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**BIOLOGY, MORPHOLOGY,  
AND SYSTEMATICS OF HYDROBIONTS**

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## **Anatomy and Morphology of Vegetative Organs and Inflorescence of *Stratiotes aloides* L. (Hydrocharitaceae)**

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**Abstract**—The results of studies on the structure of vegetative organs of *Stratiotes aloides* L. are presented. An organographic analysis and detailed morphological and anatomical descriptions of the root system, shoot system, and inflorescences have been made. It is demonstrated that the *S. aloides* shoot system is characterized by high vegetative mobility. The main histological topographical complexes, their proportions, and histochemical features are determined. The shoot system of *S. aloides* is characterized by underdeveloped xylem. Lignification of the epidermal and exodermal cell wall is a compensatory adaptation providing additional reinforcing properties. The development of diffuse collenchyma and general aerenchymatization of *S. aloides* tissues are effective mechanisms of adaptations to the aquatic habitat.

**Keywords:** *Stratiotes aloides*, morphology, anatomy, shoot, leaf, root, inflorescence, lignin

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### INTRODUCTION

The article supplements our previous investigations of the morphology and anatomy of reproductive organs of *Stratiotes aloides* L. [6]. The presented materials analytically generalize the data on the structure of vegetative organs of this species. The methods used have been described in detail previously [6].

### RESULTS

**Root system.** *S. aloides* possesses a fibrous—strap-like, secondary-homorrhizous root system. There are  $7 \pm 2$  roots per rosette offset. The length greatly depends on the depth of the water body. On an average, that of the longest root is  $110 \pm 20$  cm at a diameter of  $2.8 \pm 0.2$  mm. The growth rate of roots is high, up to 5 cm/day [14]. *S. aloides* retains a rather long primary root (Fig. 1a). At the 10th–15th day the sprout develops the first adventive endogenous roots separated from parenchyma by the “root pocket” (Fig. 1d). Early stages of root development correspond to the *Allium* type [16, 22, 26]. By the end of the first vegetative season, the root system fully decomposes as the basal part of the sprout dies off. In the beginning of the second year of vegetation overwintered rosette spouts emerge and the adventive roots develop in the open water. Later on, they immerse into the ground and fix the plant to a certain site.

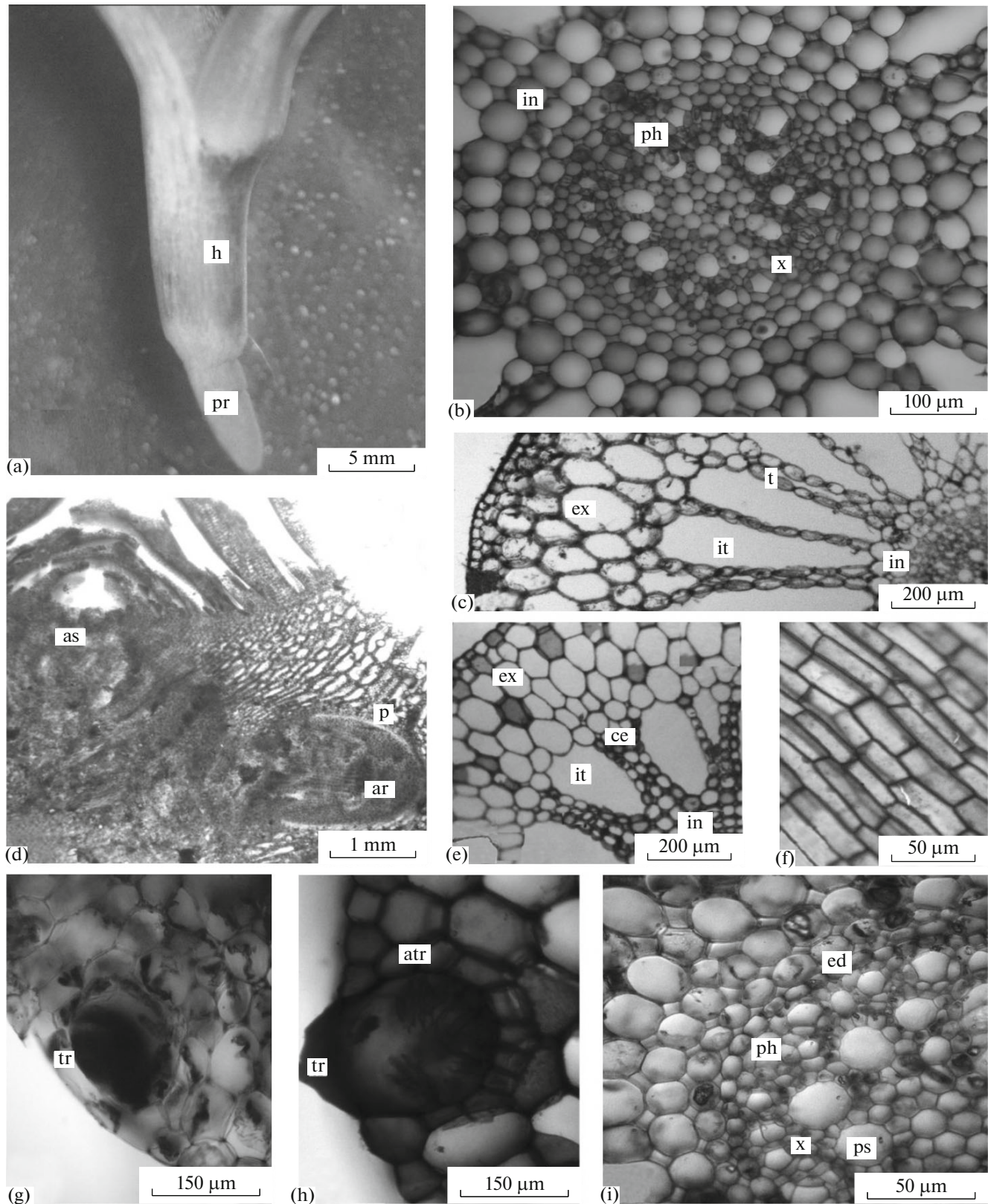
Principal histologic—topographic zones in the root of *S. aloides* are easily differentiated. In the division zone, the cells of apical meristem are small-vacu-

lated. The rootcap is reduced to two to three layers of slimy cells with weakly undulating anticlinal walls. Starch grains are confined to the “central column.”

In the growth zone, parenchymatous strands, trabeculae, are well expressed; histogens are clearly isolated. The outer bark is isocytic and the central parts are filled with aerenchyma (principal cells are  $28 \pm 5$   $\mu$ m in diameter). The inner parenchyma of the bark is two to three layered, with diffuse intercellular spaces. The stele has solitary air-bearing cavities [4].

In the absorption zone, the one-layered epiblast is formed by three cell populations: typical atrichoblasts, atrichoblasts of root hair sheath, and trichoblasts. Typical atrichoblasts are polygonal,  $26 \pm 4$   $\mu$ m long,  $12 \pm 3$   $\mu$ m wide (Fig. 1f). Cells of root hair sheath are smaller and radially arranged. Some of them have intracellular shield-shaped protuberances, which increase the general functional surface and provide additional reinforcement (Fig. 1h) [13, 16]. Trichoblasts are  $200 \pm 40$   $\mu$ m at the base,  $6 \pm 2$   $\mu$ m long (Figs. 1g, 1h). The average density of trichoblasts in the absorption zone is  $3.2 \pm 0.7$  per  $\text{mm}^2$ . Root hair index is 5.8%, somewhat less in the proximal area: 2.1%.

In the absorption zone the primary bark is differentiated in to several structure parts. The outer bark is represented by five to six rows of weakly differentiated parenchyma with small solitary intercellular spaces. The central part is filled with aerenchyma with 12–18 lens—narrow trapezoid intercellular spaces (Fig. 1e). Aerenchyma is of the lysigenous type (term suggested by Siago [26]). In histogenesis, the groups of



**Fig. 1.** Root of *Stratiotes aloides*: (a) radicle, (b) root stele in the absorption zone, (c) conducting zone (fragment), (d) intraparenchymal stage of development of the adventive root, (e) absorption zone (fragment), (f) epiblema, (g) early stages of development of trichoblast, (h) differentiated trichoblast (partially removed), (i) root stele in the conducting zone (fragment), (pr) radicle, (ar) root apex, (as) stem apex, (atr) sheath atrichoblast, (ce) elements of loose collenchyma, (ed) endodermis, (ex) outer bark, (h) hypocotyl, (in) inner bark, (it) intercellular space, (p) rootcap, (ph) elements of phloem, (ps) air channel, (t) trabecula, (tr) trichoblast, and (x) elements of xylem.

radial cells are divided anticlinously. A big part of newly formed cells are destroyed and produce a large intercellular space. The cells of parenchyma of the outer and central bark often have numerous chloroplasts. Inner parts of bark are often represented by three to four rows of isodiametric parenchyma with small intercellular spaces and single units of loose collenchyma (Figs. 1b, 1e). Endoderm is one to two layered; Casparian strips contain F-lignin. The pericycle is formed of the layer of thin-walled polygonal cells. The stele is polyarch, with eight to ten rays. Xylem is exarch and includes tracheids and vessels (Fig. 1b). Cell walls of conducting elements of metaxylem contain M-lignin. Interxylem groups of meta- and proto-phloem are represented by several sieve tubes with satellite cells. Conducting bundles have large tracheae.

In the conducting zone, the epiblema is replaced by exoderm, whose anticlinal coats have angular thickenings. The outer and anticlinal cell walls contain F-lignin; no suberin is found. The parenchyma of bark is differentiated into outer, central, and inner, represented mainly as aerenchyma and topographic zones (Fig. 1c). Elements of angular collenchyma contributing to the support of architecture of the organ are developing. Conducting elements of xylem are represented by tracheids and vessels; elements of xylem are partly replaced by air cavities. Parenchymatization and aerenchymatization of the stele are retained (Fig. 1i).

**The system of sprouts.** The system of sprouts of *S. aloides* develops as a result of iteration of a sprout of  $n$ -order and is characterized by the alteration of vegetative and generating sites (Fig. 2). The following structural-functional zones may be discerned in the structure of the sprout [8]: inhibition, vegetative, generative-vegetative, and the zone of secondary vegetative accretion. The inhibition zone comprises the lower metamers of the rosette part without axillary structures and the plagiotropic shoot (for diaspores of vegetative origin). This zone performs assimilatory function; adventive roots are also formed here. The vegetative zone is part of the sprout with alternating metamers bearing vegetative axillary complexes of stolon-rosette sprouts and turions (or without them) (Fig. 2). In the generative-vegetative zone, the generative buds are formed simultaneously with vegetative buds. The zone of secondary vegetative accretion comprises a part of the sprout above the metamer with the last inflorescence. This part of the sprout provides renewal in the next vegetation season. With growth, the structural-functional zones are displaced apically.

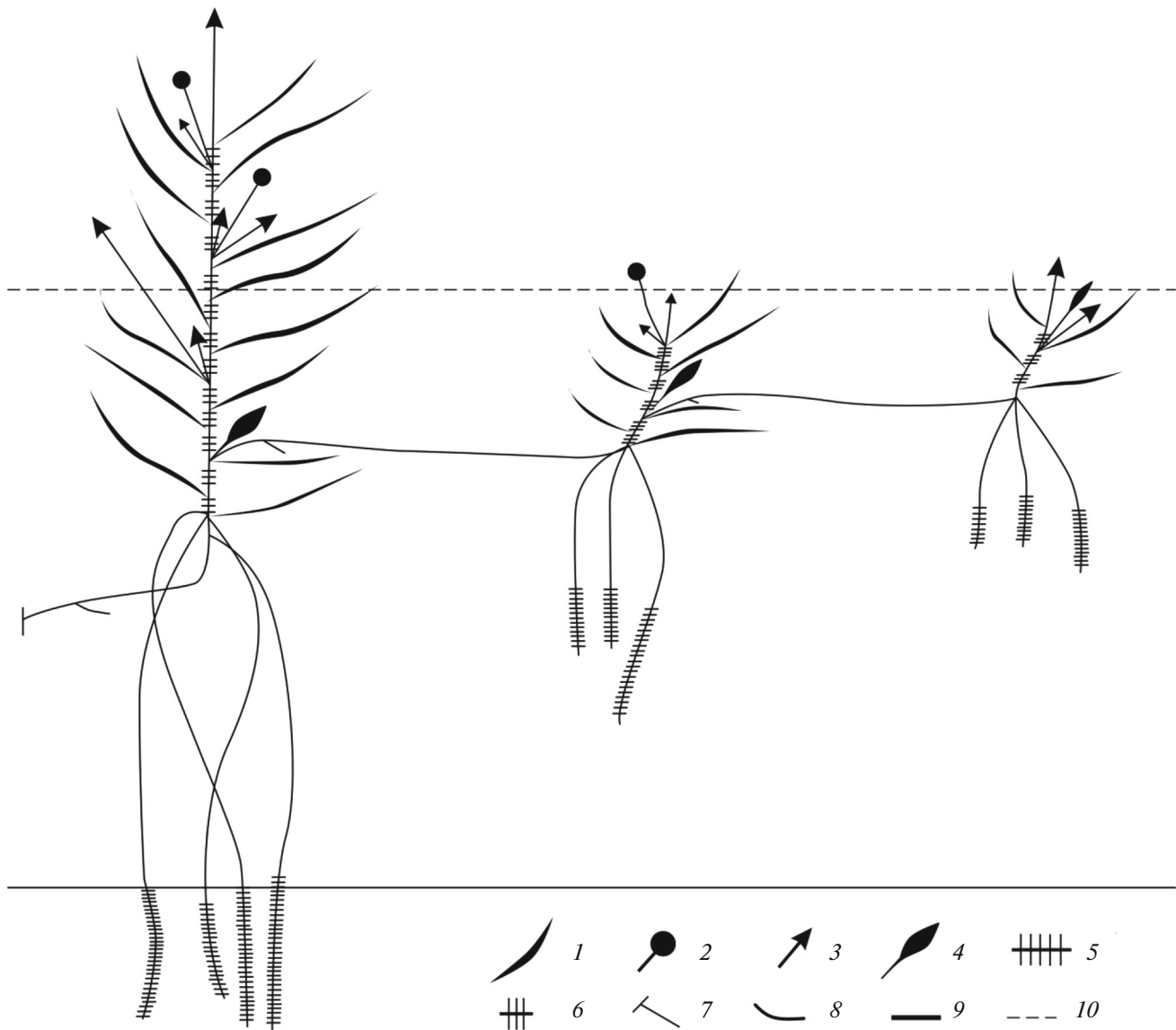
With consideration for structural-functional specialization, the following types of sprouts may be discerned in *S. aloides*: axial young rosette sprout, specialized sprouts of vegetative renewal, stolons performing an accessory function in vegetative propagation, and flower-bearing sprouts. The stem of the sprout of *S. aloides* is formed predominantly of hypocotyl tissues (Fig. 3b). The sprout is elongated by the forma-

tion of new short metamers; it grows in thickness due to activities of meristematic zones situated between the leaf base and pericycle. The sprouts of  $(n + 1)$ -order are formed intravaginally, in pairs. The formed anlagen are polymeric; one of them noticeably retards in development (Fig. 3a). Stem epiblema is isocytic, there are no stomata, the outer covers contain some F-lignin. The bark is formed of multifunctional parenchyma. Its outer parts consist of isocytic cells, intercellular spaces are small, diffuse. Four to five deeper layers have elements of angular collenchyma. The inner bark consists of aerenchyma, intercellular spaces are large, idioblasts produce slime (as confirmed by staining with neutral red, methylene blue, and copper sulfate) and tannins (as confirmed by ferric chloride), solitary. Atactostele with wide air channels. The xylem component is represented by vessels (absent in *S. aloides* f. *demersa*) with annular, spiral thickening or tracheidal elements containing M-lignin in coats. In phloem there are numerous companion cells of sieve-like elements. The cells of the sheath of conducting bundle contain numerous small starch grains.

Monopodality of the principal young sprout is compensated by polymeric iteration accompanied by formation of specialized vegetative sprouts. Thus, turions are rosette sprouts with a prolonged juvenile stage specialized for hibernation under ice, vegetative renewal, and propagation. They are  $2.4 \pm 0.1$  cm long and  $0.6 \pm 0.1$  cm wide and have one to two axial buds. Turions remain in the leaf axil until the next vegetation season or hibernate in the free state. The slime covering them, produced by parenchymal idioblasts, prevents the contact of living tissues with ice. The parenchyma of turion leaf is anisocytic, anisodiametric, conductive bundles small, and with one to two spiral tracheids and a small-celled phloem-parenchymal part; epiderm is without stomata. The stem bark consists of isocytic parenchyma (inner layers of aerenchyma), with small diffuse intercellular spaces. The parenchyma of stem and leaf of developing turions contains numerous small starch grains often occupying  $>50\%$  of the cell volume.

While the formation of turions of *S. aloides* is related to the preparation for the unfavorable period, the formation of structurally similar but stronger lateral shoots having no extended rest period is related to vegetative distribution. As the stolon internode grows, the rosette  $n + 1$  is carried out beyond the mother sprout (Fig. 2). As the weight of rosette sprouts increases, the stolons become fragile and break off, which is inflicted mechanically, thus providing efficient distribution. Anatomically, lateral sprouts are similar to turions; however, the tissues of the former are more differentiated.

The stolon of *S. aloides* is a modified intravaginal; two-metameric sprout with elongated and shortened internodes [3, 8], having no cataphylls in a definitive state. In plants at the generative stage of ontogenesis,

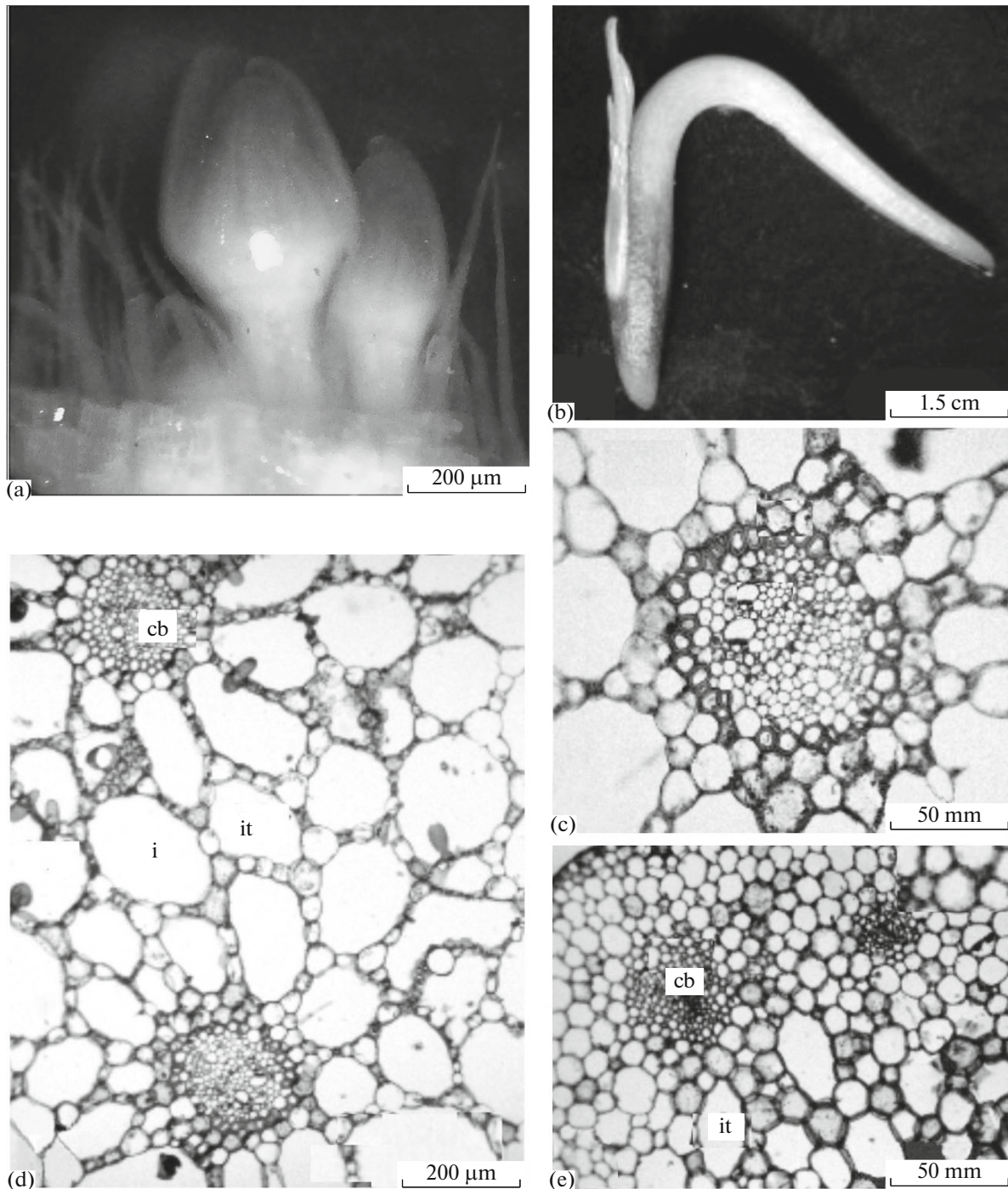


**Fig. 2.** System of sprouts of *Stratiotes aloides*: (1) leaf, (2) inflorescence, (3) vegetative sprout, (4) turion, (5) root, (6) sprout with short internodes, (7) sprout with elongated internodes, (8) scalelike leaf, (9) level of the ground, and (10) water level.

the stolons are not branching, they are  $25 \pm 6$  cm long, the large diameter is  $4.6 \pm 0.6$  mm, and the small diameter is  $2.4 \pm 0.3$  mm. Stomata not developed; anticlinal and periclinal cell walls contain F-lignin. The outer parts of bark are formed by photosynthesizing parenchyma with angular thickenings (main cells  $65 \pm 8$   $\mu\text{m}$  in diameter); inner parts are formed by non-photosynthesizing aerenchyma (main cells  $80 \pm 10$   $\mu\text{m}$  in diameter and intercellular spaces up to 150–200  $\mu\text{m}$ ). Elements of diffuse collenchyma are presented by fulcral cells at trabecule bases. Idioblasts producing slime and tannins are solitary. The atactostele is represented by amphivasal conductive bundles with starch sheaths; smaller conductive bundles are collateral with mechanical sheathing. Vascular elements of xylem

have annular thickenings, partly replaced by air channels with large lumens (Fig. 3e).

The flower stalk is an intravaginal apogeotropic or hemiapogeotropic two-metameric sprout. It is  $1/3$ – $1/5$  shorter than the leaves; in its upper part with short denticles, two large keels are clearly expressed and two to three smaller keels are situated perpendicularly. Main cells of epidermis are  $39 \pm 8$   $\mu\text{m}$  wide; outer walls contain F-lignin; and stomata are not numerous, predominantly in the distal zone. The outer parts of bark are represented by photosynthesizing parenchyma and inner parts by aerenchyma (Fig. 3d). Idioblasts are predominantly as residual bodies; their density is 9.3 per  $\text{mm}^2$ . The atactostele is formed by amphivasal conducting bundles with a one- to two-layered starch-



**Fig. 3.** Stem and specialized sprouts of *Stratiotes aloides*: (a) axillar complex, (b) two-day old sprout, (c) conductive bundle of flower stalk, (d) transverse section of flower stalk (fragment), and (e) outer bark of stolon; (cb) conductive bundle, (i) idioblast, and (it) intercellular space.

bearing sheath. Xylem comprises vessels and tracheid elements (contain M-lignin), solitary air channels, and phloem is parenchymatized (Fig. 3c).

**Leaf.** In a typical case the rosette sprouts of *S. aloides* have  $43 \pm 9$  leaves obliquely directed upwards, bifacial, sessile, triquetrous-ensiform, with short axial

bases. Venation is parallel with numerous diagonally ascending or descending anastomoses. Phyllotaxis is spiral, leaf formula  $3/8$ , divergence angle  $135^\circ$ . The leaf series comprises the cotyledon (for genets), bud scales, cataphylls (photosynthesizing, with marginal trichomes, retained for a rather long time even in

definitive specimens or nonphotosynthesizing, scale-like in stolons), typical trophophylls, bracts, and bracteoles (reduced in inflorescences of pistillate flowers).

The cotyledon is solitary,  $5.2 \pm 0.9$  cm long and  $4 \pm 1$  mm wide, bifacial, semicylindrical, photosynthesizing, retained for 1–2 (3) months (Fig. 3b). It is considerably larger than the first true leaves, collenchymatized, void of marginal spinules.

The leaves of middle formation definitive rametes demonstrate significant morphological distinctions permitting one to discern the following four leaf fractions: (1) lower trophophylls with photosynthesizing bases of the last vegetation season; (2) underwater assimilating slightly spiral trophophylls, more flattened and wide; (3) typical immersed trophophylls; and (4) photosynthesizing trophophylls emerging to air in their upper third. Expression of a certain fraction much depends on environmental conditions (first and foremost, submergence) and on the ontogenesis stage.

A typical trophophyll is characterized by differences in the proximal and distal parts and the leaf may be subdivided into the pseudopeduncle (well developed in underwater leaves) and the leaf blade [3]. The underwater part of leaf persists for more than one vegetative season; it has structural traits similar to the juvenile leaf: large mesophyll cells, one to two layers of intercellular spaces in the median area, the absence or scarcity of stomata (distal areas), and often anomalous ones. The part of leaf exposed to air differs in a well-developed lateral area, less developed keel, many-layered mesophyll, lesser aerenchymatization, and more numerous normal stomata.

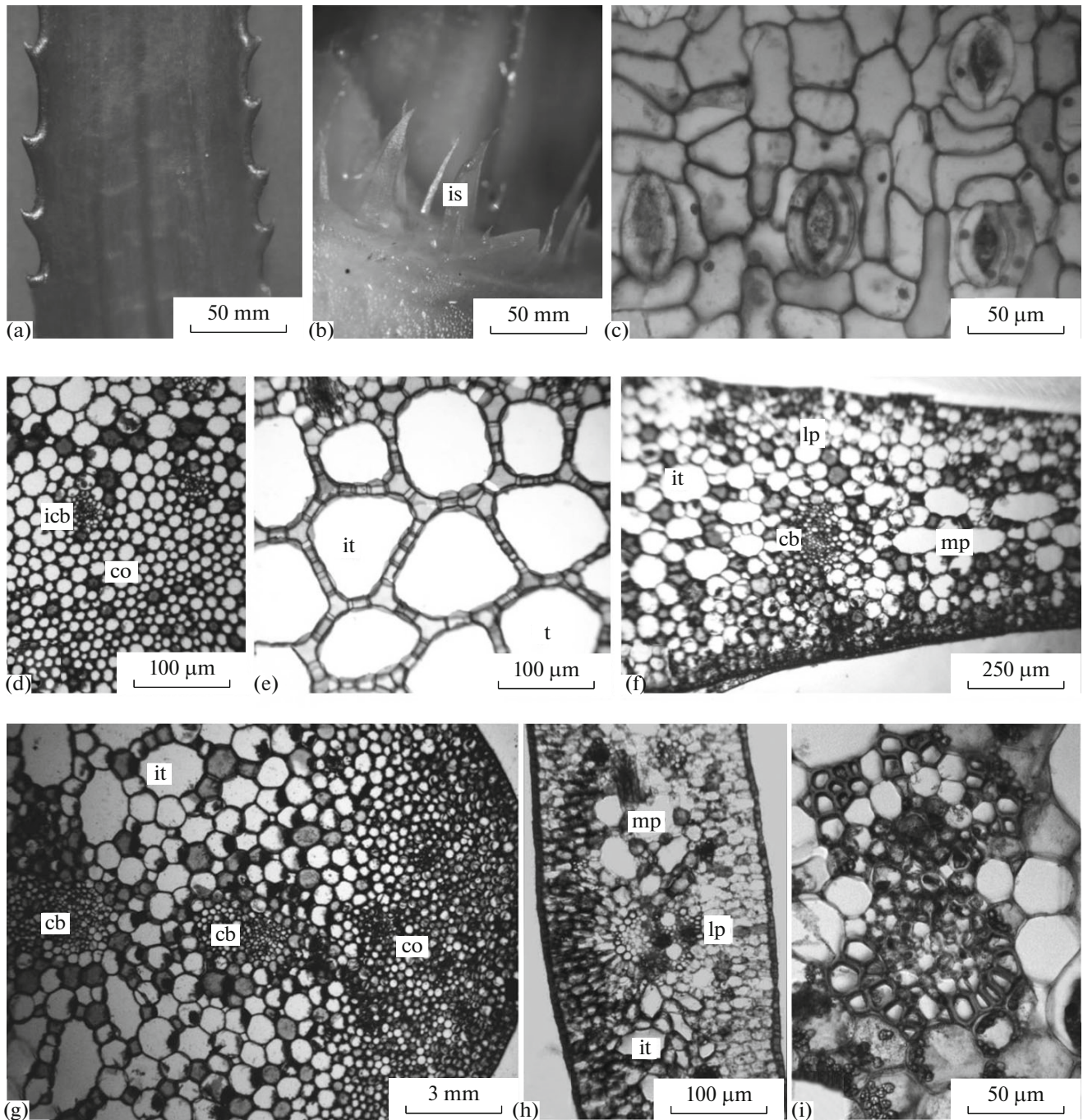
In West Siberian plants at the generative stage of ontogenesis, the length of a leaf of median formation is  $49 \pm 6$  cm; the width at the base is  $1.5 \pm 0.1$  cm and in the middle it is  $2.7 \pm 0.3$  cm. The marginal spinules and the spinules of abaxial keel are of epidermal–subepidermal origin, impregnated with silicates (Fig. 4a). The leaf blade is of the amphistomatic type. The principal cells of epidermis belong to the curvilinear clan, nonline group, curvivalled type (after Aneli [1]),  $160 \pm 10$   $\mu\text{m}$  long,  $35 \pm 5$   $\mu\text{m}$  wide. Cell walls of main cells contain F-lignin, weakly cutinized and suberitized. Stomata of the boat-shaped type, guard cells are reniform–fabiform ( $97 \pm 8$   $\mu\text{m}$  long,  $27 \pm 6$   $\mu\text{m}$  wide), with normal chloroplasts. The satellite cells are of the dissect clan, paracytic–parallel cell group (Fig. 4c). Along with a typical paracytic type of the stomatal apparatus, in *S. aloides*, there are stomata of the anamocytic [11] and diacytic types. The total number of stomata is significantly higher ( $t_p = 34.3$ ,  $p \leq 0.05$ ) on the leaf adaxial epidermis ( $42 \pm 1$  per  $\text{mm}^2$ ) than on the leaf abaxial epidermis ( $27 \pm 1$  per  $\text{mm}^2$ ). The functional morphology and number of stomata correlate with the exposition level of the leaf in the aerial environment ( $r = 0.87$ ,  $p \leq 0.05$ ). On the submerged part the stomata are scarce, functionally inactive, and often atypical.

The leaf mesophyll is represented by several histological–topographic complexes: polyfunctional lateral parenchyma, polyfunctional median aerenchymatized parenchyma, collenchymatized keel parenchyma (Figs. 4f, 4h). In the mesophyll there are small rare raphides characteristic of some Hydrocharitaceae [24]. The main cells of lateral parenchyma are photosynthesizing,  $90 \pm 10$   $\mu\text{m}$  in diameter. In the pseudopetiolar zone, numerous diffuse idioblasts are seen. The median parenchyma consists mainly of polyfunctional aerenchyma of the lysigenous etiology. Its main cells are  $140 \pm 30$   $\mu\text{m}$  long and  $120 \pm 20$   $\mu\text{m}$  wide, full-coral cells with irregularly thickened cell walls, intercellular spaces 150–450  $\mu\text{m}$  in diameter (Fig. 4e). The aerenchyma transports gases, performs photosynthesis, comprises liquid solutions and gases, saves plastic material, decreases specific weight, and provides buoyancy [2, 25]. The leaf keel consists of anisocytic collenchyma (the inner layers are of the angular type, the outer layers are lamellar), the main cells are  $28 \pm 7$   $\mu\text{m}$  in diameter (Figs. 4g, 4d). The armed leaves supply additional rigidity and contribute to the safety of hibernacles preventing their immersion to anaerobic ground in winter.

The level of filling and the kind of conductive bundles change depending on the ontogenesis stage and topographic situation. In a typical case the bundles are of amphivasal type with the interrupted outer xylem ring; the median bundle is 300–350  $\mu\text{m}$  in diameter. Smaller bundles are collateral with mechanical sheathing. Elements of primary xylem are represented by numerous vessels or tracheids (of proto- and metaxylem) with annular or spiral thickenings containing M-lignin. Often, they are replaced by wide air channels. Sieve tubes are with solitary companion cells. The cells of the starch-bearing sheath are filled with starch grains by 5–70%, depending on the season (Fig. 4i). Similarly to other Hydrocharitaceae [28], in *S. aloides* there are numerous small marginal inverted conductive bundles confined to the lateral area. They consist of solitary tracheids of xylem and of conductive elements of phloem and other Hydrocharitaceae [28],

Cataphylls and scales are 0.8–2.5 cm long and 0.2–1.2 cm wide. Morphologically, they are weakly differentiated, from scalelike keeled conduplicate ones (with or without trichomes) to photosynthesizing thickened ones. Parenchyma is many-layered, diffusely collenchymatized, mesophyll weakly differentiated, epidermis without stomata. Conductive bundles (one to five) small.

Bracts and bracteoles are similar to juvenile leaves. Bracteoles differ from bracts in a smaller proportion of weakly differentiated multifunctional parenchyma, in a smaller volume of air cavities, and extremely low-developed mechanical and conductive tissues. There is one median bundle and three to four lateral ones; inverted conductive bundles are not numerous. Bracteoles have almost lost the assimilative function and

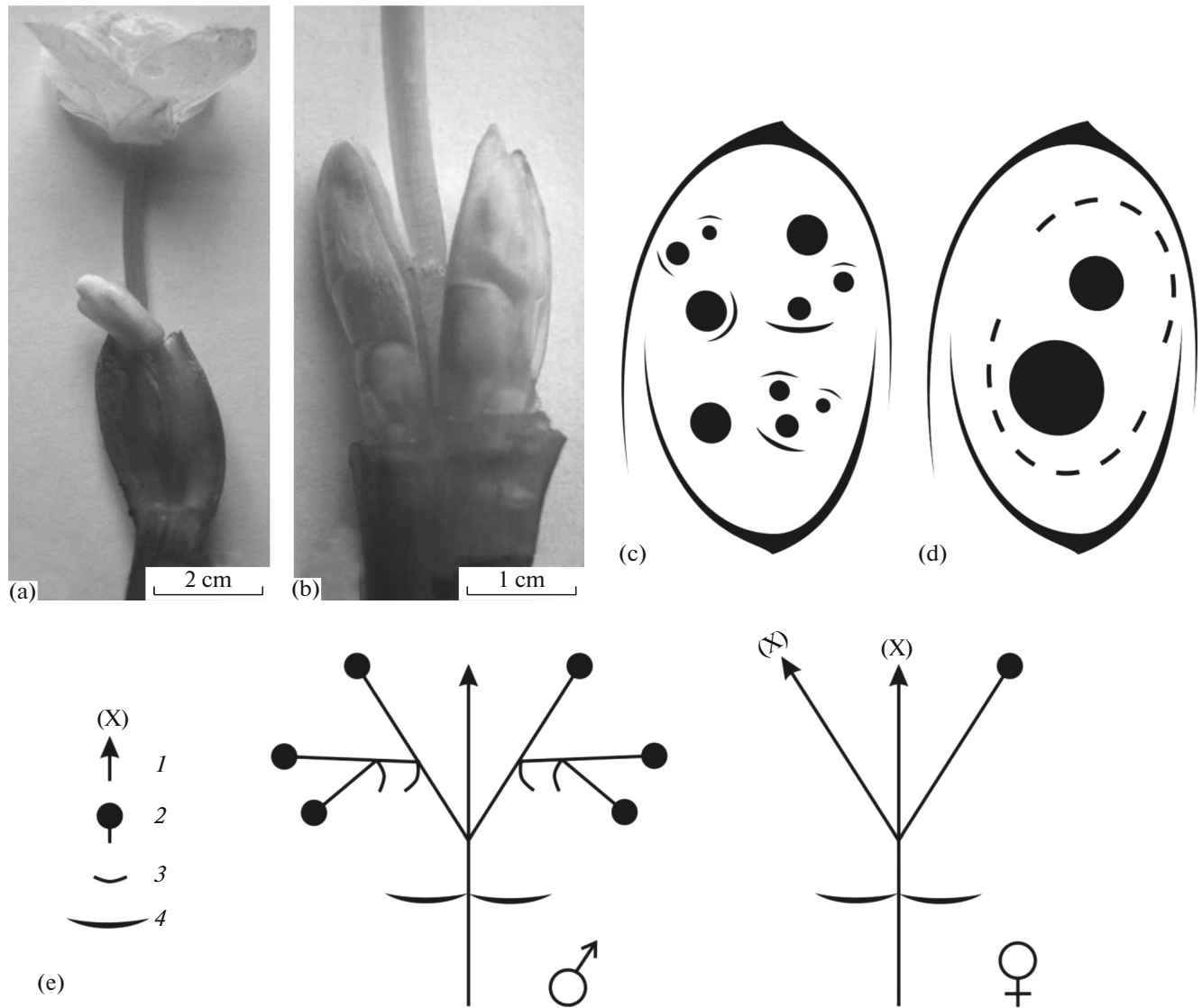


**Fig. 4.** Leaf of *Stratiotes aloides*: (a) general view of a young leaf (fragment), (b) intrafoliar scale, (c) epidermis, (d) keel collenchyma, (e) aerenchyma, (f) the zone of pseudopetiole (lateral area), (g) keel, (h) leaf blade (midrib), and (i) lateral conductive bundle; (co) collechyma, (icb) inverted conductive bundle, (is) intrafoliar scale, (lp) lateral parenchyma, and (mp) median parenchyma. Other designations are the same as in Figs. 1 and 3.

mechanically protect developing flower buds, also preventing excessive moisture loss.

Like many representatives of Helobiae, *S. aloides* is characterized by the presence of intrafoliar scales (squamae intrafoliaceae, according to Arber [12]) having an axillary nature [12, 19] (Figs. 3a, 4b). Morphogenetically, they are related to the leaf situated

above and have an epidermal–subepidermal origin. The intrafoliar scales are one- to two-layered, formed from undifferentiated parenchyma; conductive tissues are not developed. The notion that the scales are functionally related to slime secretion [16, 19] is erroneous because idioblasts producing slime and typical of parenchyma of many organs are not found here. The



**Fig. 5.** Inflorescences of *Stratiotes aloides*: (a, b) inflorescence of pistillate flowers ((a) general view and (b) bracts removed), (c) inflorescence diagram of pistillate flowers, (d) diagram of two-flower inflorescence of pistillate flowers, and (e) scheme of phylomorphogenesis; (1) reduced flower, (2) flower, (3) bract, and (4) bracteole.

function of these structures may be related to the protection of axial structures. The number of intrafoliar scales in a node varies. Generally, this number increases along the principal genetic spiral [12, 19].

**Inflorescences.** In the course of ontogenesis, the inflorescences of *S. aloides* undergo numerous bifurcations defining the dichasial architecture of an inflorescence [23]. The products of bifurcation possess different potentials: one takes part in development of an individual flower, another takes part in the development of a bracteole (a foliar structure). This results in the formation of a system which is a pseudomonochaesium. In a pistillate flower the apex of a lateral bud yields elements of a flower and only sometimes undergoes branching (Fig. 5e).

The inflorescences of staminate flowers contain from two to ten (on an average  $4.6 \pm 0.9$ ) flowers and a flower stalk ( $46 \pm 8$  cm long) emerging from water only in its upper third. The pedicels of pistillate flowers  $40 \pm 10$  mm long. The spathe of an inflorescence consists of two free overlapping conduplicative bracts. The large bract is  $35 \pm 5$  mm long and  $14 \pm 3$  mm wide. The small bract is  $31 \pm 4$  mm long and  $9 \pm 2$  mm wide. There are smaller semitransparent bracteoles varying in number (Figs. 5a–5c). In the distal direction, the bracteoles tend to decrease in size in proportion to the abaxial keel and spinules [4].

The inflorescence of pistillate flowers is 1 (2)-flowered (on an average  $1.1 \pm 0.3$ ), protected by a spathe of two bracts. The flower stalk is  $13 \pm 4$  cm long, fully



**Table 1.** Principal qualitative and quantitative parameters of the histological–topographic zones of the root of *Stratiotes aloides*

Parameter	Zones of			
	division	growth	absorption	conduction
Relative length, %	0.01	0.03	36.56	63.40
Proportions of, %:				
periblem	68	–	–	–
plerome	32	–	–	–
bark	–	73	89	93
stele	–	27	13	7
aerenchyma	–	21	36	58
Number of rays in:				
phloem	–	5–7 (8)	8–10	8–12
xylem	–	5–7 (8)	8–10	8–12
Diameter of elements of xylem, $\mu\text{m}$	–	$35 \pm 6$	$83 \pm 8$	$86 \pm 9$
M-lignin	Not detected	Not detected	Metaxylem	Metaxylem
F-lignin	Same	Same	Casparian strips	Casparian strips, exoderm

submerged into water. The length of a large bract of the pistillate flower is  $33 \pm 5$  mm, the width at the base is  $13 \pm 3$  cm, and small bract is  $21 \pm 4$  mm long and  $10 \pm 2$  mm wide at the base. Bracteoles are reduced to a row of numerous lanceolate–linear outgrowths (Fig. 5d). The flower stalk of a pistillate flower is  $9 \pm 2$  mm long. The inflorescence of pistillate flowers is an extreme variant of impoverishment of lateral axes; a modified bracteole is situated on the principal axis. The flower is pseudoterminal (Fig. 5e).

## DISCUSSION

**Root system.** Related to *S. aloides* species (*Hydrocharis morsus-ranae* L., *H. dubia* (Blume) Backer, *Elo-dea canadensis* Michx., *Limnobium spongia* (Bosc) Rich. ex Steud.), have similar morphoanatomical traits of structure of the root system: root hairs (even in the basal zone), aerated bark, one-layered endodermis, stele of a small volume [9, 11, 14, 26]. Presence of collenchyma and a well-developed aerenchyma are generally characteristic of the root system of Hydrocharitaceae [11]. A distinctive trait of *Stratiotes aloides* is the stele of a polyarch type. In the root of *S. aloides*, from the apex to the conductive zone, there is a tendency toward an increasing aerenchymatization, a proportional increase in the bark volume, and a decrease in the volume of the stele. The number of rays of xylem and phloem in the stele increase and vessels appear along with tracheids; some elements of xylem are replaced by wide air channels (Table 1). Development of the system of diffuse intercellular spaces and general aerenchymatization of the bark reflect the principal tendencies of evolution of hydrophytes.

Lignins are identified for the first time in the absorption zone only; small-scale distribution of hydrophilic polysaccharides and of hydrophobic lignin redistributes mechanical properties of tissues [7] and provides an additional reinforcing effect. Lignification of exodermis, which is not characteristic of hydromacrophytes, is a compensatory adaptation.

**System of sprouts.** The vegetative axes sprouts of *S. aloides*, similarly to other species of the fam. Hydrocharitaceae, are characterized by the presence of intercalary continuous meristems [18], which ensure annual renewal and iterative branching [5]. A special trait of *S. aloides* is the capacity to produce several generations of sprouts of subordinate order [8, 10, 21]. Lateral buds form an axillary complex of stolon–rosette sprouts (which are also characteristic of the genera *Hydrocharis* L., *Limnobium* Rich., *Vallisneria* L. [11]). This complex may also include an inflorescence [15]. Turions and lateral sprouts, as vegetative diaspores, ensure efficient vegetative propagation. Generally, the system of sprouts may be characterized as a stolon–rosette vegetatively mobile system, clearly polycentric, with early complete specialization and with nonspecialized morphological disintegration.

The axial parts of sprouts of *Stratiotes aloides* also manifest a tendency to aerenchymatization and diffuse localization of mechanical elements (hydrophytic direction of morphogenesis). A comparatively high proportion of the outer bark is characteristic of the main axis and of the axial part of turion, while in the stolon and flower stalk the inner bark prevails (Table 2).

Diversification of leaf development in *S. aloides* depends on external factors: when the leaf is submerged into water, the pseudopetiole develops predominantly; the leaf blade develops in the air. Along

**Table 2.** Principal qualitative and quantitative parameters of elements of the sprout system (axial structures) of *Stratiotes aloides*

Parameter	Axis of principal sprout	Turion (axial part)	Stolon	Flower stalk
Proportions of, %:				
outer bark	33	38	21	8
inner bark	21	35	64	78
aerenchyma	21	35	64	78
Stele	46	27	15	14
M-lignin	Elements of xylem	—	Elements of xylem	Elements of xylem
F-lignin	Epidermis	—	Epidermis	Epidermis

**Table 3.** Qualitative and quantitative parameters of main histological–topographic zones of the leaf of *Stratiotes aloides*

Parameter	Formations			
	lower	middle		upper (bractea)
		false leafstalk	blade	
Proportions of, %:				
lateral parenchyma	69	$\frac{24}{66}$	$\frac{68}{81}$	$\frac{12}{47}$
median parenchyma	28	$\frac{67}{34}$	$\frac{30}{19}$	$\frac{85}{53}$
keel parenchyma	3	$\frac{9}{0}$	$\frac{2}{0}$	$\frac{3}{0}$
aerenchyma	6	$\frac{63}{17}$	$\frac{36}{8}$	$\frac{83}{34}$
Number of lateral bundles	2–4	$\frac{1-2}{2-6}$	$\frac{0-1}{4-8}$	$\frac{0}{2-6}$
Number of median conductive bundles	1	1 + 1	1	1
F-lignin	Epidermis	Epidermis	Epidermis	—
M-lignin	—	Sometimes elements of xylem	Elements of xylem	—

The value for the median area is above the line, and the value under the line is for the lateral area of the leaf.

the principal genetic spiral, there are an increasing aerenchymatization, more profound differentiation of leaf mesophyll, and an increasing number of stomata.

The apparatus of stomata is paracytic-parallel celled (paracytic and anamocytic types of the apparatus of stomata are characteristic of the fam. Hydrocharitaceae [11]). There are the following tendencies in distribution of lignins: M-forms are confined to conducting elements; F-forms occur in walls of epidermal cells. Lignification of walls of epidermal cells, not typical of hydromacrophytes but characteristic of *S. aloides*, compensates a partial reduction of mechanic tissues. Addition rigidity of the leaf also prevents the distribution of specimens of other hydromacrophytes on the area occupied by *S. aloides* [17].

The leaf is characterized by a high structural lability manifesting itself in proportional relationships of dif-

ferent histologic–topographic complexes and in the development level of particular elements (Table 3). Xylem possesses more progressive traits in comparison with other Hydrocharitaceae [11].

**Inflorescences.** Similarly to other Hydrocharitaceae, the inflorescences of *S. aloides* demonstrate a range of morphological adaptations to environmental conditions and efficient pollination [20]. According to Caul [20], irrespective of the position of the first flower, the inflorescence in Hydrocharitaceae evolutionarily lost bracts, except one or two terminal bracts; condensed symposium; and progressively lost later formed flowers, leading to an extreme variant to a solitary flower.

In ontogenesis of the pistillate inflorescence of *S. aloides*, the meristem initially forms two bracts. Then the apex is bifurcated, producing a lateral bud

and a bracteole which may be aborted, which is common in Alismatidae [27]. The formed lateral buds of *S. aloides* undergo a few subsequent inequivalent bifurcations and produce aggregations of flowers. The general tendency toward the reduction of the pistillate inflorescence in *S. aloides* to the uniflorous one is compensated by polyspermy and the formation of a fleshy fruit.

**Biomorph.** The biomorph of *S. aloides* has no analogs in the fam. Hydrocharitaceae [11], confirming the systematic isolation of this taxon. In the vegetation season, *S. aloides* simultaneously exploits the resources several environmental media. Most rosette sprouts are submerged to water, while leaf tops and distal parts of reproductive sprouts are exposed to air. Only 10% of the assimilatory surface of a rosette sprout is exposed to air. During the vegetation season, the rosette sprouts are fixed to the bottom of a water body with straplike roots, which are lost in winter. The system of sprouts of *S. aloides* is a long-growing one, sympodial, anisotropic, consisting of young monopodial sprouts of the principal and subordinate orders [5, 10]. Fragmentation in autumn results in a simplification of the sprout system of clonal specimens and in vegetative propagation [5, 17]. In wintering rosette sprouts, the tops are destroyed during vegetation under ice. Upon the oncoming of each new vegetative season, the axillary buds on rosette sprouts are activated and, by the early summer, each specimen forms a complex system of sprouts (Fig. 2). In the beginning of the vegetation season, the developing adventive roots penetrate the ground and fix the rosette sprouts to a certain area [17].

The biomorph of *S. aloides* should be defined as a perennial (vegetative-oligoannual) polycarpic rooted rosette stolon-turion vegetatively mobile flowering above-water hydathophyte [17].

## CONCLUSIONS

The vegetative organs of *S. aloides* manifest a range of structural adaptations related to specific conditions of the aquatic environment. *S. aloides*, as is typical of the fam. Hydrocharitaceae, is characterized by the presence of stomata of the paracytic type, of trabeculae in aerenchyma of all vegetative organs, of weakly developed xylem partly replaced by air cavities, and of chlorophyll-bearing tissues in almost all vegetative organs. Vessels along with tracheids are present both in the sprout and in the root; there are tannin-bearing and slime producing cells and lignification of exodermis is present. Lignification of epidermis and exodermis is a compensatory adaptation supplying additional reinforcement. The development of diffuse collenchyma and general aerenchymatization of tissues in *S. aloides* are efficient adaptations to the aquatic environment. Dynamics of the water level and the accompanying changes in the complex of ecological factors entail a complex of morphoanatomical adaptations.

The formation of turions and fragmentation of individuals into wintering solitary rosette sprouts contributes to the high vegetative mobility of this species.

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