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Embryology of *Polycnemum arvense* L. (lower core Caryophyllales)

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Summary: Polycnemum arvense has almost all embryological attributes of core Caryophyllales. It shows in total equal affinity with Amaranthaceae and Chenopodiaceae, if the latter are considered separate families. It is somewhat closer to Amaranthaceae because of its 1-celled female archesporium, but it shares the *Polycnemum*/*Paronychia* pollen type with some Chenopodiaceae (and Caryophyllaceae), but not with Amaranthaceae. Bisporangiate anthers of *Polycnemum* and Gomphrenoideae of Amaranthaceae, which has long been considered of great taxonomic importance, are almost certainly homoplasies, not synapomorphies. The outer integument structure of *Polycnemum* differs from those of Amaranthaceae as well as Chenopodiaceae. *Polycnemum* is similar to some Caryophyllaceae in the type of anther development, but not to Amaranthaceae and Chenopodiaceae. It sharply contrasts with all core Caryophyllales in fibrous exothecium which is also inherent in some Frankeniaceae and Polygonaceae of non-core Caryophyllales. *Polycnemum* is certainly close to Amaranthaceae and Chenopodiaceae concerning the complex of its embryological characters. Nevertheless, it is too specific to be included in any of these families. Restoration of Menge's family Polycnemaceae for *Polycnemum* alliance would be more appropriate.

Keywords: *Polycnemum*, Polycnemaceae, Caryophyllales, plant embryology, anther development, exothecium, ovule development, embryogenesis, seed coat

Polycnemum and its related genera poorly fit characteristic features of the main core Caryophyllales. Accordingly, they were included in Polygonaceae together with some chenopodiaceous and paronychious genera (Jussieu 1789) or in Paronychiaceae (Moquin-Tandon 1837) or in the separate family Polycnemaceae between Amaranthaceae and Paronychiaceae (Menge 1839). *Polycnemum* alliance was usually included in the family Amaranthaceae until the middle of the 19th century (Adanson 1763; Endlicher 1836–1840; Lindley 1846; Moquin-Tandon 1849), though even then, few botanists (Linné 1830; Dumortier 1827) nested it in Chenopodiaceae. This alliance has normally been kept in Chenopodiaceae since the middle of the 19th century (Bentham & Hooker 1880; Volkens 1893; Ulbrich 1934; Takhtajan 1987; Kühn et al. 1993; Ogundipe & Chase 2009).

Separation of Amaranthaceae and Chenopodiaceae was repeatedly questioned in the 19th and 20th centuries (Baillon 1888; Schinz 1934; Rodman et al. 1984), recently on the basis of DNA sequence data (Downie et al. 1997). These families were implicitly united by ardent molecular systematists ([APG] 1998; Cuénoud et al. 2002; [APG III] 2009; Crawley & Hilu 2012; [APG IV] 2016), but such a uniting needs further substantiation (Kadereit et al. 2003; Shepherd 2008). In Amaranthaceae-Chenopodiaceae assemblage, *Polycnemum* alliance is usually a sister to traditional Amaranthaceae (Kadereit et al. 2003; Masson & Kadereit 2013) and is included into the latter ([APG] 1998; [APG III] 2009; Takhtajan 2009; [APG IV] 2016). However, it is either a sister to the clade Betoideae-Coryspermoideae-Chenopodioideae (Kadereit et al. 2006) or a sister to the whole Amaranthaceae-Chenopodiaceae assemblage (Müller & Borsch 2005; Masson & Kadereit 2013). Neither of above-mentioned relations is well supported (Kadereit

et al. 2003; Müller & Borsch 2005; Masson & Kadereit 2013). Nevertheless, *Polycnemum* alliance is certainly among the basal lineages of Amaranthaceae-Chenopodiaceae assemblage.

Amaranthaceae and Chenopodiaceae were long considered advanced core Caryophyllales (Ehrendorfer 1976; Takhtajan 1966, 1987), even the terminal in the pectinate cladogram of the latter (Rodman et al. 1984). However, DNA sequence data have confirmed their basal position in core Caryophyllales (Downie & Palmer 1994; Kadereit et al. 2003). Thus, *Polycnemum* alliance is among basal lineages of the core Caryophyllales which could bear plesiomorphic characters that could elucidate evolutionary pathways of core Caryophyllales' attributes.

Basal position and weakly supported relations of *Polycnemum* alliance would have provoked comprehensive research of these plants. Surprisingly, only secondary thickening of stems and roots has recently been scrutinized (Timonin 2011; Hecklau et al. 2012). Other features of these plants have to be found out of taxonomic surveys mostly dating back to the early 19th century.

As to embryology of *Polycnemum* alliance, *Polycnemum* has been told to have bilocular anthers (Endlicher 1836–1840) (unilocular according to Baillon 1888), longitudinal introrse dehiscence of the anther (Baillon l.c.), campylotropous (Baillon l.c.) solitary ovule on long bent funicle, upward micropyle (Moquin-Tandon 1837; Baillon 1888), circular embryo (Menge 1839; Moquin-Tandon 1837) encircling abundant starchy (perisperm) and ascendant hilumward radicle (Moquin-Tandon 1837). Anther development, sporogenesis, embryogenesis etc. have not been studied so far. We have embryologically investigated the type species *Polycnemum arvense* L. to fill this gap.

Materials and methods

Plants of *Polycnemum arvense* L. have solitary axillary flowers, so one shoot usually bears all developmental stages from early flower buds to mature fruits. Wild plants from the Rostov region, South European Russia, were totally fixed with FAA fixative in 2014. The fixed material was washed with 70% ethyl alcohol, dehydrated and embedded in paraffin wax according to standard protocols (Barykina et al. 2004). 8 to 12 µm thick sections were dewaxed, rehydrated and stained by Alcian Blue with Rawitz's haematoxylin or by Procyonic Blue (for proteins) or processed either with PAS reaction (for polysaccharides) or with Ferric chloride reaction (for tannic substances) according to Barykina et al. (2004). The preparations thus processed were dehydrated and embedded into Canada Balm. Photomicrographies were taken under light microscope Univar (Reichert) equipped with digital camera DCM-510.

Results

Flowers. (Fig. 1) solitary, axillary, complete, 3-staminate; anthers ?monothecal, bisporangiate; anther wall 5-layered; pistil with short style and short bipartite stigma; papillate tissue functioning as transmitting tissue or as obturator continuous from stigma terminals through stylar channel to ovary roof; ovary superior, 1-locular, 1-ovulate; ovary wall 4-layered, its inner subepidermal layer crystalliferous.

Anther and pollen development. Primary archesporium produces outwards the primary parietal layer and inwards the secondary archesporium by means of periclinal divisions of its cells. The cells of the primary parietal layer divide periclinally to give rise to 2 secondary parietal layers (Fig. 2 A). The cells of the latter divide nearly synchronously (Fig. 2 B). The outer secondary

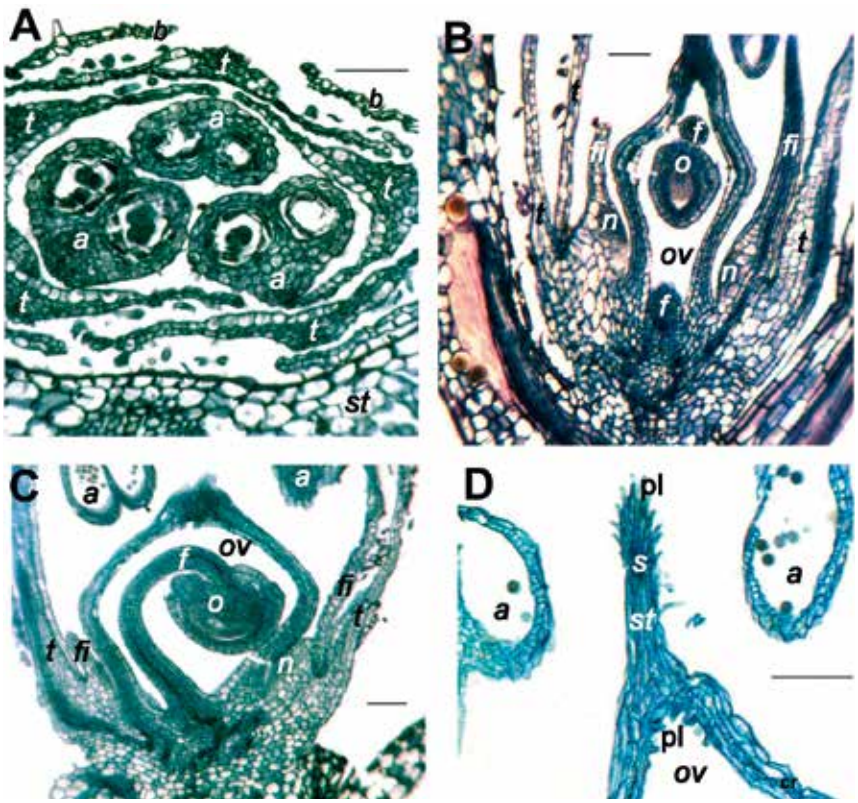

Figure 1. Flower. A – transverse section at the level of anthers; B, C – longitudinal section; D – papillate tissue of the pistil, longitudinal section. a – anther; b – bract; cr – crystalliferous cells; f – funicle; fi – stamen filament; n – nectary; o – ovule; ov – ovary; pl – papillae; s – stigma; st – style; t – tepalum. Scale bars = 50 µm.

parietal layer gives rise to the endothecium and outer middle layer (Fig. 2 B, C). The inner one forms the inner middle layer and the tapetum (Fig. 2 B). The anther development thus matches Davis' Basic type (1966).

Both middle layers are usually ephemeral. They begin to degenerate before sporogenesis (Fig. 2 C, D). However, one middle layer partly remains near the endothecium in some mature anthers (Fig. 3 A). Its cells have slightly thickened cell walls.

The cells of endothecium develop fibrous thickenings in their anticlinal transverse cell walls (Fig. 3 B, C). Similar thickenings are also on the cell walls of connective cells adjacent to the locule. Cell wall thickenings are also developed in the epidermal cells, but they occupy their anticlinal longitudinal walls (Fig. 3 D, E). The thickenings of the endothecial cells are perpendicular to their counterparts of the epidermal ones.

Glandular tapetum consists of the cells which increase and become 2-nucleate at the stage of meiosis in archesporial cells (Fig. 2 D). The tapetum dissolves at the stage of 2-celled pollen and leaves behind a film with Ubisch bodies (Fig. 3 D).

Crystalliferous cells are in connective tissue.

Simultaneous meiosis results in tetrahedral or isobilateral spore tetrads (Fig. 3 F). The pollen grains are spherical, pantoporate, 3-celled (Fig. 3 G).

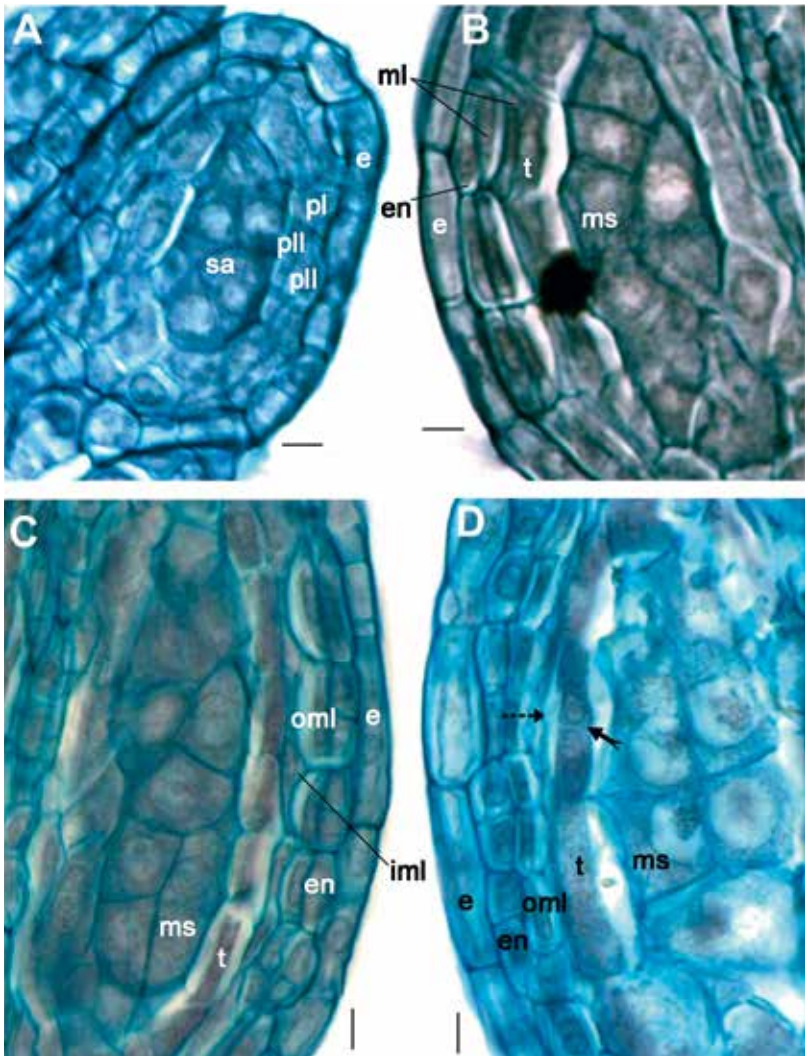

Figure 2. Anther wall development. A – 2–3-layered anther wall; B – 5-layered anther wall; C – beginning of degeneration of the inner middle layer; D – degenerated inner middle layer, glandular tapetum. e – epidermis; en – endothecium; iml – inner middle layer; ml – middle layer; ms – microsporocyte (late secondary archesporium); oml – outer middle layer; pI – primary parietal layer; pII – secondary parietal layer; sa – early secondary archesporium; t – tapetum. Solid arrow – binucleate tapetal cell; dotted arrow – collapsed inner middle layer. Scale bars = 5 µm.

The septum between the anther locules dissolves after the pollen has matured. The anther dehisces introrsely longitudinally (Fig. 3H).

Ovule development. The solitary basal ovule is originally orthotropous, but is lifted by a long funicle. Growing funicle begins to bend before closure of the ovary (Fig. 4A). The ovule is resultantly rotated. The inner integument is clearly visible all around the nucellus at this stage, whereas the outer one is identifiable opposite the future raphe side (Fig. 4B). The ovule rotation progresses to make the ovule pensile at the stage of meiosis of its sporocyte (Fig. 4C). The nucellus is nearly enclosed by the inner integument at that time, but the micropyle is still undeveloped. The outer integument is clearly visible all around. The integuments are 2-layered. The micropyle is formed by the inner integument at the megaspore developmental

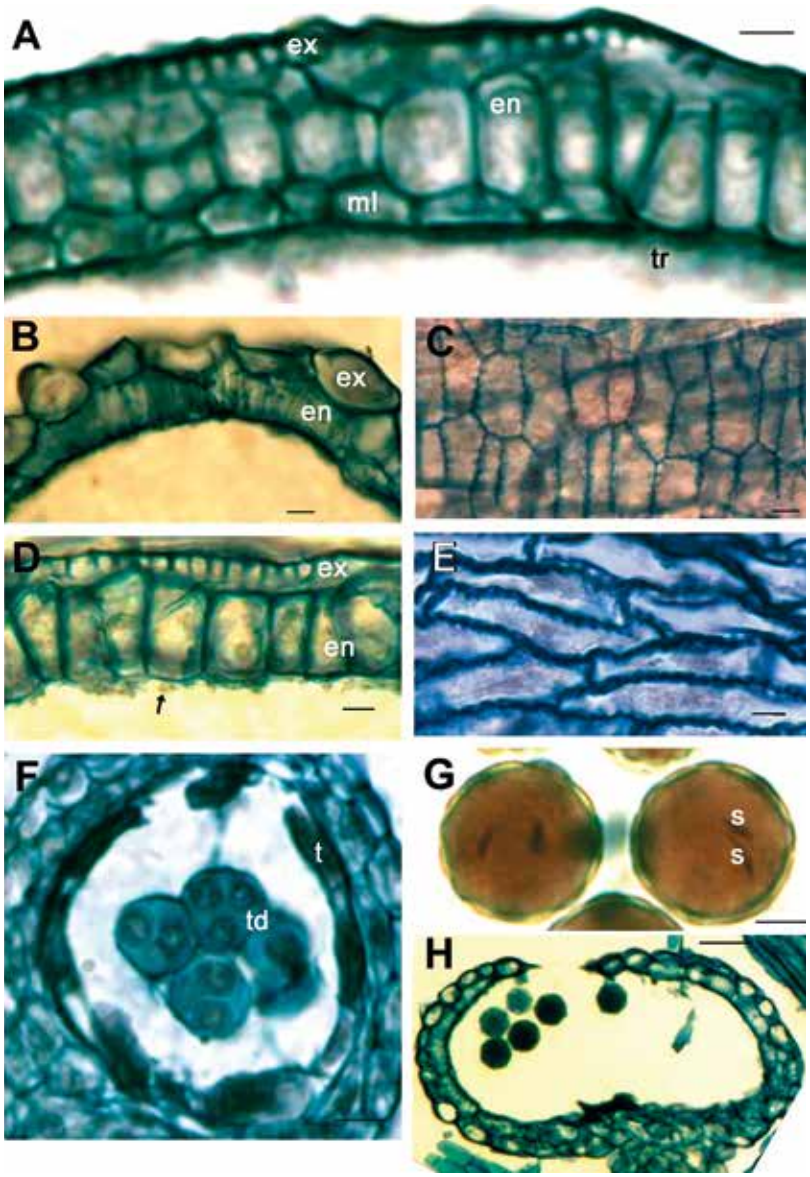

Figure 3. Mature anther. A – extant middle layer of the anther wall; B – endothecium in transverse section of the anther; C – endothecium in paradermal section; D – exothecium in longitudinal section of the anther; E – exothecium from the surface; F – pollen tetrads in the anther locule; G – 3-celled pollen grains in the mature anther; H – dehisced anther. en – endothecium; ex – exothecium; ml – middle layer; s – sperm cell; t – tapetum; td – microspore tetrad; tr – tapetum remnants. Arrow – Ubisch body. Scale bars = 5 µm (A–G); 25 µm (H).

stage (Fig. 4 D). The ovule rotates 180° again during megaspore development to mature embryo sac to become anacampylotropous circinnotropous (Fig. 4 E). Its micropyle is orientated upwards (Fig. 4 E, F). The ovule changes into amphitropous after fertilization and rotates back 90°, its micropyle is turned sidewards (Fig. 4 G).

The solitary archesporial cell divides into parietal cell and megasporocyte (Fig. 5 A). The former one gives rise to 2–3 layers of ephemeral parietal cells (Fig. 5 B). There are 2 areas of proliferation in the growing nucellus, viz. micropylar and chalazal ones. 5–8-layered nucellar cap results from

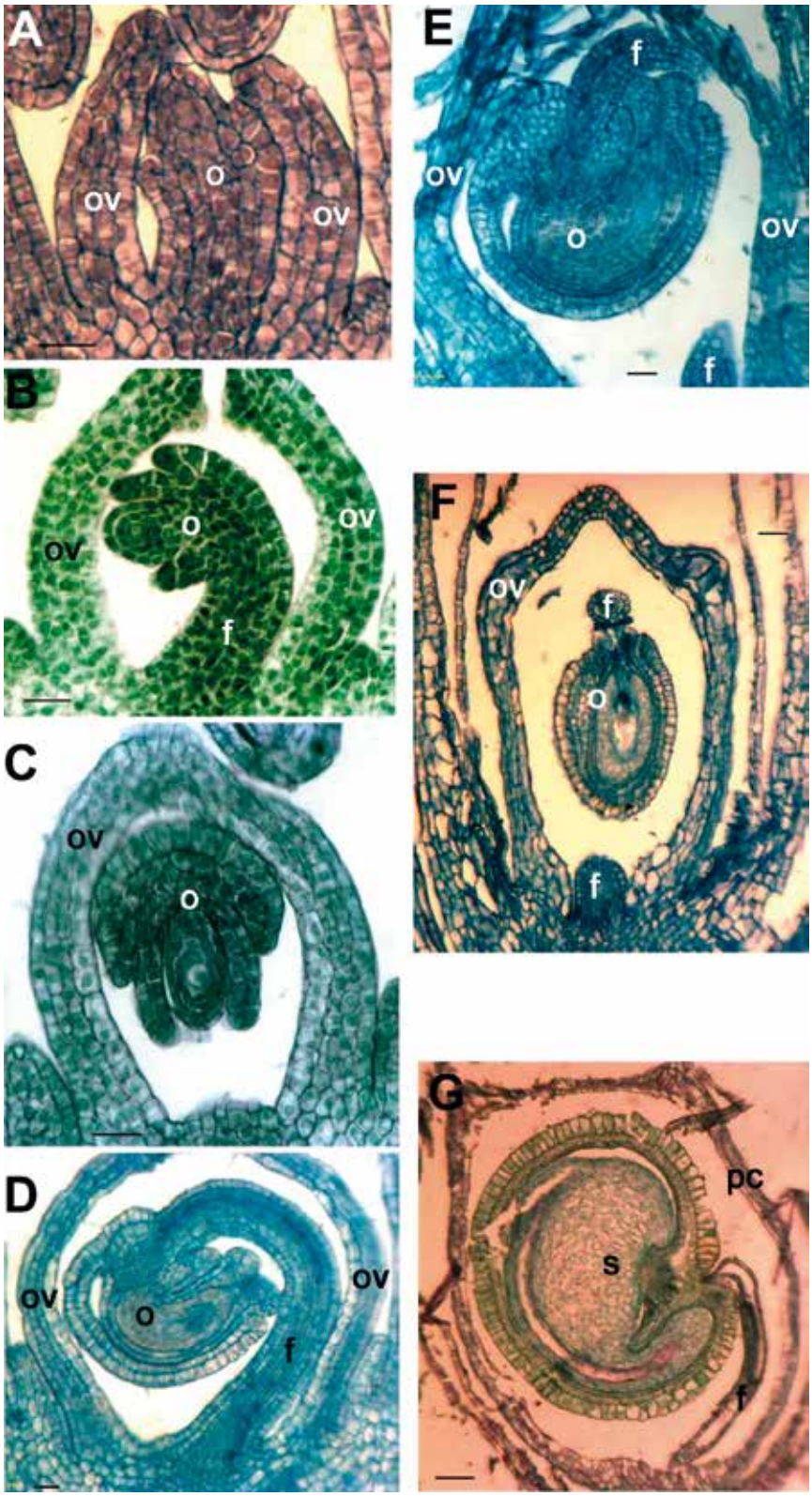

Figure 4. Changes of direction of developing ovule. f – funicle; o – ovule; ov – ovary; pc – pericarp; s – immature seed. Scale bars = 25 µm (A–E); 50 µm (F); 100 µm (G).

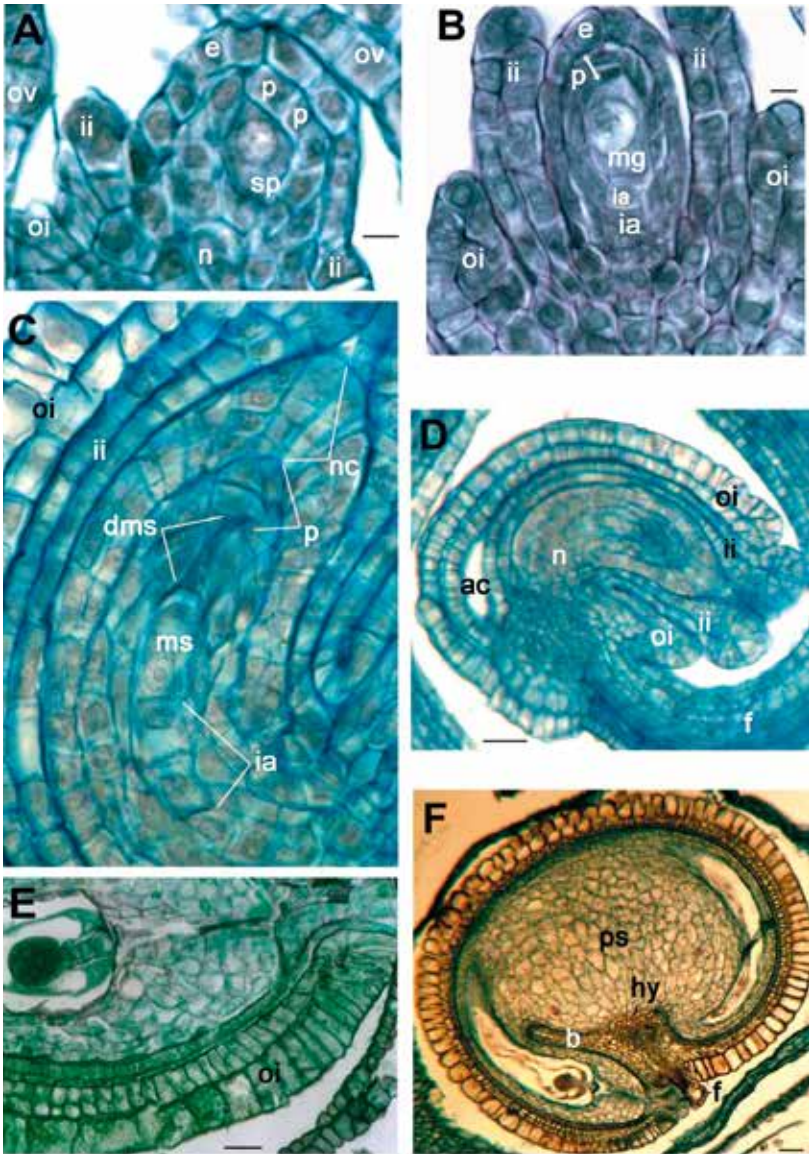

Figure 5. Ovule development. A – sporogeneous and parietal cells; B – megasporocyte, parietal cells and inferior axial cells; C–D – ovule at the stage of megaspore; E – outer integument near the micropyle; F – basal body in the ovule. ac – air chamber; b – basal body; dms – degenerated megaspores; e – epidermis; f – funicle; hy – hypostasis; ia – inferior axial cell; ii – inner integument; mg – megasporocyte; ms – megaspore; n – nucellus; nc – nucellar cap; ov – ovary wall; oi – outer integument; p – parietal cell; ps – developing perisperm; sp – sporogeneous cell. Scale bars = 5 µm (A–C, E); 20 µm (D); 50 µm (F).

the divisions of epidermal cells and their derivatives in the micropylar area (Fig. 5 C). Inferior axial cells develop below the chalaza end of the megasporocyte (Fig. 5 B, C).

Mature ovule is crassinucellate, bitegmic. The inner integument remains 2-layered over the entire length except for its endostome area (Fig. 5 D). The outer integument is mostly 2-layered, but also 3-layered here and there caused by local periclinal divisions of its inner cells (Fig. 5 E). The cells of the outer integument divide anticlinally near micropyle to become palisade-like (Fig. 5 E). The outer integument moves apart from the inner one in the chalazal area of the ovule. The

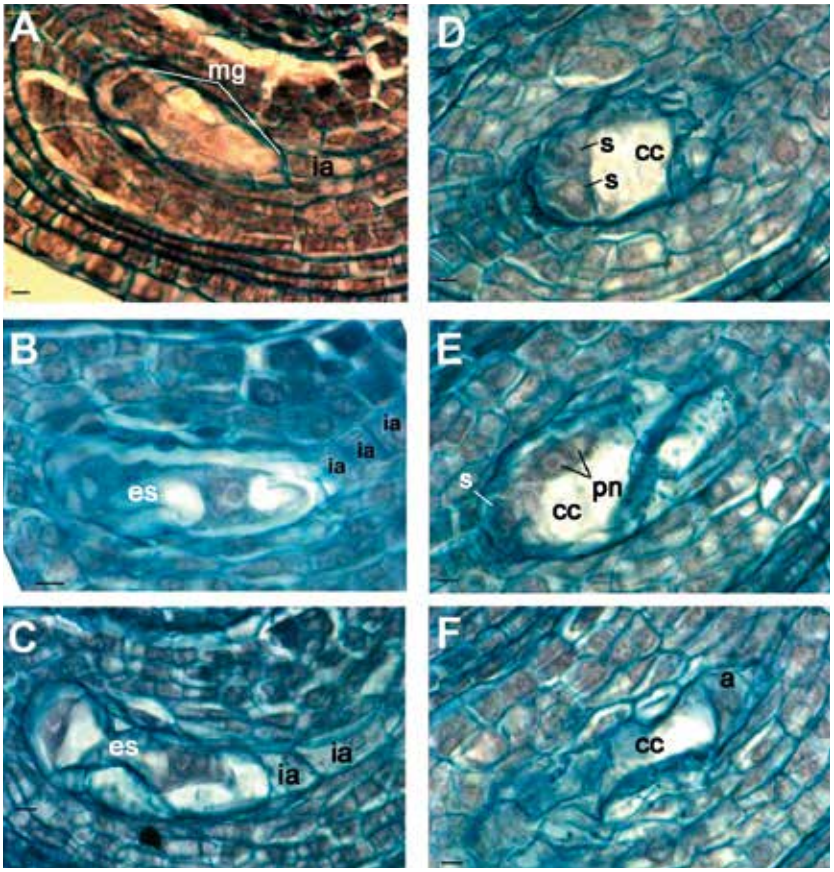

Figure 6. Embryo sac development. A – megaspore tetrad; B – 2-nucleate developing embryo sac; C – 4-nucleate developing embryo sac; D–F – mature embryo sac. a – antipodal cell; cc – central cell; e – egg cell; es – embryo sac; ia – inferior axial cell; mg – megaspores; pn – polar nuclei; s – synergid. Scale bars = 5 µm.

large air cavity is thus developed (Fig. 5 D). The basal body differentiates in the chalazal part of the ovule during campylotropus to amphitropous transformation of the ovule after fertilization (Fig. 5 F). It is clearly limited by the inner cell layer of the inner integument.

Meiosis of the megasporocyte results in a linear tetrad (Fig. 6 A) or rarely a triad of cells. The chalazal cell grows into embryo sac of Polygonum type (Fig. 6 B–F); other cells degenerate (Fig. 5 C). The egg apparatus is typical (Fig. 6 D, E); the synergids have a filiform apparatus (Fig. 7 A). Fusion of the polar nuclei occurs before fertilization (Fig. 7 A). There are three small antipodal cells or one 3-nucleate one (Fig. 6 F). The antipodal cells are ephemeral. Mature embryo sac has no antipodal cells. A series of 1–3 large inferior axial cells abuts on the chalazal tip of the embryo sac (Figs 5 C; 6 B, C; 7 B). Their cell walls are thicker than those of the nucellar cells.

The mature embryo sac is sheathed by large cells without nucleus but with polysaccharide bodies (Fig. 7 B). The latter are likely to be unutilized transitory starch granules. These cells are enlarged probably because of destruction of some cell walls between them. Small starch granules are also around the secondary nucleus of the central cell (Fig. 7 A).

Endosperm development. Circular arc of thin-walled cells with starch-filled amyloplasts develops along the dorsal part of the nucellus after fertilization. Nuclear endosperm soon grows into this

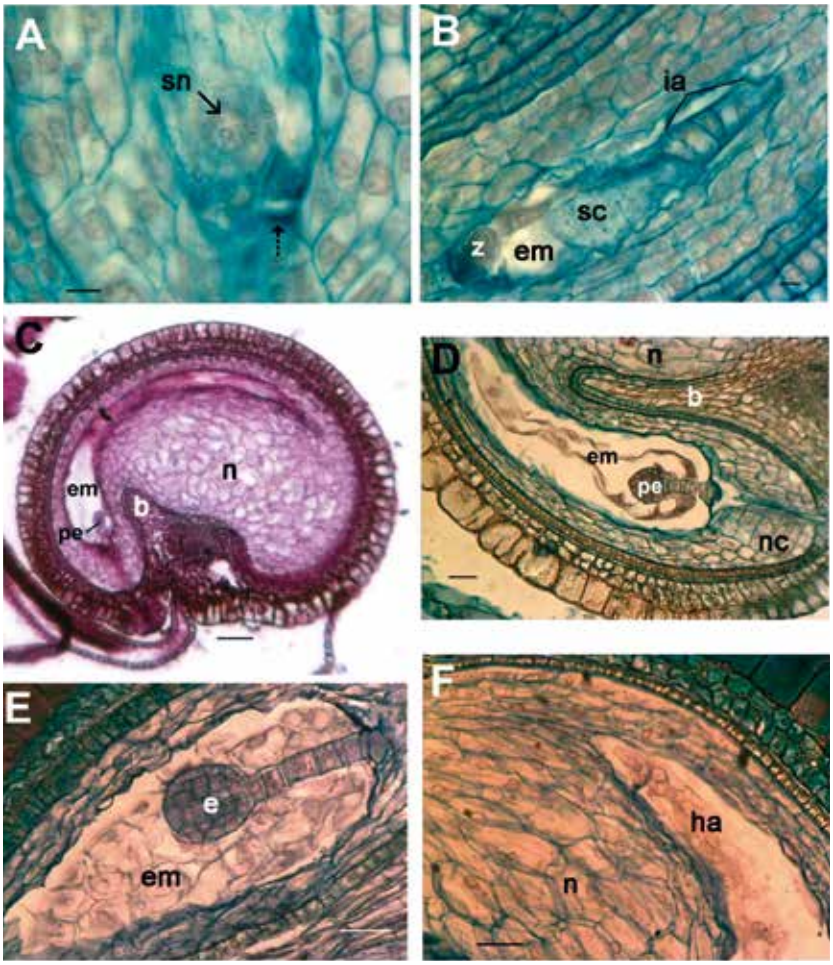

Figure 7. Endosperm development. A – micropylar part of the mature embryo sac; B – post-fertilization embryo sac; C – growing endosperm; D – micropylar part of nuclear endosperm; E – cellular endosperm around the embryo; F – endosperm haustorium. b – basal body; e – embryo; em – endosperm; ha – haustorium; ia – inferior axial cells; n – nucellus; nc – nucellar cap; pe – proembryo; sc – sheathing cells of the nucellus; sn – secondary nucleus of embryo sac and surrounding starch granules; z – zygote. Dotted arrow – filiform apparatus of the synergid. Scale bars = 5 µm (A, B); 30 µm (C–F).

arc to replace the cells there (Figs 7 C; 5 F). Most endosperm nuclei are concentrated around the proembryo, few of them are peripheral in cytoplasmic strands (Fig. 7 D). Cellular zone of the endosperm develops around the late globular proembryo (Fig. 7 E). Cell formation gradually extends into the middle part of the growing endosperm, however, its chalazal part remains nuclear. Its very tip is an endospermal haustorium (Fig. 7 F) of opaque cytoplasm with condensed large nuclei which often fuse with each other. This haustorium is separated from the nucellus by rather thickened cell walls, which seem to maintain transfer function. The endosperm contains almost no reserve substances (Fig. 7 E). It is likely to be a digesting and transferring formation.

Proembryo development. The zygote divides transversely into terminal (*ac*) and basal (*bc*) cells of 2-celled proembryo (Fig. 8 A). Each of them divides transversely again to give rise to the cells *l* and *l'* and the cells *m* and *ci*, respectively. Linear 4-celled proembryo resultantly originates (Fig. 8 B). Longitudinal divisions of *l* and *l'* result in the secondary cell tetrad of 2-celled storeys *l* and *l'*

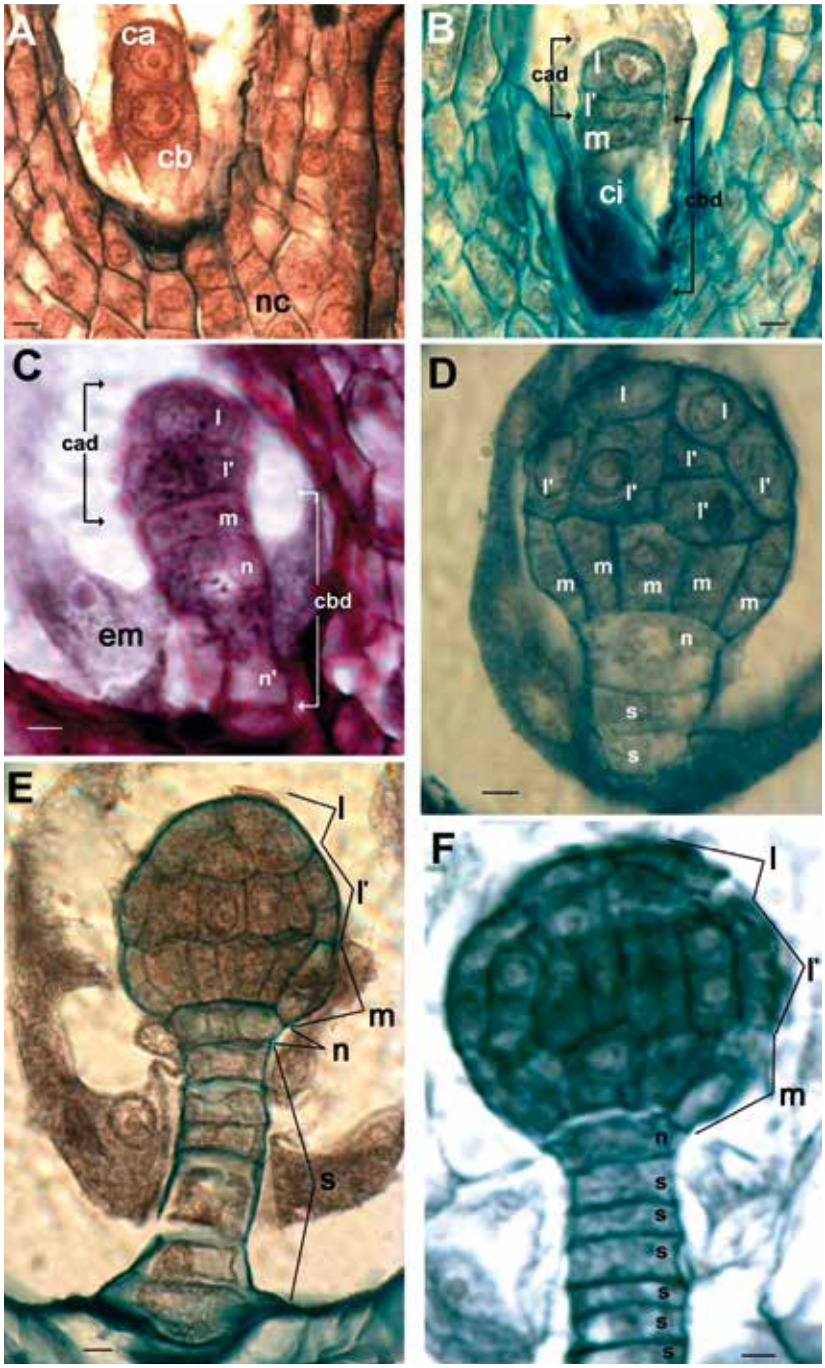

Figure 8. Embryogenesis. A – 2-celled proembryo; B – 4-celled linear proembryo; C – tetrad of l and l' cells; D–F – globular proembryo. ca – terminal cell; cad – terminal cell derivatives; cb – basal cell; cbd – basal cell derivatives; em – endosperm; nc – nucellar cap; s – suspensor. Scale bars = 5 µm.

(Fig. 8 C) which become later few-celled storeys (Fig. 8 D–F). The cell *m* tangentially divides to produce basipetally cell *n* (Fig. 8 C). Then it divides longitudinally to produce 4(5)-celled storey *m* (Fig. 8 D–F). The cell *n* gives rise to the hypophysis by means of longitudinal cell divisions. The cell *ci* repeatedly divides transversely to result in uniseriate 7–8-celled suspensor (Fig. 8 D–F).

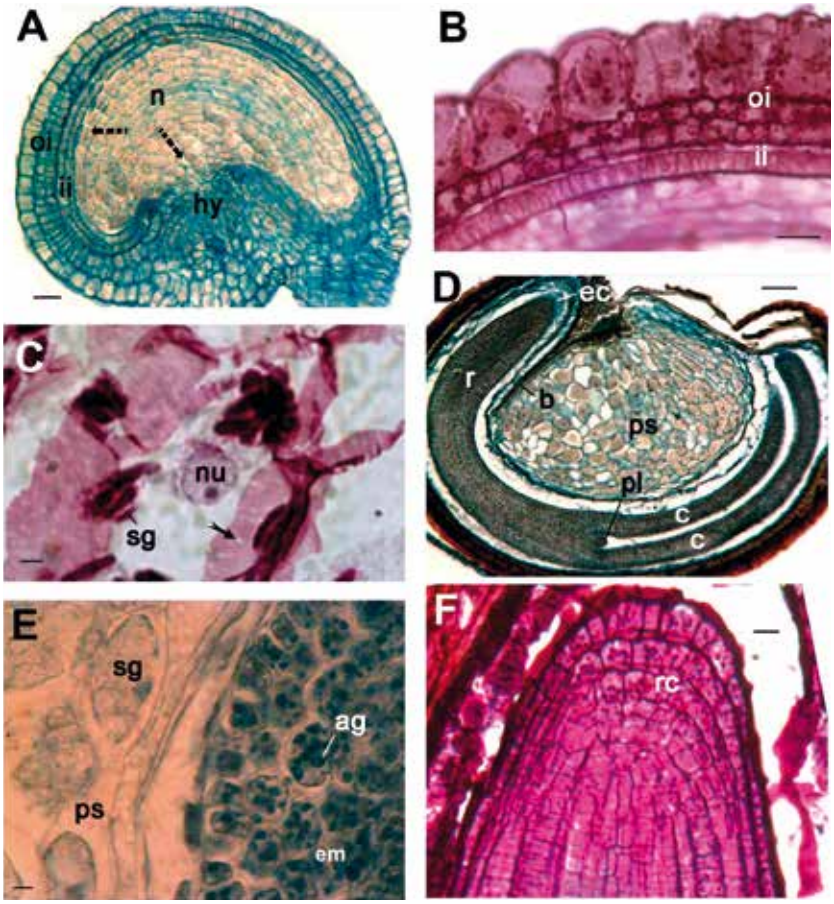

Figure 9. Seed development. A – growth zones of fertilized ovule; B – starch granules in the integument cells; C – nucellus cells; D – unripe seed; E – store substances in the embryo and perisperm; F – radicle. ag – aleuronic granule; b – basal body; c – cotyledon; ec – endosperm cap; em – embryo; ii – inner integument; hy – hypostasis; n – nucellus; nu – nucleus; oi – outer integument; pl – plumule; ps – perisperm; r – radicle; rc – radicle cap; sg – starch granule. Solid arrow – pit; dotted arrow – growth zones. Scale bars = 5 µm (C, E); 10 µm (F); 20 µm (A, B); 100 µm (D).

The embryogenesis in *P. arvense* fits Chenopodiad type. The basalmost suspensor cell has a larger nucleus. Its broad base is adherent to the nucellar cap (Fig. 8 E). Small starch granules are in the proembryo cells (Fig. 8 C).

Seed development. The basal body develops in the chalazal part of nucellus after fertilization, when campylotropous ovule transforms to amphitropous one. It intrudes into the nucellus (Figs 5 F; 7 C). There are 2 zones of cell proliferation in the nucellus (Fig. 9 A). The first one is just below the inner integument mostly in the chalazal part of the nucellus and opposite the hilum. The second one abuts the hypostasis. Activities of these zones cause the nucellus to become convex (Fig. 9 A). Abundant transitory starch granules arise in the ovule after fertilization, especially in the integuments (Fig. 9 B), in the chalazal part of the nucellus below the hypostasis and in the basal body. Small starch granules are in the nucellar cap. Central part of the nucellus is starch-free at this developmental stage (Fig. 7 C, F), but it starts accumulating oval, slightly tapered compound starch granules at the torpedo embryo stage (Fig. 9 C). The latter increase in sizes as the seed grows and ripens (Fig. 9 E).

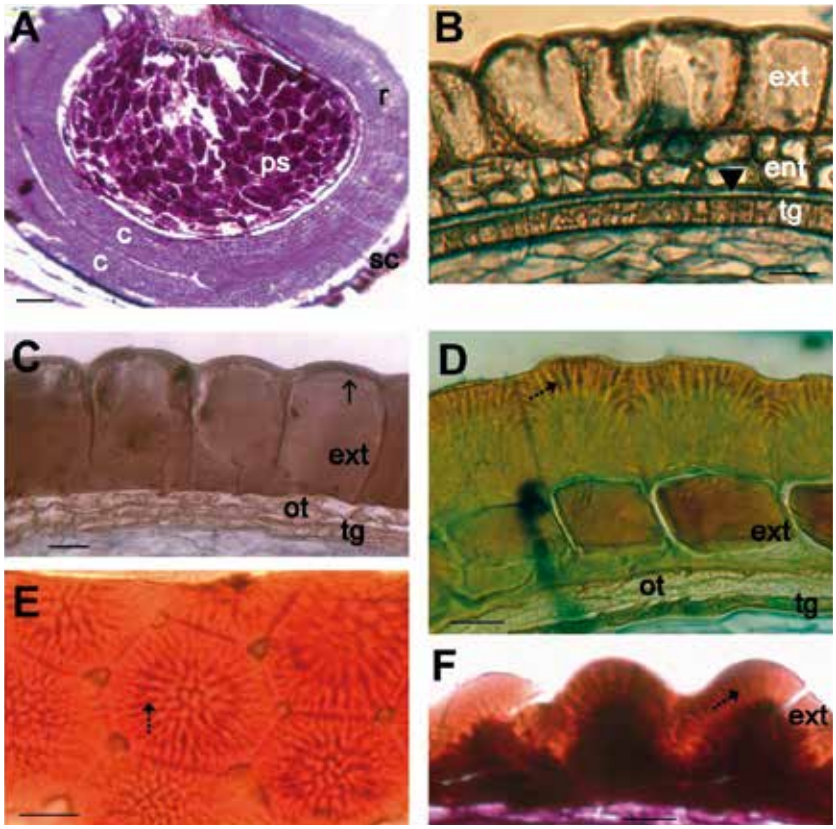

Figure 10. Mature seed and developing seed coat. A – mature seed, longitudinal section; B – prospective tissues of the seed coat; C – initial stage of the outer cell wall thickening in developing exotesta; D – thickened outer cell wall of exotesta cells; E – developed exotesta from the surface; F – developed exotesta in cross-section. c – cotyledon; ent – prospective endotesta; ext – (prospective) exotesta; ot – obliterated tissues of the seed coat (exotegmen and endotesta); ps – perisperm; r – radicle; sc – seed coat; tg – (prospective) endotegmen. Solid arrow – papillate inner surface of the outer exotesta cell wall; dotted arrow – stalactite; arrowhead – obliterated exotegmen. Scale bars = 100 μm (A); 20 μm (B–F).

The nucellar cells have clearly visible roundish nuclei and irregularly shaped large pits in their cell walls in immature seeds (Fig. 9 C). These cells are overfilled by tightly packed compound starch granules in the mature seeds, whereas their nuclei are small and misshapen. The nucellus is thus changed into the perisperm, the specific storage tissue of the core Caryophyllales. It occupies the central part of the seed. The basal body is compressed and becomes filmy (Fig. 9 D). Mostl of it is replaced by the nucellus. Developed circular embryo nearly completely surrounds the perisperm (Fig. 10 A). The cotyledons take about half of the embryo length (Figs 9 D; 10 A). The plumule is represented by apex without leaf primordia. There are distinctive provascular strands in the cotyledons, hypocotyl and radicle. Small starch granules fill the cells of early embryo, but they are replaced by the aleurone grains in the mature one (Fig. 9 E) throughout except for the root cap whose cells contain starch granules maintaining statolith function (Fig. 9 F). The endosperm remains as protein-containing endosperm cap around the radicle in the mature seed (Fig. 9 D).

Seed coat development. The seed coat comprises both integuments. The cells of the partly 3-layered outer integument, especially those of prospective exotesta, are larger than their counterparts of the 2-layered inner integument at the developmental stage of mature embryo sac (Fig. 9 B). Large

starch granules are deposited in all integument cell layers being more numerous in those of the developing testa (Fig. 9 B). These granules gradually disappear during seed development.

Tannins are detectable in the prospective exotesta and endotegmen cells at the early globular proembryo developmental stage. Tannins are later detected in cells of hypostasis and chalaza part of the seed. The outer cell layer of the inner integument firstly collapses and disappears (Fig. 10 B). Thin-walled inner cells of the outer integument secondarily lose their starch granules and obliterate (Fig. 10 C, D). Neither exotegmen nor endotesta thus develop in the seed coat. Small-celled inner layer of the inner integument remains alive pretty long to develop into the endotegmen (Fig. 10 D) with characteristic numerous striate thickenings of its cell walls. The outer cell layer of the outer integument changes into the exotesta. Its cells form a thickened outer cell wall permeated by tannic stalactites (Fig. 10 D). The inner surface of this cell wall under development is initially papillate (Fig. 10 C) just as in *Amaranthus retroflexus* L. (Dzhalilova et al. 2015). It becomes smooth later. The exotesta cells are dead in the mature seed.

The seed coat of the mature seed is exotestal endotegminal. It consists of protective exotesta and empty compressed endotegmen and endotesta remnants (Fig. 10 D). The stalactites in the outer cell walls of exotesta cells are perpendicular to the surface of the seed coat. They are parallel to each other in the flat cell walls, but they seem oblique converging inwards in the convex ones (Fig. 10 E, F).

The mature seeds are reniform, laterally flattened, dark brown and easily fall out of the membranous pericarp.

Discussion

The core Caryophyllales show a well-defined complex of embryological attributes, though some exclusions do occur (Veselova 1990). Non-core Caryophyllales are diverse embryologically (Kamelina 2009), but in general they are very different from the core Caryophyllales. Only a few characteristic features of the latter are scattered among representatives of the non-core Caryophyllales. The families Asteropeiaceae, Physenaceae, Simmondsiaceae and Rhabdodendraceae (Brockington et al. 2009) or Simmondsiaceae, Frankeniaceae and Tamaricaceae (Schäferhoff et al. 2009) were shown to be the closest to the core Caryophyllales. Of them, the family Asteropeiaceae has not been embryologically investigated, but it is reported to have no perisperm (Kamelina 2009). Simmondsiaceae (Naumova 1981), Frankeniaceae (Kamelina 1983a) and Tamaricaceae (Kamelina 1983b) do not have common embryological attributes with the core Caryophyllales. Physenaceae (Kamelina 2009) are similar to the core Caryophyllales in a campylotropous ovule, but quite dissimilar in 4-layered inner and 6-layered outer integuments, straight embryo and an absent perisperm. Rhabdodendraceae are the most similar to core Caryophyllales, viz. campylotropous ovule, 2–3-layered perisperm and circular embryo (Kamelina 2009). However, it has neither a nucellar cap nor a filiform apparatus in the synergids, only its inner integument is 2-layered, whereas the outer one is 3–5-layered[1], the embryo sac is of specific variation of the Polygonum type (Kamelina 2009).

Anther development matches with Davis' Monocotyledonous type in most core Caryophyllales families (Phytolaccaceae s.l., Cactaceae, Portulacaceae s.l., Talinaceae, Basellaceae, Didiereaceae,

[1] Ovules of Rhabdodendraceae are unitegmic according to Shamrov (1985).

Molluginaceae, Amaranthaceae, Chenopodiaceae) (Davis 1966; Poddubnaya-Arnoldi 1982; Yakovlev 1983). Anther development in *Polycnemum arvense* matches with Davis' Basic type which is in contrast to most core Caryophyllales. However, this type of anther development prevails in Caryophyllaceae (Tursunov & Matyunina 1983; Veselova 1990), another basal core Caryophyllales (Brockington et al. 2009; Schäferhoff et al. 2009). Basic type of anther development is also revealed in some members of Nyctaginaceae s.l. and Aizoaceae s.l. (Davis 1966; Iljina 1984; Veselova 1989) of the higher core Caryophyllales. This type of anther development is widely distributed among Dicotyledons, but it has not been reported in non-core Caryophyllales so far (Kamelina 2009). Therefore, the Basic type of anther development in *Polycnemum* and members of Nyctaginaceae and Aizoaceae should be better considered as autapomorphies of these taxa.

Bisporangiate ?monothecal anther inherent in *Polycnemum arvense* is typical of Gomphrenoideae (Amaranthaceae) (Schinz 1934; Endress & Stumpf 1990; Takhtajan 2009), but the synapomorphic status of this character still needs to be confirmed. 2-nucleate glandular tapetum in the anther, simultaneous tetrad development and 3-celled pollen of *Polycnemum arvense* are quite typical of the core Caryophyllales (Veselova 1990).

Fibrous thickenings on the cell walls of endothecium and exothecium (epidermis) cells are a nearly unique character of *Polycnemum arvense*. Such thickenings as well as bisporangiate anther is only revealed in *Arceuthobium* spp. (Viscaceae), highly reduced parasitic plants affecting conifers (Johnson 1888; Dowding 1931). Fibrous thickenings in the exothecium cells instead of endothecium were found in *Empetrum nigrum* L. and *Corema album* (L.) D. Don. ex Steud. (Empetraceae) (Freiberg 1983) and *Anemone* and *Aquilegia* (Ranunculaceae) (Teryokhin et al. 2002). No core Caryophyllales with fibrous exothecium have been known so far, but a fibrous exothecium sometimes develops in representatives of Frankeniaceae (Kamelina 1983a) and in *Oxyria* (Polygonaceae) (Teryokhin et al. 2002) of non-core Caryophyllales. Further research is needed to find out if the fibrous exothecium of *Polycnemum arvense* is a plesiomorphic character.

Anacampylotropous (circinnotropous), bitegmic, crassinucelate ovule of *Polycnemum arvense* is quite typical of core Caryophyllales. Most Amaranthaceae and Chenopodiaceae have two 2-layered integuments which are 3–4-layered around the micropyle (Konycheva & Kadyrova 1983; Savina 1983). The outer integument of *P. arvense* is partly 3-layered, but it is invariably 2-layered around the micropyle; it consists of palisade cells there. Supernumerary cell layers in the outer integument are revealed in some species of *Atriplex* L. of Chenopodiaceae (Popova & Kamaeva 1977) as well as in *Amaranthus retroflexus* L. of Amaranthaceae (Veselova et al. 2014). Besides, supernumerary cell layers in the integument are in *Stegnosperma halimifolium* Benth. of Stegnospermataceae (Kamelina & Proskurina 1985), another basal core Caryophyllales. Thus, the integument structure does not elucidate affinities of *Polycnemum*.

The female archesporium of *Polycnemum arvense* is 1-celled. Such an archesporium is characteristic of Amaranthaceae (Savina 1983), but not typical of Chenopodiaceae (Konycheva & Kadyrova 1983). However, both families have exceptional representatives (Savina 1983; Veselova & Kondorskaya 1990). Meiotic division of the micropylar cell of cell dyad is often suppressed in *Polycnemum arvense* to result in 3 cells instead of a megaspore tetrad. Such a suppression of cell division often takes place in different families of core Caryophyllales (Yakovlev 1983). The campylotropous ovule develops into an amphitropous seed which is typical of many core

Caryophyllales (Yakovlev 1983). The embryogenesis in *P. arvense* fits Chenopodiad type and is typical of many core Caryophyllales.

Polycnemum arvense is similar to other core Caryophyllales in destruction of the outer cell layer of the inner integument usually followed by the destruction of the inner cell layer of the outer integument in the developing seed coat. Various seed coat structures are known in Chenopodiaceae and Amaranthaceae (Butnik 1991; Butnik & Zhapakova 1991). The seed coat of *Polycnemum arvense* is exotestal endotegminal with stalactites in the outer cell walls of exotesta cells. It is similar to that of *Atriplex*, *Chenopodium* and *Oxybasis* of Chenopodiaceae (Sukhorukov & Zhang 2013) and *Amaranthus* of Amaranthaceae (Tikhomirov & Fedorova 1997; Veselova et al. 2014), but also to that of *Talinum* (Talinaceae) (Veselova et al. 2012;) and of *Cryptocarpus pyriformis* Kunth (Nyctaginaceae) (Sukhorukov et al. 2015), etc.

The inner surface of the outer cell wall of stalactite bearing exotesta cells is papillate in *Polycnemum arvense* at the initial stage of thickening. Similar but more conspicuous papillae were previously revealed in developing outer exotesta cell walls of *Amaranthus retroflexus* L. (Dzhalilova et al. 2015). Formation of papillae on the inner surface of early developing outer exotesta cell wall is likely to be universal in core Caryophyllales whose exotesta cells have stalactites in their outer cell walls.

The mature seeds of *Polycnemum arvense* are typical of core Caryophyllales.

Polycnemum arvense is thus embryologically a typical member of core Caryophyllales. Its relations to Chenopodiaceae and Amaranthaceae are almost equal. Only the 1-celled female archesporium could indicate a greater affinity to Amaranthaceae. However, the bisporangiate anthers of *Polycnemum arvense* and members of Gomphrenoideae (Amaranthaceae) are unlikely to be synapomorphic because the basal lineages of Amaranthaceae (Ogundipe & Chase 2009) have ordinary bithecal tetrasporangiate anthers. Furthermore, *Polycnemum arvense* shares its *Polycnemum* / *Paronychia* pollen type with some Chenopodiaceae (and Caryophyllaceae), but not with Amaranthaceae (De Klerk & Joosten 2007). *Polycnemum arvense* sharply contrasts with the majority of core Caryophyllales in ?autapomorphic Basic type of anther development and ?symplesiomorphic exothecium. Restoration of Menge's (1839) family Polycnemaceae nested near Amaranthaceae and Chenopodiaceae would be more appropriate than inclusion of the *Polycnemum* alliance either in Amaranthaceae or in Chenopodiaceae.

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References

Adanson M. (1763): Familles des plantes. T. 2. – Paris: Vincent.

[APG] Bremer K., Chase M. W., Stevens P. F., Anderberg A. A., Backlund A., Bremer B., Briggs B. G., Endress P. K., Fay M. F., Goldblatt P., Gustafsson M. H. G., Hoot S. B., Judd W. S., Källersjö M., Kellog E. A., Kron K. A., Les D. H., Morton C. M., Nickrent D. L.,

Olmstead R.G., Price R.A., Quinn Ch.J., Rodman J.E., Rudall P.J., Savolainen V., Soltis D.E., Soltis P.S., Sytsma K.J. & Thulin M. (1998): An ordinal classification for the families of flowering plants. – Ann. Missouri Bot. Gard. **85**(4): 531–553.

[APG III] **Bremer B., Bremer K., Chase M.W., Fay M.F., Reveal J.L., Soltis D.E., Soltis P.S., Stevens P.F., Anderberg A.A., Moore M.J., Olmstead R.G., Rudall P.J., Sytsma K.J., Tank D.C., Wurdack K., Xiang J.Q.-Y. & Zmarzty S. (2009):** An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. – Bot. J. Linn. Soc. **161**(2): 105–121.

[APG IV] **Byng J.W., Chase M.W., Christenhusz M.J.M., Fay M.F., Judd W.S., Mabberley D.J., Sennikov A.N., Soltis D.E., Soltis P.S., Stevens P.F., Briggs B., Brockington S., Chautems A., Clark J.C., Conran J., Haston E., Möller M., Moore M., Olmstead R., Perret M., Skog L., Smith J., Tank D., Vorontsova M. & Weber A. (2016):** An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. – Bot. J. Linn. Soc. **181**(1): 1–20.

Baillon H. (1888): Histoire des plantes. T. 9. Aristolochiacées, Cactacées, Mésembryanthémacées, Portulacacées, Caryophyllacées, Chénopodiacées, Elatinacées, Frankéniacées, Droséracées, Tamaricacées, Salicacées, Batidacées, Podostemacées, Plantaginacées, Solanacées, Scrophulariacées. – Paris: Hackette & Cie.

Barykina R.P., Veselova T.D., Devjatov A.G., Dzhalilova Kh.Kh., Iljina G.M. & Chubatova N.V. (2004): Spravochnik po botanicheskoy mikrotekhniki. Osnovy i metody. [Botanical microtechnique manual. Principles and methods.] – Moscow: Moscow Univ. Press. [In Russian]

Bentham G. & Hooker J.D. (1880): Genera plantarum: ad exemplaria imprimis in Herbariis Kewensibus servata definita. Vol. 3. Pars 1. Sistens dicotyledonum monochlamydearum ordines XXXVI. Nyctagineas – Ceratophylleas et Gymnospermearum ordines III. Gnetaceas – Cycadaceas. – London: L. Reeve & Co.

Brockington S.F., Alexandre R., Ramdial J., Moore M.J., Crawley S., Dhingra A., Hilu Kh., Soltis D.E. & Soltis P.S. (2009): Phylogeny of the Caryophyllales sensu lato: Revisiting hypotheses on pollination biology and perianth differentiation in the core Caryophyllales. – Int. J. Plant Sci. **170**(5): 627–643.

Butnik A.A. (1991): Semeistvo Chenopodiaceae. [Family Chenopodiaceae] – In: Takhtajan A.L. [ed.]: Anatomia seminum comparativa. T. 3. Dicotyledones. Caryophyllidae – Dilleniidae: 77–82. – Leningrad: Nauka. [In Russian]

Butnik A.A. & Zhapakova U.N. (1991): Semeistvo Amaranthaceae. [Family Amaranthaceae] – In: Takhtajan A.L. [ed.]: Anatomia seminum comparativa. T. 3. Dicotyledones. Caryophyllidae – Dilleniidae: 74 –77. – Leningrad: Nauka. [In Russian]

Crawley S.S. & Hilu Kh.W. (2012): Caryophyllales: Evaluating phylogenetic signal in *trn*K intron versus *mat*K. – J. Syst. Evol. **50**(5): 387–410.

Cuénoud P., Savolainen V., Chatrou L.W., Powell M., Grayer R.J. & Chase M.W. (2002): Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbc*L, *apt*B, and *mat*K DNA sequences. – Amer. J. Bot. **82**(1): 132–144.

Davis G.L. (1966): Systematic embryology of Angiosperms. – New York: John Wiley and Sons.

de Klerk P. & Joosten H. (2007): The difference between pollen types and plant taxa: a plea for clarity and scientific freedom. – Eiszeitalter und Gegenwart **56**(3): 162–171.

Dzhalilova Kh.Kh., Timonin A.C. & Veselova T.D. (2015): Stalactite development in the exotesta cell walls of *Amaranthus retroflexus* L. (Amaranthaceae): an unusual way of cell wall lysis. – Wulfenia **22**: 113–125.

Dowding E.S. (1931): Floral morphology of *Arceuthobium americanum*. – Bot. Gaz. **91**(1): 42–54.

Downie S. R., Katz-Downie D. S. & Cho K. Y. (1997): Relationships in the Caryophyllales as suggested by phylogenetic analyses of partial chloroplast DNA ORF2280 homolog sequences. – Amer. J. Bot. **84**(2): 253–273.

Downie S. R. & Palmer J. D. (1994): A chloroplast DNA phylogeny of the Caryophyllales based on structural and inverted repeat restriction site variation. – Syst. Bot. **19**(2): 236–252.

Dumortier B.-C. (1827): Florula Belgica, operis majoris prodromus. Staminacia. – Tournay: J. Casterman.

Ehrendorfer F. (1976): Closing remarks: Systematics and evolution of Centrospermous families. – Pl. Syst. Evol. **126**(1): 99–105.

Endlicher S. (1836–1840): Genera plantarum secundum ordines naturales disposita. – Wien: F. Beck.

Endress P. K. & Stumpf S. (1990): Non-tetrasporangiate stamens in the angiosperms: Structure, systematic distribution and evolutionary aspects. – Bot. Jahr. Syst. **112**(2): 193–240.

Freiberg T. E. (1983): Semeistvo Empetraceae. [Family Empetraceae] – In: Yakovlev M. S. [ed.]: Comparative embryology of flowering plants. Phytolaccaceae – Thymelaeaceae: 209–213. – Leningrad: Nauka. [In Russian]

Hecklau H., Gasson P., Schweingruber F. & Baas P. (2012): Wood anatomy of Chenopodiaceae (Amaranthaceae s.l.). – IAWA J. **33**(2): 205–232.

Iljina G. M. (1984): Embryology of the family Aizoaceae s. lat. in connection with its systematics (the survey of literature). – Moscow Univ. Biol. Bull. **2**: 52–59. [In Russian]

Johnson T. (1888): *Arceuthobium oxycedri*. – Ann. Bot. **2**(6): 137–160.

Jussieu A. L. de (1789): Genera plantarum secundum ordines naturales disposita, juxta methodum in Horto Regio Parisiensi exaratam, anno 1774. – Paris: Herissant et Th. Barrois.

Kadereit G., Borsch T., Weising K. & Freitag H. (2003): Phylogeny of Amaranthaceae and Chenopodiaceae and the evolution of C4 photosynthesis. – Int. J. Plant Sci. **164**(6): 959–986.

Kadereit G., Hohmann S. & Kadereit J. W. (2006): A synopsis of Chenopodiaceae subfam. Betoideae and notes on the taxonomy of *Beta*. – Willdenowia. **36**(Special Issue): 9–19.

Kamelina O. P. (1983a): Semeistvo Frankeniaceae. [Family Frankeniaceae.] – In: Yakovlev M. S. [ed.]: Comparative embryology of flowering plants. Phytolaccaceae – Thymelaeaceae: 175–179. – Leningrad: Nauka. [In Russian]

Kamelina O. P. (1983b): Semeistvo Tamaricaceae. [Family Tamaricaceae] – In: Yakovlev M. S. [ed.]: Comparative embryology of flowering plants. Phytolaccaceae – Thymelaeaceae: 179–185. – Leningrad: Nauka. [In Russian]

Kamelina O. P. (2009): Sistematicheskaya embriologiya tsvetkovykh rasteniy. Dvudolnye. [Systematic embryology of flowering plants. Dicotyledons.] – Barnaul: Artika. [In Russian]

Kamelina O. P. & Proskurina O. B. (1985): Embryology of *Stegnosperma halimifolium* (Stegnospermataceae): Distribution of embryological features in Caryophyllales. – Bot. Zhurn. **70**(6): 721–730. [In Russian]

Konycheva V. I. & Kadyrova R. U. (1983): Semeistvo Chenopodiaceae. [Family Chenopodiaceae.] – In: Yakovlev M. S. [ed.]: Comparative embryology of flowering plants. Phytolaccaceae – Thymelaeaceae: 49–52. – Leningrad: Nauka. [In Russian]

Kühn U., Bittrich V., Carolin R., Freitag H., Hedge I. C., Uotila P. & Wilson P. G. (1993): Chenopodiaceae. – In: Kubitzki K. [ed.]: The families and genera of vascular plants. Vol. 2: Kubitzki K., Rohwer J. G. & Bittrich V. [eds]: Flowering plants – Dicotyledons: Magnoliid, Hamamelid and Caryophyllid families: 253–281. – Berlin et al.: Springer.

Lindley J. (1846): The vegetable kingdom or the structure, classification, and uses of plants illustrated upon the natural system. – London: Bradbury and Evans.

Linné C. (1830): Genera plantarum: eorumque characteres naturales secundum numerum, figuram, situm, et proportionem omnium fructificationis partim. T. 1. Classis 1–18. [9th ed. by Sprengel K.] – Göttingen: Dieterich.

Masson R. & Kadereit G. (2013): Phylogeny of Polycnemoideae (Amaranthaceae): Implications for biogeography, character evolution and taxonomy. – Taxon **62**(1): 100–111.

Menge A. (1839): Catalogus plantarum phanerogamicarum regionis Grudentinensis et Gedanensis. – Grudziądz: C.G. Röthe.

Moquin-Tandon A. (1837): Note sur le genre *Polycnemum* et sur une nouvelle tribu de la famille des Paronychiées. – Ann. Sci. Natur. 2 sér. 7. Bot.: 33–42.

Moquin-Tandon A. (1849): Amaranthaceae. – In: de Candolle A. [ed.]: Prodromus systematis naturalis regni vegetabilis, sive enumeratio contracta ordinum generum specierumque plantarum huc usque cognitarum, juxta methodi naturalis, normas digesta. 13(2): 231–424. – Paris: Treuttel et Würtz.

Müller K. & Borsch T. (2005): Phylogenetics of Amaranthaceae based on *mat*K/*trn*K sequence data: Evidence from parsimony, likelihood, and Bayesian analysis. – Ann. Missouri Bot. Gard. **92**(1): 66–102.

Naumova T.N. (1981): Semeistvo Simmondsiaceae. [Family Simmondsiaceae] – In: Yakovlev M.S. [ed.]: Comparative embryology of flowering plants. Winteraceae – Juglandaceae: 182–183. – Leningrad: Nauka. [In Russian]

Ogundipe O.T. & Chase M. (2009): Phylogenetic analyses of Amaranthaceae based on *mat*K DNA sequence data with emphasis on West African species. – Turk. J. Bot. **33**: 153–161.

Poddubnaya-Arnoldi V.A. (1982): Kharakteristika semeystv pokrytosemennykh rasteniy po tsytoembriologicheskim priznakam. [Cytoembryological characteristics of the families of Angiosperms] – Moscow: Nauka. [In Russian]

Popova L.N. & Kamaeva G.M. (1977): Morfologo-anatomicheskie osobennosti semyan i plodov roda *Atriplex* L. [Morphological and anatomical characters of the seeds and fruits in the genus *Atriplex* L.] – In: Sheljag-Sosonko J.R. [ed.]: Aktualnye voprosy sovremennoy botaniki [Topical issues of modern botany]: 124–126. – Kiev: Naukova dumka. [In Russian]

Rodman J.E., Oliver M.K., Nakamura R.R., McClammer J.U. jr. & Bledsoe A.H. (1984): A taxonomic analysis and revised classification of Centrospermae. – Syst. Bot. **9**(3): 297–232.

Savina G.I. (1983): Semeistvo Amaranthaceae. [Family Amaranthaceae.] – In: Yakovlev M.S. [ed.]: Comparative embryology of flowering plants. Phytolaccaceae – Thymelaeaceae: 47–49. – Leningrad: Nauka. [In Russian]

Schäferhoff B., Müller K.F. & Borsch T. (2009): Caryophyllales phylogenetics: disentangling Phytolaccaceae and Molluginaceae and description of Microteaceae as a new isolated family. – Willdenowia **39**: 209–228.

Schinz H. (1934): Amaranthaceae. – In: Engler A., Prantl K., Pax F.A. & Harms H. [Hrsg.]: Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen. Bd. 16c [2. Aufl.]: 7–85. – Leipzig: Wilhelm Engelmann.

Shamrov I.I. (1985): Semeistvo Rhabdodendraceae. [Family Rhabdodendraceae] – In: Yakovlev M.S. [ed.]: Comparative embryology of flowering plants. Brunelliaceae – Tremandraceae: 137. – Leningrad: Nauka. [In Russian]

Shepherd K.A. (2008): Consensus or complacency? A discussion of the proposed new collection sequence at the WA Herbarium. – Austral. Syst. Bot. Soc. Newslett. **135**: 5–8.

Sukhorukov A.P., Mavrodiev E.V., Struwig M., Nilova M.V., Dzhalilova Kh.Kh., Balandin S.A., Erst A. & Krinitsyna A.A. (2015): One-seeded fruits in the core Caryophyllales: their origin and structural diversity. – PLoS One **10**(2): 1–38.

Sukhorukov A.P. & Zhang M. (2013): Fruit and seed anatomy of *Chenopodium* and related genera (Chenopodioideae, Chenopodiaceae / Amaranthaceae): Implications for evolution and taxonomy. – PLoS One **8**: 1–18.

Takhtajan A. L. (1966): Sistema i filogeniya tsvetkovykh rasteniy. [Systema et phylogenia Magnoliophytorum.] – Moscow, Leningrad: Nauka. [In Russian]

Takhtajan A. L. (1987): Sistema magnoliofitov. [Systema Magnoliophytorum.] – Leningrad: Nauka. [In Russian]

Takhtajan A. L. (2009): Flowering plants. [2nd ed.] – Dordrecht: Springer Netherlands. – doi:10.1007/978-1-4020-9609-9

Teryokhin E. S., Batygina T. B. & Shamrov I. I. (2002): New approach to classifying modes of microsporangium wall formation. – In: Batygina T. B. [ed.]: Embryology of flowering plants. Terminology and concepts. V. 1. Generative organs of flowers: 32–39. – Enfield, NH: Oxford & IBH Publishing Co.

Tikhomirov V. N. & Fedorova T. A. (1997): The comparative anatomy of the seed coat in the representatives of the genus *Amaranthus* (Amaranthaceae). – Bot. Zhurn. **82**(1): 16–23. [In Russian]

Timonin A. C. (2011): Anomalnoe vtorichnoe utolshchenie tsentrosemennykh: Specifika morfofunktsionalnoy evolutsii rasteniy. [Anomalous secondary thickening in Centrosperms: Specificity of the morphological and functional evolution of plants.] – Moscow: KMK Scientific Press. [In Russian]

Tursunov D. Zh. & Matyunina T. E. (1983): Semeistvo Caryophyllaceae. [Family Caryophyllaceae.] – In: Yakovlev M. S. [ed.]: Comparative embryology of flowering plants. Phytolaccaceae – Thymelaeaceae: 39–47. – Leningrad: Nauka. [In Russian]

Ulbrich E. (1934): Chenopodiaceae. – In: Engler A., Prantl K., Pax F. A. & Harms H. [Hrsg.]: Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen. Bd. 16c [2. Aufl.]: 379–584. – Leipzig: Wilhelm Engelmann.

Veselova T. D. (1989): The embryological characteristics of cleistogamous flowers in *Oxybaphus nyctagineus* (Michx.) Sweet (Nyctaginaceae). – Biol. Nauki. **6**: 68–74. [In Russian]

Veselova T. D. (1990): O sistematicheskom polozhenii tsentrosemennykh v svyazi s dannymi embriologii. [On systematic position of the Centrosperms as evidenced by embryological data.] – In: Tikhomirov V. N. & Sladkov A. N. [eds]: Morfologiya tsentrosemennykh kak istochnick evolutsionnoy informatsii. [Morphology of the Centrosperms as a source of evolutionary information]: 28–48. – Moscow: Nauka. [In Russian]

Veselova T. D., Dzhalilova Kh. Kh. & Timonin A. C. (2012): Structure of funicle and seed coat in *Talinum paniculatum* (Jacq.) Gaerth. and *Talinum triangulare* (Jacq.) Willd. (Portulacaceae s. ampl.). – In: Timonin A. C. [ed.]: Leonid Vasilievich Kudrjashov. Ad memoriam: 195–207. – Moscow: MAKS Press. [In Russian]

Veselova T. D., Dzhalilova Kh. Kh. & Timonin A. C. (2014): Development of seed coat in species of *Amaranthus* L. subgenus *Amaranthus* (Amaranthaceae). – In: Lotova L. I. & Timonin A. C. [eds]: Kaden's memorial book: 54–66. – Moscow: MAKS Press. [In Russian]

Veselova T. D. & Kondorskaya V. R. (1990): Razvitie generativnykh organov *Atriplex nitens* Schkuhr. [Development of the generative organs in *Atriples nitens* Schkuhr] – In: Tikhomirov V. N. & Sladkov A. N. [eds]: Morfologiya tsentrosemennykh kak istochnick evolutsionnoy informatsii. [Morphology of the Centrosperms as a source of evolutionary information]: 48–65. – Moscow: Nauka. [In Russian]

Volkens G. (1893): Chenopodiaceae. – In: Engler A. & Prantl K. [Hrsg.]: Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen. Teil 3. Abt. 1a: 36–91. – Leipzig: Wilhelm Engelmann.

Yakovlev M. S. [ed.] (1983): Comparative embryology of flowering plants. Phytolaccaceae – Thymelaeaceae. – Leningrad: Nauka. [In Russian]

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