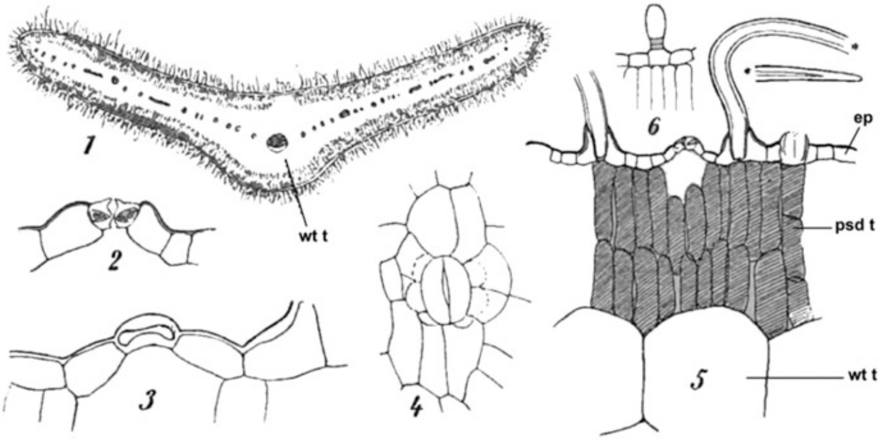


Fig. 162 *Tournefortia gnaphalodes*; 1, cross section through a leaf, general aspect; 2,3, stomata, cross section; 4, stomata, front view; 5, cross section through a leaf, detail; 6, trichome; ep, epidermis; psd t, palisade tissue; wt t, water storage tissue (Warming 1897)

roots upon which the tree depends are very numerous; the foundation of the tree is firmer, and its power of resistance to bending, which may be caused by wind or movements of the water, is greater than if the stem was the sole support (Figs. 178 and 179).

The anatomical construction of these roots agrees with the unusual nature of the demands to which they are exposed as supporting structures and deviates from that of most other roots in that the mechanical tissue is made to assume a tubular arrangement around large pith (Fig. 180). Similar prop roots are possessed by *Ceriops* and *Acanthus ilicifolius*. The lower parts of these prop roots are often beset with algae.

b. Respiratory Roots (Pneumatophores)

Respiration is a process under difficulty in the soil, which is water-logged, rich in organic bodies, and poor in oxygen. For this reason all the mangrove plants have a strongly developed system of aerenchyma; the submerged parts are very spongy and soft in structure; stomata and unusually large lenticels on parts projecting above water place the atmosphere in communication with the intercellular spaces. The prop roots of *Rhizophora* serve as respiratory roots. Other species possess quite peculiar respiratory roots (pneumatophores). *Avicennia* has erect, unbranched “asparagoid” roots a foot in height; these stand in very long rows, which radiate from the tree and indicate the position of the horizontal roots from which they emerge (Figs. 181, 182, and 183). Their respiratory role is revealed by anatomical structure (Fig. 184).

Similar respiratory roots are found in *Sonneratia acida*, *Laguncularia racemosa* (Figs. 185 and 186), *Bruguiera caryophyllaeoides* (Fig. 187a), *B. gymnorrhiza* (Fig. 187b), and *Carapa obovata* (Fig. 187c); bent knee-like roots, with the knee projecting above water, occur in *Bruguiera* and to a less extent in *Lumnitzera*, while comb-like prolongations connected with the root

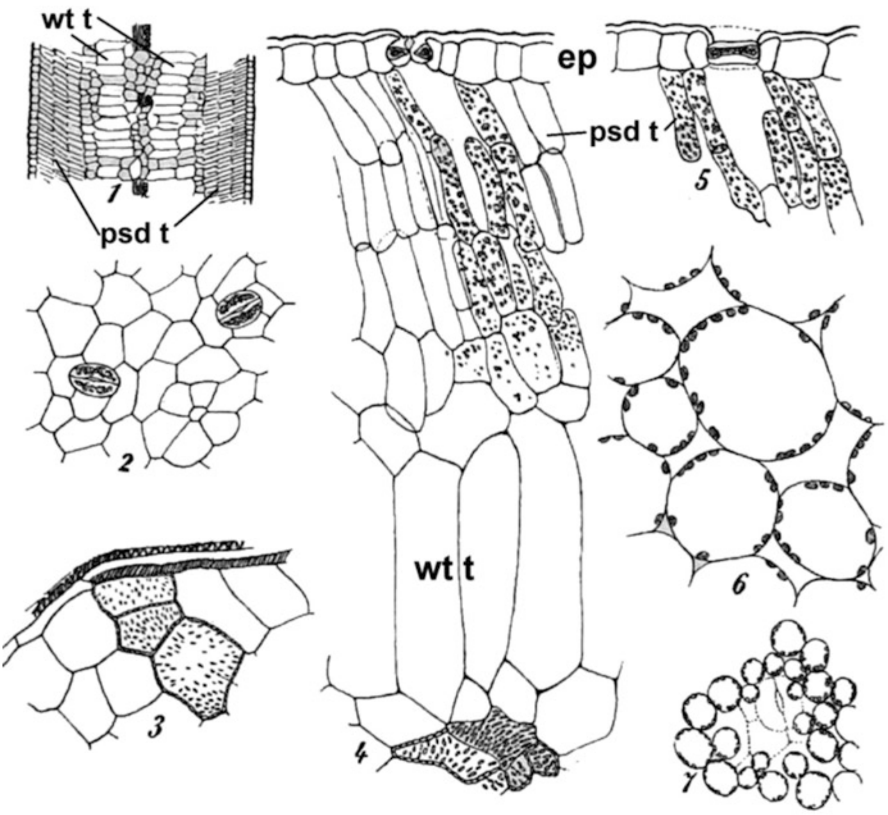


Fig. 163 *Scaevola plumieri*; 1, cross section through a leaf, general aspect; 2, epidermis, front view; 3, tracheids, attached to nervures; 4,5, cross section through a leaf, details; stomata, cross section; 6,7, palisade cells, cross section; tr, trichome; ep, epidermis; psd t, palisade tissue; wt t, water storage tissue (Warming 1897)

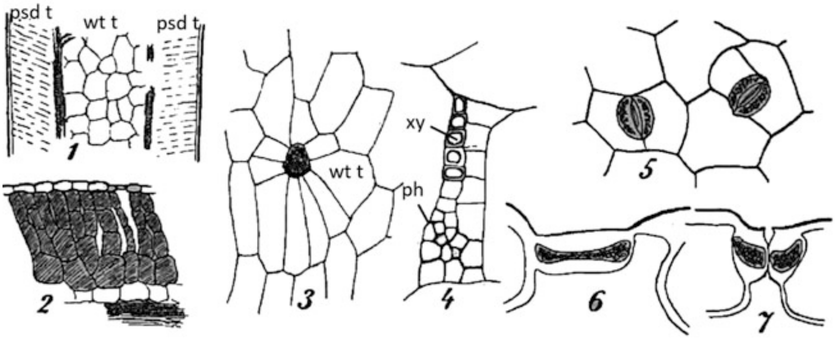


Fig. 164 *Sesuvium portulacastrum*; 1, cross section through a leaf, general aspect and detail (2); 3, water storage tissue (wt t) and a vascular bundle, cross section; 4, cross section through a nervure; 5, stomata, front view; 6,7, stomata, cross section; psd t, palisade tissue; wt t, water storage tissue; xy, xylem; ph, phloem (Warming 1897)

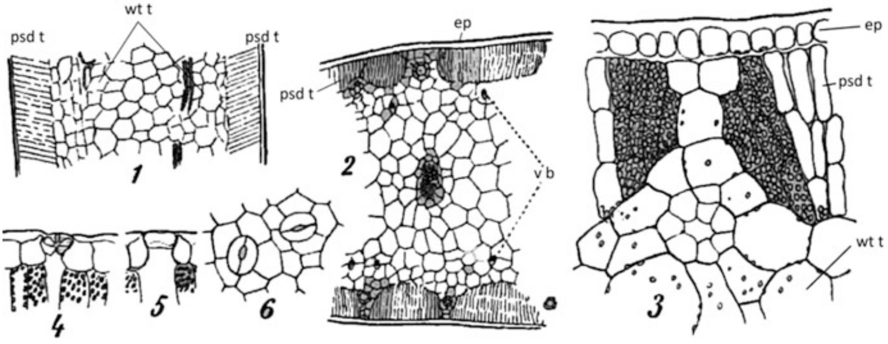


Fig. 165 *Borrichia arborescens*; 1, cross section through a leaf, general aspect and details (2; 3); 4–5, stomata, cross section; 6, stomata, front view; ep, epidermis; v b, vascular bundle; psd t, palisade tissue; wt t, water storage tissue; xy, xylem; ph, phloem (Warming 1897)

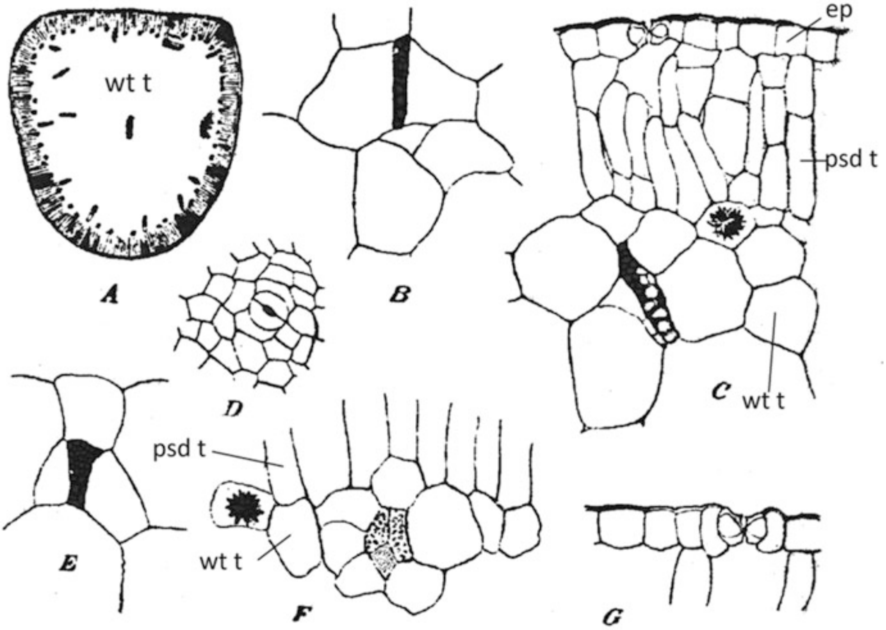


Fig. 166 *Batis maritima*; **A**, cross section through a leaf, general aspect and details (**C**; **F**); **B**, **E**, cross section through a nervure; **D**, stomata, front view and cross section (G); ep, epidermis; psd t, palisade tissue; wt t, water storage tissue (Warming, 1891)

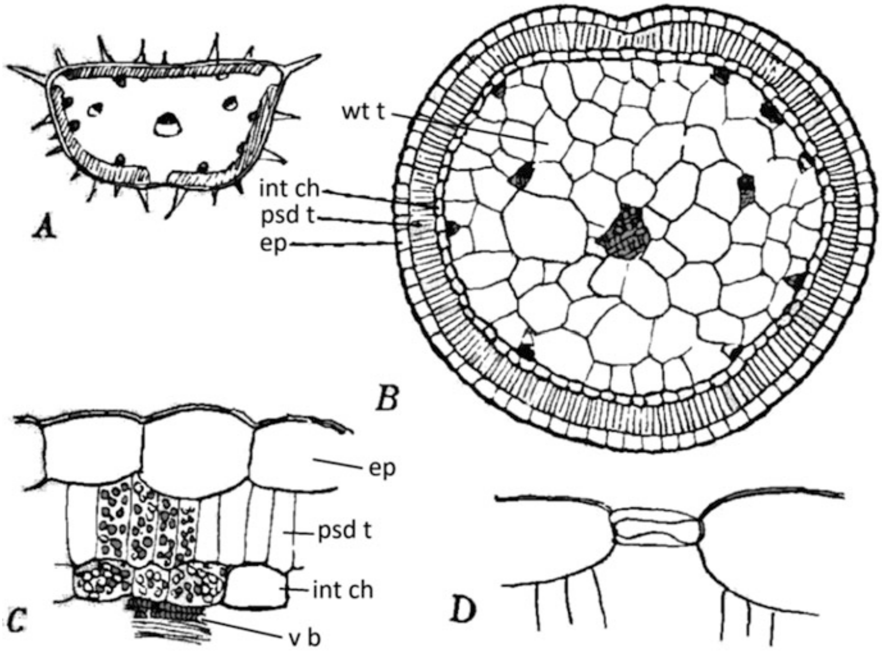


Fig. 167 *Salsola kali*; **A**, cross section through a leaf, general aspect and details (**B**, **C**); **D**, stomata, cross section; ep, epidermis; psd t, palisade tissue; wt t, water storage tissue; int ch, internal chlorenchyma; v b, vascular bundle (Warming 1906)

occur in *Carapa*. Anatomical configuration supports this function. In *Laguncularia racemosa*, the primary cortex develops initially as air-storing tissue, and the inner part of cortex is delimited by a distinct endodermis; in its growth, the primary cortex diminishes, and the large area of phloem acquires an air-storing function (Fig. 188). Idioblasts (trichoblasts) like those evidenced in *Rhizophora* are also found in *Sonneratia* (Fig. 189) and *Bruguiera gymnorrhiza* (Fig. 190).

c. Germination and Vivipary

Vivipary is defined as the process in which the seed remains attached in the fruit to the mother tree, germinates into a protruding embryo with a long hypocotyl, and finally falls from the tree (Robyns 1971). That means the embryo plant, while still attached and nourished by the parent tree, grows into a more or less developed plant without undergoing any resting period (Warming 1909). Several series of stages may be evidenced:

i. In *Aegiceras* the embryo emerges from the seed but remains inside the fruit; it has a large stem and is green.

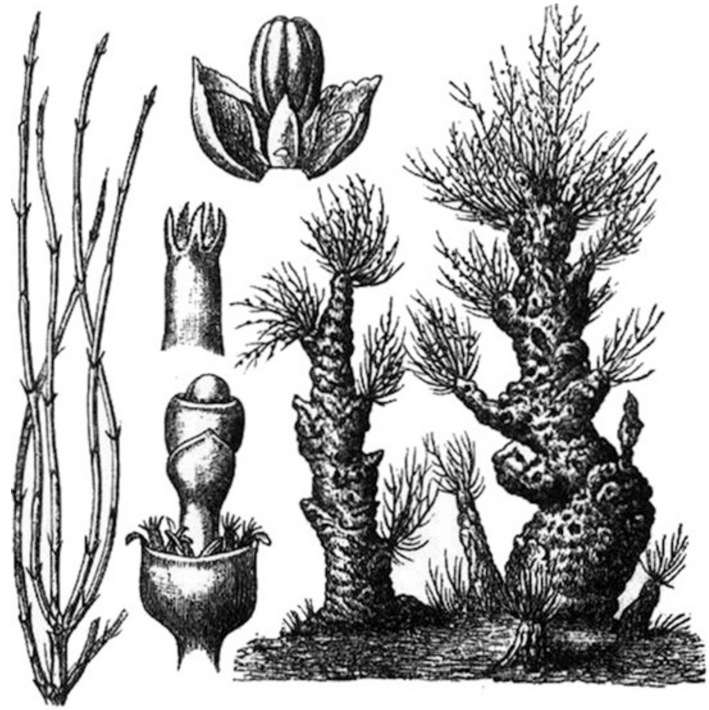


Fig. 168 *Haloxylon ammodendron* (Meyer 1905)

ii. In *Avicennia* (Figs. 191 and 192) the endosperm and subsequently the embryo emerge from the seed and lie uncovered within the chamber of the ovary. The embryo is green and obtains food from the parent plant by means of a long, repeatedly branched, hypha-like haustorial cell, which traverses the placenta.

iii. In *Rhizophora* (Figs. 193 and 194) and allied genera (*Bruguiera caryophylloides*, Fig. 193; *B. parviflora*, Fig. 195; *Kandelia rheedii*, Fig. 196; and *Ceriops*), the embryo grows not only out of the seed but also out of the fruit and projects from the latter in the form of a green seedling displaying the hypocotyl and root, which in some species exceed one-third of a meter; then, the full-formed seedlings hang down from the branches. The cotyledons serve as a haustorium, sucking food from the parent plant. Finally, the seedling breaks loose from the cotyledons (*Rhizophora* has only one cotyledon), which remain behind inside the fruit and shrivel with it. Seedling falls into the water or mud; its club shape and pointed root end help it to penetrate the mud, into which it rapidly thrusts lateral roots that had previously been initiated. If the seedling does not succeed in fixing itself, it floats and may strike root on some distant shore; in this way the species is provided with means of dispersal by water.

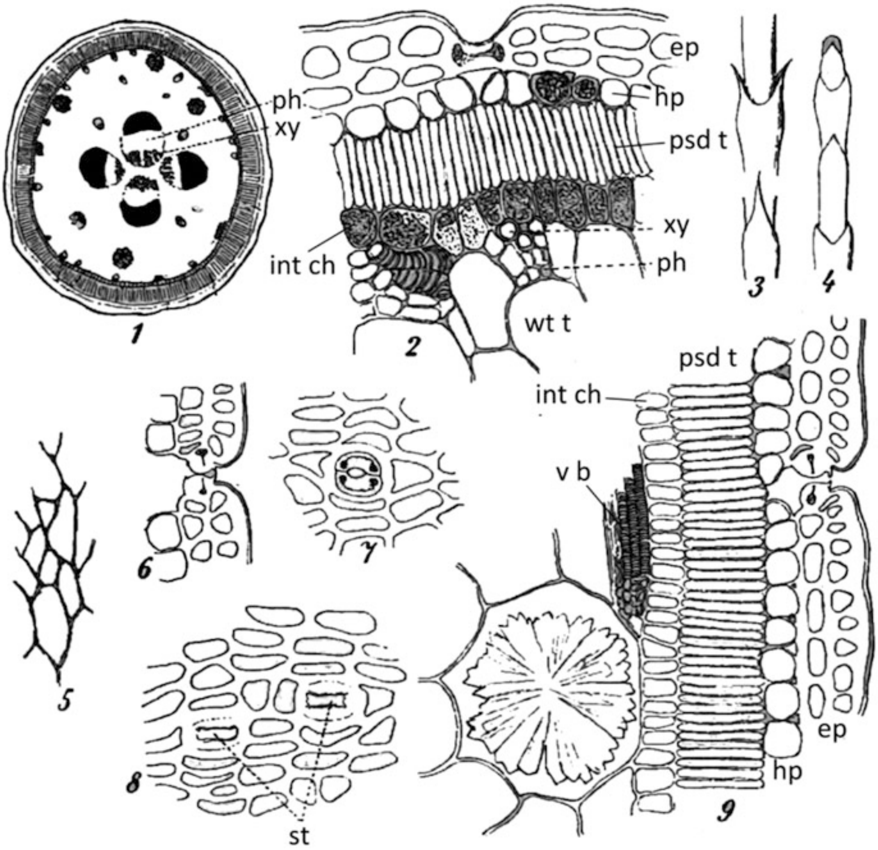


Fig. 169 *Haloxylon ammodendron*; 1, cross section through a succulent segment, general aspect and details (2,9); 3,4, articulated segments; 5, cells from water storage tissue; 6, stomata (st), cross section and front view (7,8); ep, epidermis; psd t, palisade tissue; wt t, water storage tissue; int ch, internal chlorenchyma; v b, vascular bundle; hp, hypodermis; xy, xylem; ph, phloem (Warming 1897)

d. Means of Migration

The mangrove includes approximately the same species along all the tropical shores from Australia to East Africa. This is due in part to the fact that the medium temperature remains uniform throughout and in part to the efficient means of dispersal. Due to air-containing spaces in the integument or in other parts and to the consequent decrease in specific gravity, fruits, seeds, and seedlings of mangrove plants can float for a very long time, without losing their germinative power (Warming 1909).

e. Xerophytic Structure

The great majority of mangrove species are shrubs and trees. Despite the circumstance that these plants grow in flooded muddy soil, their shoots display a number

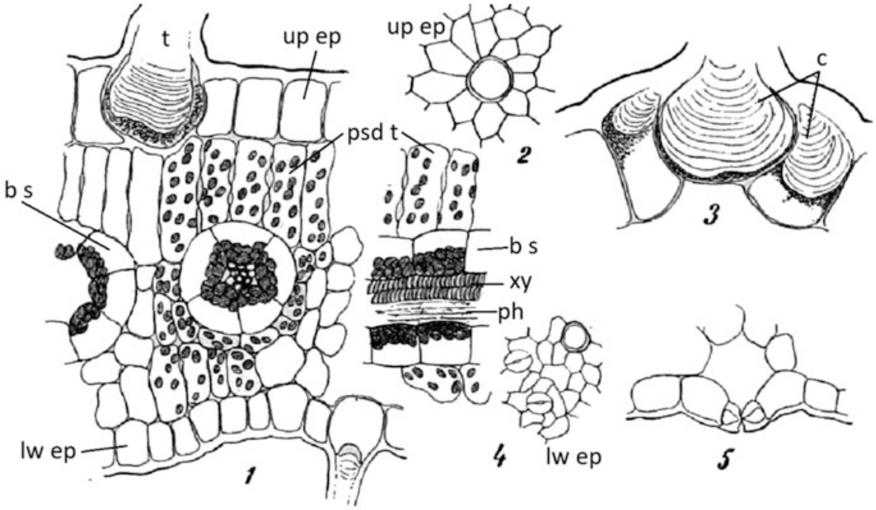


Fig. 170 *Heliotropium fruticosum*; 1, cross (left) and longitudinal (right) section through a leaf; 2, upper epidermis, front view; 3, trichome; 4, lower epidermis, front view; 5, stomata, cross section; up ep, upper epidermis; lw ep, lower epidermis; psd t, palisade tissue; wt t, water storage tissue; xy, xylem; ph, phloem; b s, bundle sheath; c, cystolith (Warming 1897)

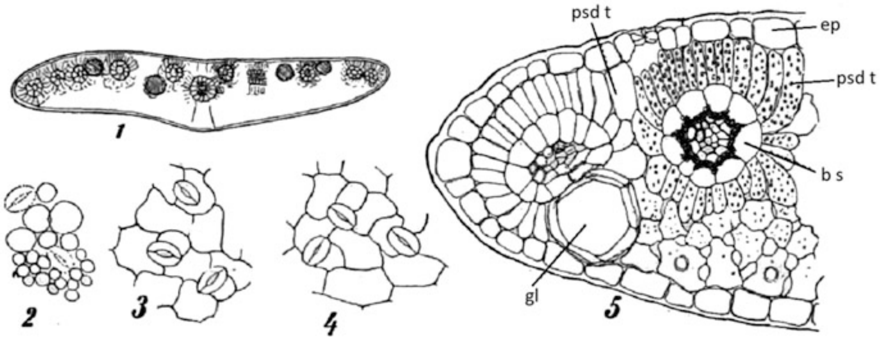


Fig. 171 *Pectis humifusa*; 1, cross section through a leaf, general aspect and details (5); 2, cross section through palisade tissue; 3, upper epidermis, front view; 4, lower epidermis, front view; ep, epidermis; psd t, palisade tissue; b s, bundle sheath; gl, gland (Warming 1897)

of structural features that occur in plants adapted to withstand drought. In other words, as already underlined in this chapter, their habitat is affected by physiological drought conditions (Warming 1909; Schimper 1891, 1903; Grigore 2008; Grigore and Toma 2010a; Grigore et al. 2014; Grigore and Toma 2017).

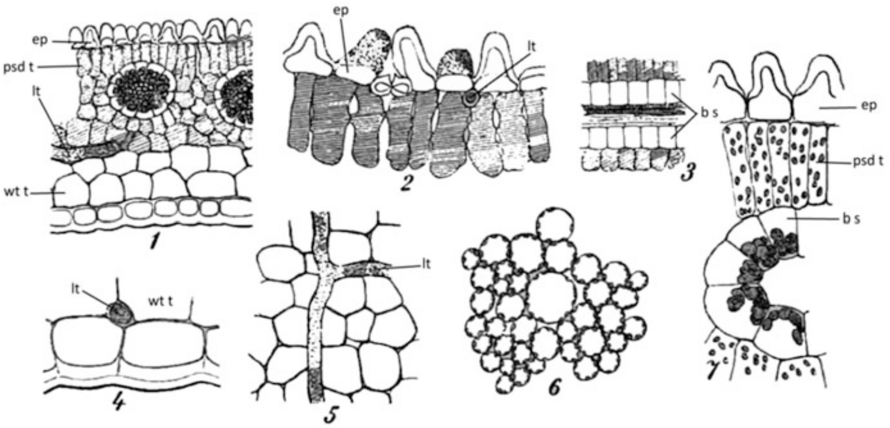


Fig. 172 *Euphorbia buxifolia*; 1, cross section through a leaf, general aspect and details (2,3,4,7); 5, laticifer (lt) from water storage tissue; 6, cross section through palisade tissue; ep, epidermis; psd t, palisade tissue; wt t, water storage tissue; b s, bundle sheath (Warming 1897)

Xeromorphic adaptations of mangroves can be found in the following structural features:

(a) The leaves are thick, coriaceous, or succulent in some extent: *Sonneratia*, *Lumnitzera* (Fig.197), *Carapa* (Fig. 198), *Rhizophora*, and *Avicennia*.
(b) The epidermis is thick-walled and strongly cutinized; the leaves are often very glossy: *Rhizophora mucronata* (Fig. 199) (Schimper 1891, 1903).
(c) Salt glands.
(d) Stomata are often sunk beneath the general surface of epidermis.
(e) Water storage tissue is always present (Fig. 198) and sometimes massive. In *Rhizophora mucronata*, the older leaves, which no longer assimilate, become thicker than younger leaves; this is caused by an enlargement of the water storage tissue, and thus the leaf changes its function.
(f) The mesophyll has few intercellular spaces, but the palisade tissue is well-developed, as main or unique chlorenchyma: *Sonneratia* (Fig. 200) and *Lumnitzera*.
(g) The ends of nervures dilate into water-storing tracheids: *Sonneratia* (Fig. 201), *Bruguiera*, *Avicennia*, and *Ceriops*.
(h) Long stone cells or bast-like mechanical cells are lodged between the palisade cells in *Rhizophora* (Fig. 199), *Sonneratia*, and *Carapa* and in the pith of *Rhizophora*.
(i) Mucilage cells occur in species of *Sonneratia* and *Rhizophora* (Fig. 199).
(j) Some species are strongly and densely clothed with hairs: *Avicennia*.

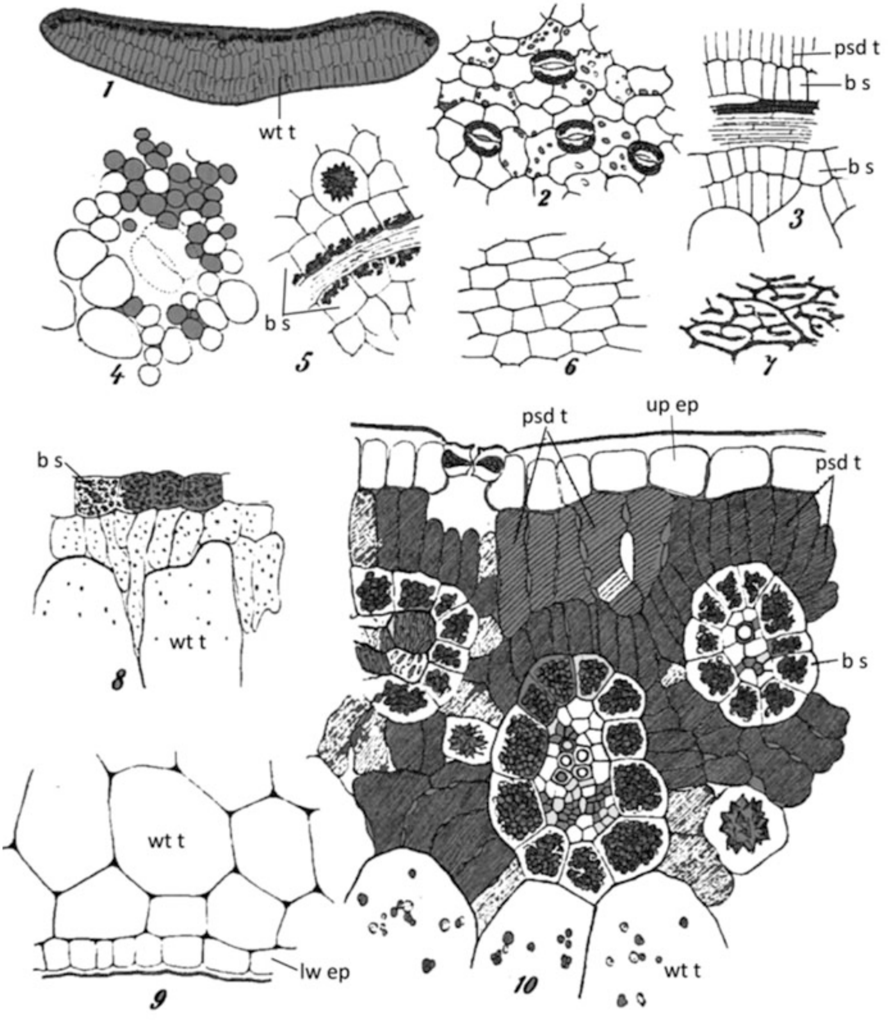


Fig. 173 *Philoxerus vermiculatus*; 1, cross section through a leaf, general aspect and details (3,5,8,9,10); 2, upper epidermis, front view; 4, cross section through palisade tissue; 6, lower epidermis, front view; 7, cross section through bundle sheath level; up ep, upper epidermis; lw ep, lower epidermis; b s, bundle sheath; psd t, palisade tissue; wt t, water storage tissue; b s, bundle sheath (Warming 1897)

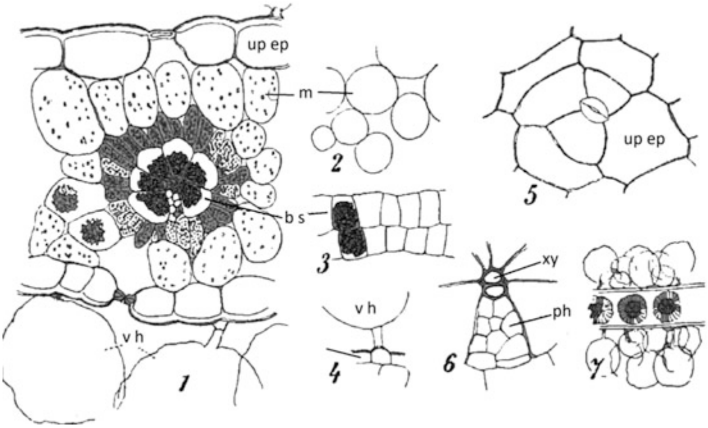


Fig. 174 *Atriplex farinosa*; 1, cross section through a leaf, details and general aspect (7); 2, cross section through mesophyll cells; 3, longitudinal section through vascular bundle; 4, epidermis and vezicular (salt) hair; 5, upper epidermis, front view; 6, cross section through vascular bundle level; up ep, upper epidermis; b s, bundle sheath; m, mesophyll; v h, vezicular (salt) hair; xy, xylem; ph, phloem (Warming 1897)

Fig. 175 *Atriplex halimus*, cross section through lamina (Grigore et al. 2014)

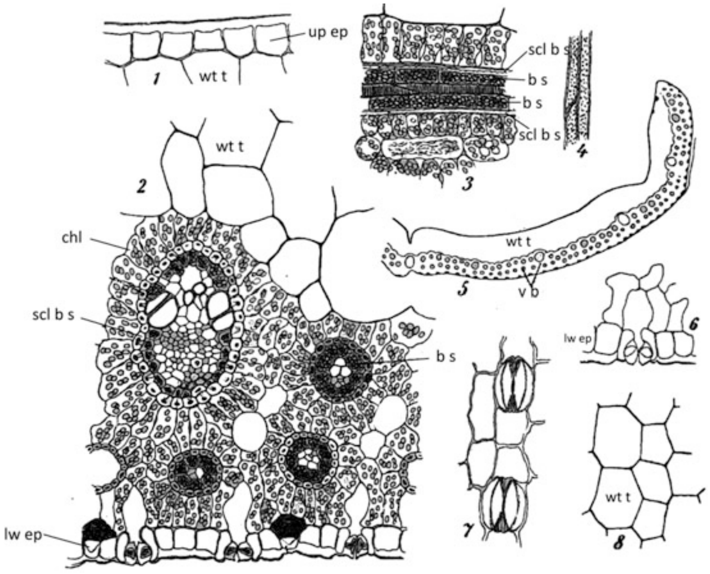


Fig. 176 *Remirea maritima*; 1,2, cross section through a leaf, details and general aspect (5); 3, cross section through bundle sheath; 4, sclerenchymatic sheath; 6, stomata, cross section; 7, epidermis, front view; 8, cross section through water storage tissue level; lw ep, lower epidermis; up ep, upper epidermis; b s, bundle sheath; scl b s, sclerenchymatic bundle sheath; chl, chlorenchyma; v b, vascular bundle (Warming 1897)

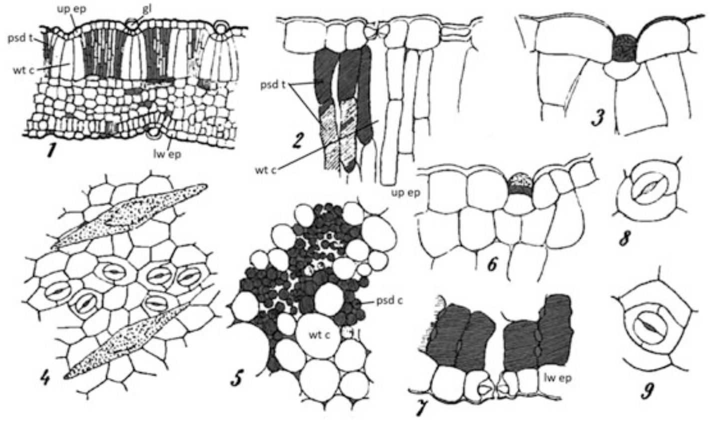


Fig. 177 *Lippia nodiflora*; 1, cross section through a leaf, general aspect and details (2,3,6,7); 4, epidermis and trichomes, front view; 5, cross section through water storage and palisade tissue level; 8,9, stomata, front view; lw ep, lower epidermis; up ep, upper epidermis; psd t, palisade tissue; wt t, water storage tissue; gl, gland (Warming 1897)

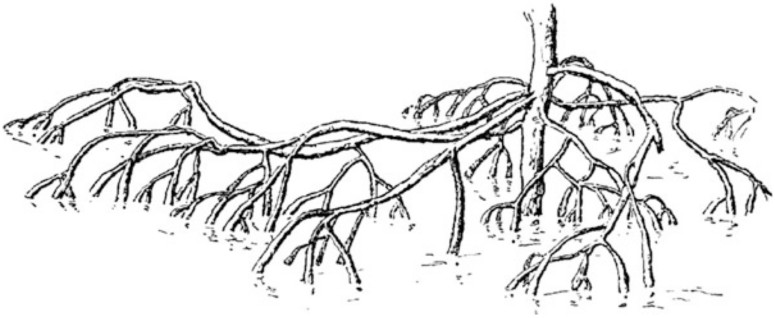


Fig. 178 General aspect of aerial prop roots on *Rhizophora mangle* (Warming, extracted from Børgesen and Paulsen 1900)

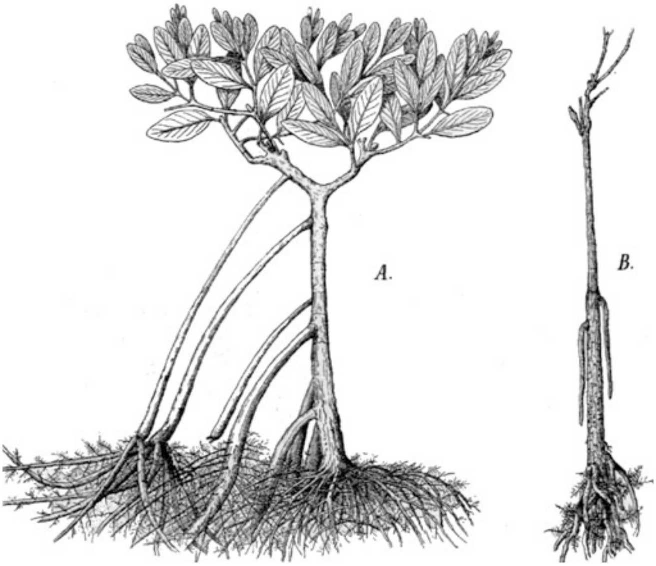


Fig. 179 Bow-like (**A**) and almost vertical aerial prop roots (**B**) on *Rhizophora mangle* (Børgesen and Paulsen 1900)

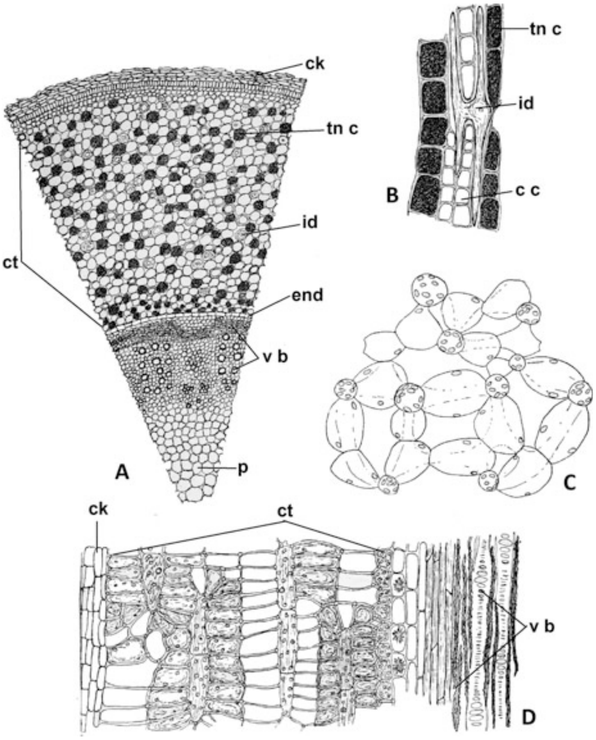


Fig. 180 *Rhizophora mangle*; **A**, cross section through aerial prop root; **B**, longitudinal section through aerial prop root; **C**, cross section through cortex of absorptive root; **D**, longitudinal section through absorptive root (ck, cork; ct, cortex; p, pith; v b, vascular bundle; end, endodermis; id, idioblasts; tn c, tannin cells; c c, cortex cells (Bowman 1917)

Fig. 181 *Avicennia nitida* – isolated plant with pneumatophores (Børgesen and Paulsen 1900)

Fig. 182 *Avicennia nitida* – horizontal (repent) root (h r) with emerging pneumatophores (pn) and absorptive roots (a r) (Børgesen and Paulsen 1900)

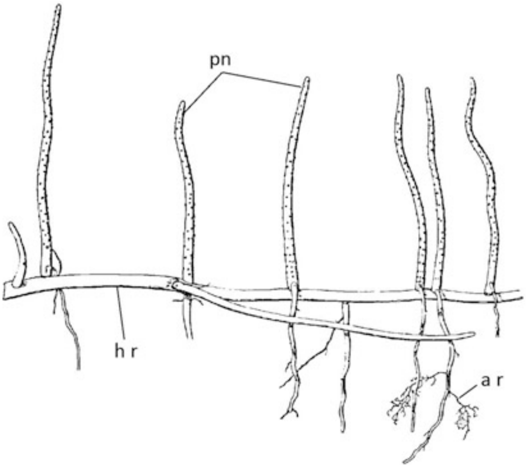


Fig. 183 *Avicennia nitida* – pneumatophores; (**A**) unbranched root; (**B**) branched root; (**C, D**, magnified details of pneumatophores – pneumatodes (lenticels) noticeable (Børgesen and Paulsen 1900)

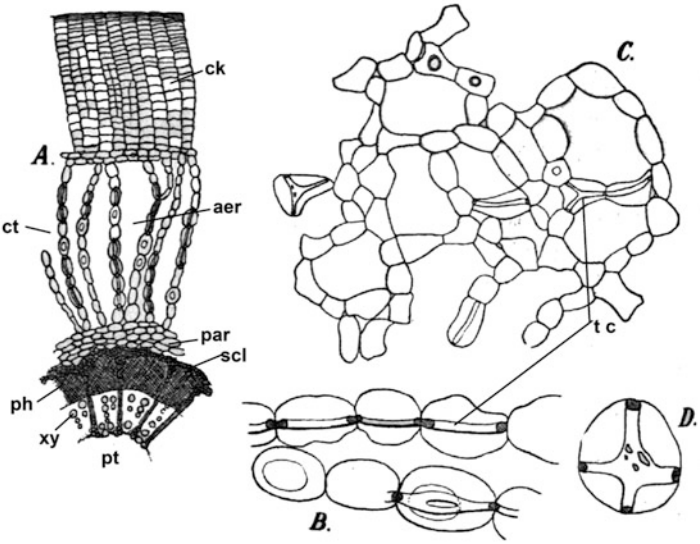
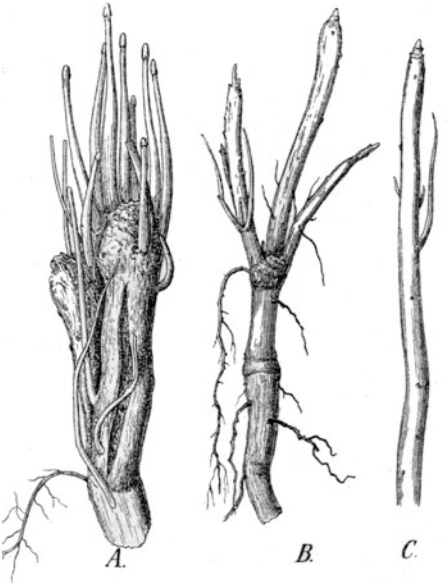


Fig. 184 *Avicennia nitida* – cross section through a pneumatophore; (**A**) general view; (**B**) thickened cells from aerenchyma; (**C**) cross section through aerenchyma level; (**D**), thickened cell from aerenchyma; ck, cork; aer, aerenchyma; ct, cortex; par, parenchyma; ph, phloem; xy, xylem; pt, pith; scl, sclerenchyma; t c, thickened cell (Børgesen and Paulsen 1900)

Fig. 185 *Laguncularia racemosa* – pneumatophores (**A**–**C**, different degrees of ramification) (Børgesen and Paulsen 1900)



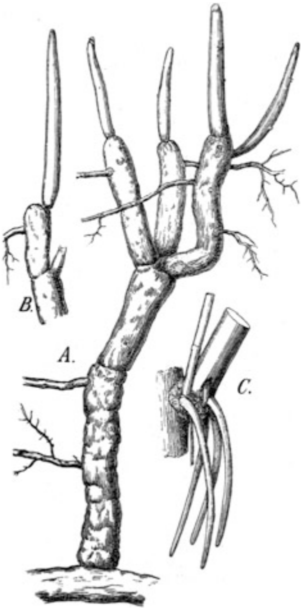


Fig. 186 *Laguncularia racemosa* – pneumatophores; (**A**–**B**), with negative geotropism; (**C**), with positive geotropism (Børgesen and Paulsen 1900)

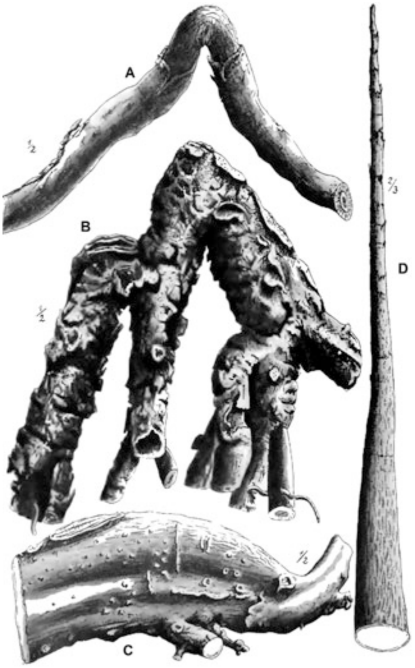


Fig. 187 Pneumatophores – *Bruguiera caryophyllaeoides* (**A**), *B. gymnorrhiza* (**B**), *Carapa obovata* (**C**), *Avicennia officinalis* (**D**) (Schimper 1903)

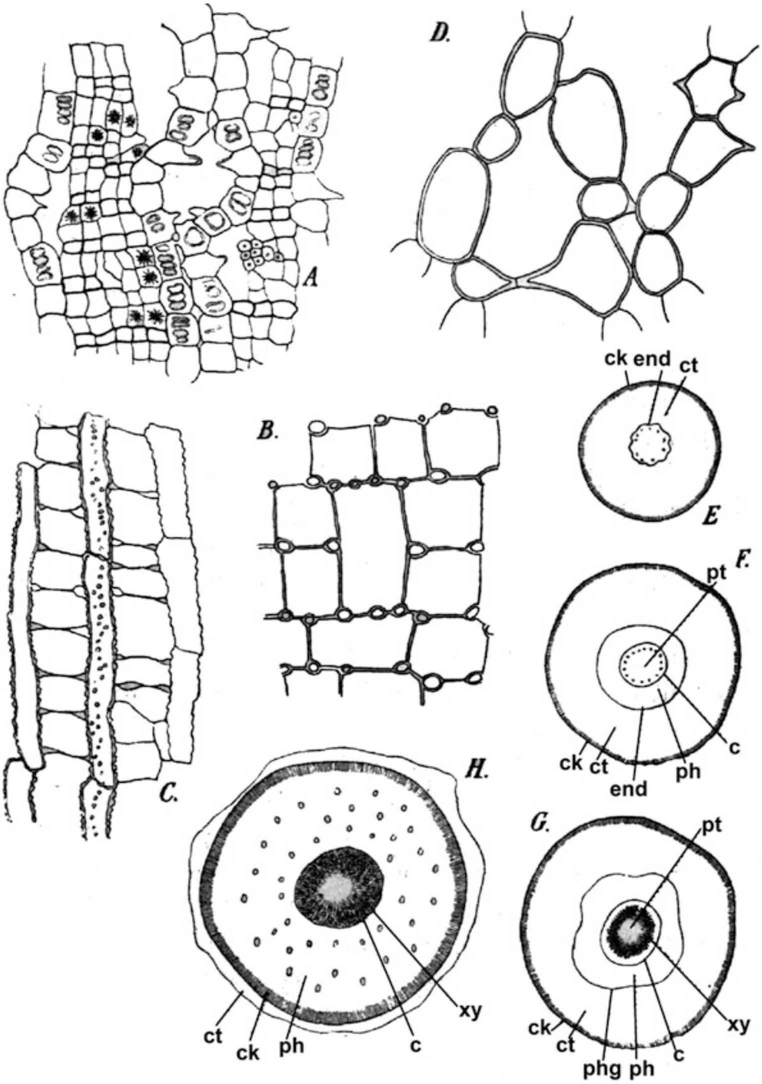


Fig. 188 *Laguncularia racemosa* – (**A**), cross section through an aerial respiratory root, phloem level; (**B**), longitudinal and radial section through phloem and through primary cortex (**C**); (**D**), cross section through primary cortex; **E–H**, different stages of development of a young aerial root, showing the formation of phloem and shedding of primary cortex; c, cambium; ct, cortex; xy, xylem; ph, phloem; ck, cork; phg, phellogen; pt, pith; end, endodermis (Børgesen and Paulsen 1900)

Fig. 189 *Sonneratia acida*, cross section through aerial respiratory root (tr, trichoblasts; a s, air spaces) (Liebau 1914)

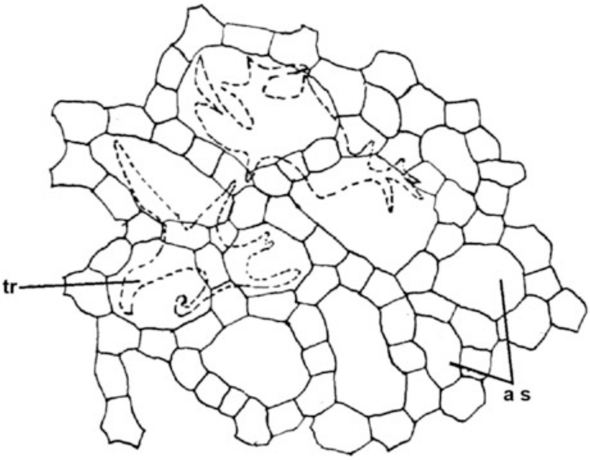


Fig. 190 *Bruguiera gymnorrhiza*, longitudinal section through aerial respiratory root; p – pith (Liebau 1914)

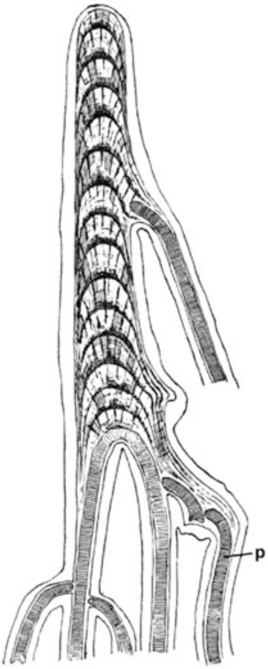


Fig. 191 *Avicennia nitida* – seedling (Børgesen and Paulsen 1900)

Fig. 192 *Avicennia tomentosa* – different stages of seedling’ development (Schimper 1891)

Fig. 193 Attached seedlings of *Rhizophora conjugata* (right) and *Bruguiera caryophylloides* (left) (Schimper 1898)

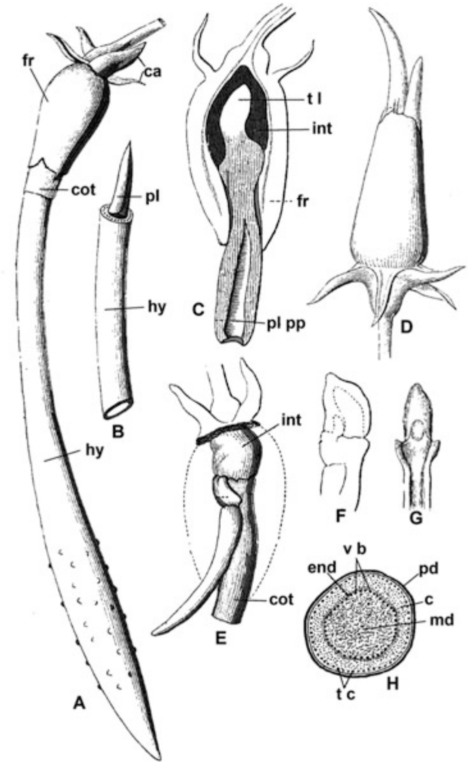
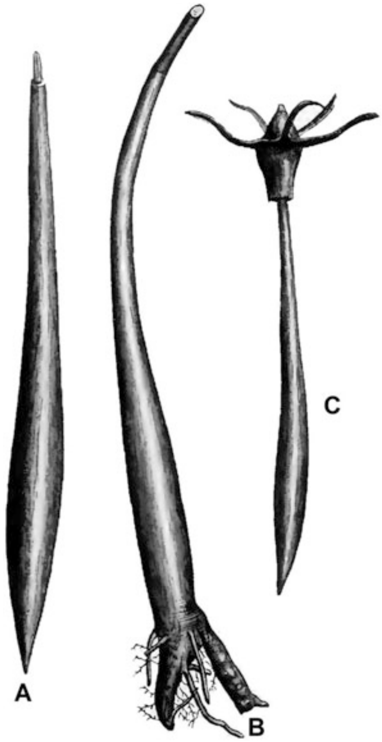


Fig. 194 Detached seedling of *Rhizophora mangle*; **A**, general aspect; **B**–**G**, details; **H**, cross section through hypocotyl; ca, calyx; fr, fruit; hy, hypocotyl; cot, cotyledon; pl, plumule; int, integument; t l, tip of the leaf; pl pp, plumule protruding place; end, endodermis; md, medulla; c, cortex; pd, periderm; v b, vascular bundle; t c, tannin cells (Warming 1877)

Fig. 195 Attached seedlings of *Bruguiera parviflora* (Schimper 1903)

Fig. 196 Seedlings of *Kandelia rheedii* (**A**, detached with plumule upward; **B**, seedling after taking root; **C**, young seedling still attached to the fruit) (Schimper 1903)



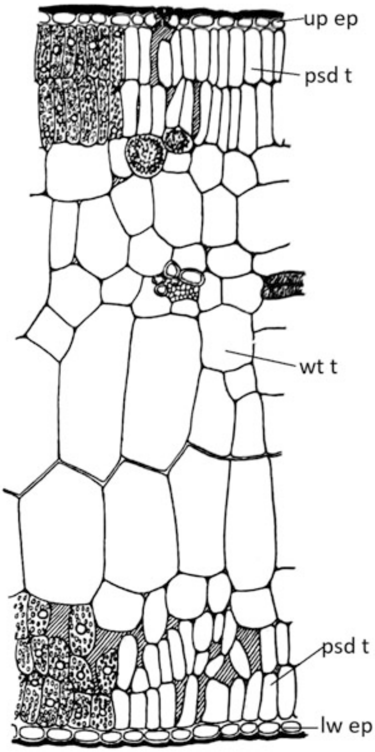


Fig. 197 *Lumnitzera racemosa*, cross section through the leaf; up ep, upper epidermis; psd t, palisade tissue; wt t, water storage tissue (Walter and Steiner 1936)

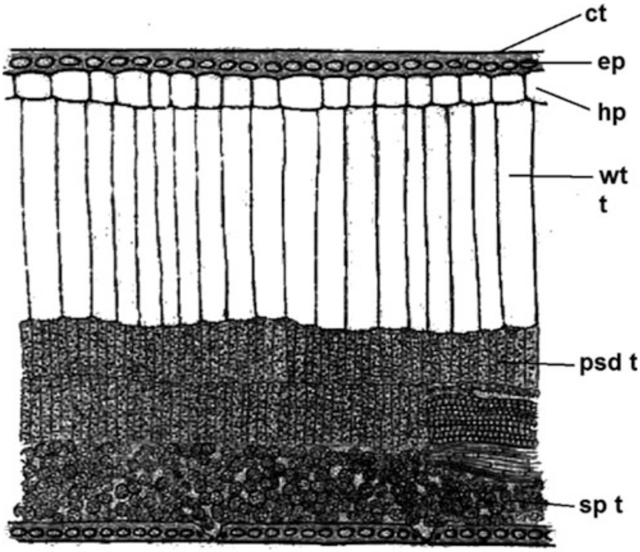


Fig. 198 *Carapa moluccensis*, cross section through the leaf; ct, cuticle; ep, epidermis; psd t, palisade tissue; wt t, water storage tissue; hp, hypodermis; sp t, spongy tissue (Schimper 1891)

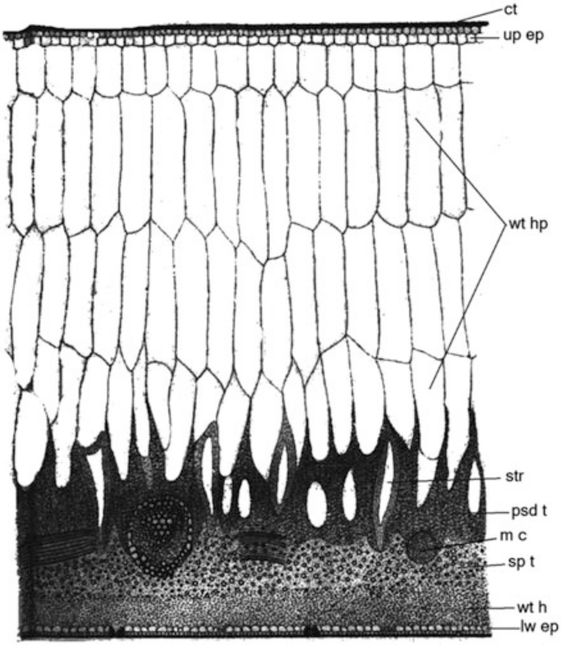


Fig. 199 *Rhizophora mucronata*, cross section through the leaf; ct, cuticle; up ep, upper epidermis; wt hp, water storage hypodermis; str, stereids (spicular cells); psd t, palisade tissue; m c, mucilage cells; sp t, spongy tissue; lw ep, lower epidermis (Schimper 1891)

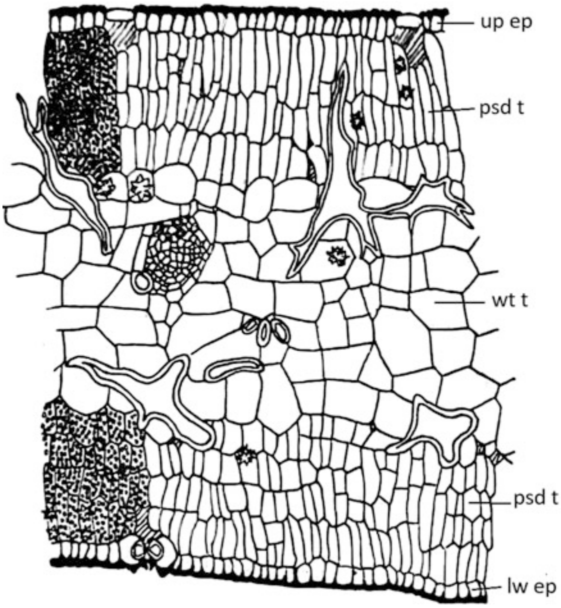
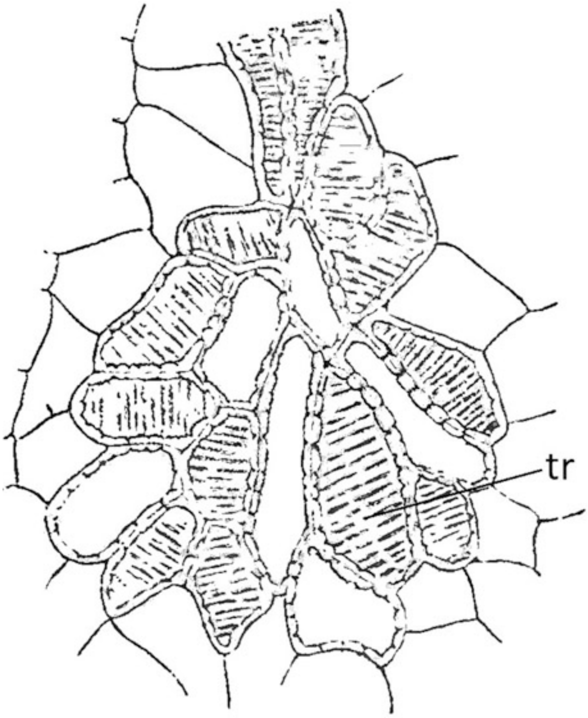


Fig. 200 *Sonneratia acida*. Cross section through the leaf; up ep, upper epidermis; lw ep, lower epidermis; psd t, palisade tissue; wt t, water storage tissue (Walter and Steiner 1936)

Fig. 201 *Sonneratia acida*, tracheids (tr) (Schimper 1903)



6 Conclusions

This contribution reinforces the idea that halophytes are – from morphological and anatomical point of view – a special case of xerophytes. For practical purposes, their adaptations were here called "general" and approached consequently; in fact, these morphological and anatomical features are xeromorphic, and this is due to the so-called physiological drought that affects all saline environments. Different described situations (nontropical salt-marsh halophytes, sea-coast halophytes, mangroves) illustrate that, without losing their xeromorphic profile, halophytes' adaptations can be regarded as the fine results of various environmental factors – not only restricted to elevated salinity – and the mangroves support perfectly this idea. They have coriaceous, thick often succulent leaves; some of them have salt glands, tracheids, mucilage cells, and well-developed palisade tissue. Because of the particular ecological conditions, mangroves are viviparous and have aerial, prop, and respiratory roots. None of the other types of halophytes have all of these last mentioned adaptations; however, halophytes free from the power of sea winds and sprays, vegetating in salt deserts or steppes, may be succulent or can possess salt glands. But all of them have in common the fact that must face the physiological drought of their environment.

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