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Anatomy of the generative structures of the Subantarctic flowering plant *Colobanthus apetalus* (Labill.) Druce

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Abstract: This study investigated the details of the morphological and anatomical structure of the generative organs of the Subantarctic flowering plant, belonging to the family Caryophyllaceae - *Colobanthus apetalus* (Labill.) Druce. The research material was collected in hostile natural conditions in Subantarctic regions, and also was grown in the incubators and the greenhouse of the University of Warmia and Mazury in Olsztyn (Poland). *C. apetalus* forms tufts with soft and grassy leaves and small greenish flowers that are more obvious than in other *Colobanthus* species. *C. apetalus* forms open (chasmogamic) flowers in greenhouse cultivation. The flowers most often form five stamens with two microsporangia. Over a dozen pollen grains are formed in each microsporangium. Studies of the plant material originated from natural conditions conducted by means of a light microscope, have shown that the ovules of the analyzed representative of the genus *Colobanthus* are anatropous, crassinucellar, and the monosporic embryo sac develops according to the Polygonum type (the most common type in angiosperms). *C. apetalus* plants underwent a full development cycle in greenhouse cultivation and produced fertile, perispermic seeds. During the *C. apetalus* growth in conditions at increased air humidity, the vivipary was also observed.

Keywords: Antarctic, vascular plants, microsporangium, ovule, vivipary.

Introduction

Antarctic and Subantarctic areas are located in the southern hemisphere of the Earth, characterized by the harsh, cold climate and poor vegetation (Edwards 1974). The only native representatives of vascular plants in the Antarctic are *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae) and *Deschampsia antarctica* Desv. (Poaceae) (Alberdi *et al.* 2002; Giełwanowska 2005; Parnikoza

et al. 2007; Androsiuk *et al.* 2015) and the invasive alien species *Poa annua* L. (Poaceae) (Olech and Chwedorzewska 2011; Chwedorzewska *et al.* 2014; Wódkiewicz *et al.* 2014). The Subantarctic zone is characterized by milder environmental conditions and more diverse plant life. One of the species found in this region is *Colobanthus apetalus* (Labill.) Druce (West and Cowley 1996). The genus *Colobanthus* consists of 25 species (The Plant List 2020) of tufted, mainly cushion-forming perennials from the Pacific region, Australasia to southern South America, Subantarctic islands, Maritime Antarctic and Hawaiian mountains. *C. apetalus* forms tufts with grassy leaves (1.5–3 cm in length), stems of up to 3 cm, and small greenish flowers (5 mm in diameter). The sepals often have purple borders, and seeds have low rounded papillae (Skottsberg 1915; Alpine Garden Society 2020). These plants are of great interest to scientists and often become model organisms to study the specific adaptations to extreme environmental conditions of the Antarctic and Subantarctic (Giełwanowska 2005; Piotrowicz-Cieślak *et al.* 2005; Kellmann-Sopyła *et al.* 2015; Kellmann-Sopyła and Giełwanowska 2015; Koc *et al.* 2018; Dulska *et al.* 2019). The anatomical structure of Antarctic and Subantarctic flowering plants, especially their structure at the level of micro- and ultrastructure, has been poorly studied so far. Only the information on anatomy, cell ultrastructure and generative reproduction of *C. quitensis* is available (Giełwanowska 2005; Giełwanowska *et al.* 2006, 2011; Kellman-Sopyła and Giełwanowska 2015; Kellman-Sopyła *et al.* 2017). However, there is no similar data on other species of the genus *Colobanthus*. The aim of this paper was to analyze microscopically the anatomy and ultrastructure of cells within the generative organs of *Colobanthus apetalus*.

Materials and methods

Plant material. — The experimental materials included flower buds and seeds of *Colobanthus apetalus* (Caryophyllaceae). The plant material was collected in 2010 in the Subantarctic, in Tierra del Fuego National Park, near Ushuaia (54°48′ S, 68°18′ W) in Argentina. In total 21 flower buds and about 200 seeds were harvested. Plant fragments with flower buds after harvesting were chemically fixed in 4% glutaraldehyde in a phosphate buffer (pH 7.0–7.2) and transported to Poland. The collected seeds, after their transfer to Poland, were sown in the incubators and the greenhouse of the University of Warmia and Mazury in Olsztyn (53°47'N, 20°30'E). Plants in greenhouse were grown in pots filled with a 1:1 mixture of soil and sand, at a temperature of 20°C.

Light and electron microscopy. — After returning to Poland, plant fragments were post-fixed in a 2.5% aqueous solution of osmium tetroxide for 8 hours. Then, after rinsing, the material was dehydrated in an alcohol series (in ethanol with increasing concentrations of 30, 50, 70, 90 and 96% — each concentration for 10 minutes, in 99.8% ethanol — 2 x 30 minutes and in acetone

— 2 x 30 minutes). Afterwards, plant parts were placed for 16 hours in the 2:1 mixture of Poly Bed 812 epoxy resin and acetone. After this time, they were transferred to pure resin for 6 hours. Resin-impregnated plant fragments were again placed in pure resin and polymerized at increasing temperature (first day at 37°C, second day at 45°C, third and subsequent days at 55°C). Semi-thin (1.5–2.0 μm) and ultra-thin (60–90 nm) sections were prepared on a Leica (Ultracut R) ultramicrotome, using glass and diamond knives. About 35–40 sections were prepared from each flower bud. Observations of ovules, microsporangia and pollen grains were planned. Each structure was observed on 22–26 sections. Semi-thin sections were stained with toluidine blue and azure B, according to Pearse (1962), and were observed under light microscope (Nikon Eclipse 80*i*). Ultra-thin sections were contrasted with a saturated aqueous solution of uranyl acetate and lead citrate, according to Reynolds (1973), and were observed using a transmission electron microscope (JEOL JEM 1400).

Statistical analysis. — One hundred manually separated seeds, collected from plants grown in the greenhouse, were weighed on the Radwag MYA 3Y microscale (to the nearest 0.1 mg) in five replications to determine 1000 seed weight. The result for every replication was multiplied by 10. Arithmetic means (X), standard deviations (SD) and coefficients of variation (V%) were calculated.

One hundred seeds of *C. apetalus* were sampled to determine their geometric parameters. Each seed was measured to determine its length, width and slenderness (length-width ratio). Length and width were measured with an accuracy of up to 1 μm under the Leica M205 C stereomicroscope with the use of the Leica Application Suite V3.8 software. Arithmetic means (X), standard deviations (SD) and coefficients of variation (V%) were calculated for each parameter. The results are presented in Table 1.

Table 1

Basic characteristics of *C. apetalus* seeds.

Species	Index	1000 seed weight [mg]	Length [mm]	Width [mm]	Slenderness
Colobanthus apetalus	X SD V%	58.4 ±3.8 6.5	0.626 ±0.041 6.533	0.460 ±0.039 8.379	1.368 ±0.143 10.459

Results

Colobanthus apetalus plants bloomed profusely, both in natural conditions (Fig. 1a) and in greenhouse cultivation (Fig. 1b), in each growing season. Flowers growing in the greenhouse were open (chasmogamic). Flower buds appeared on

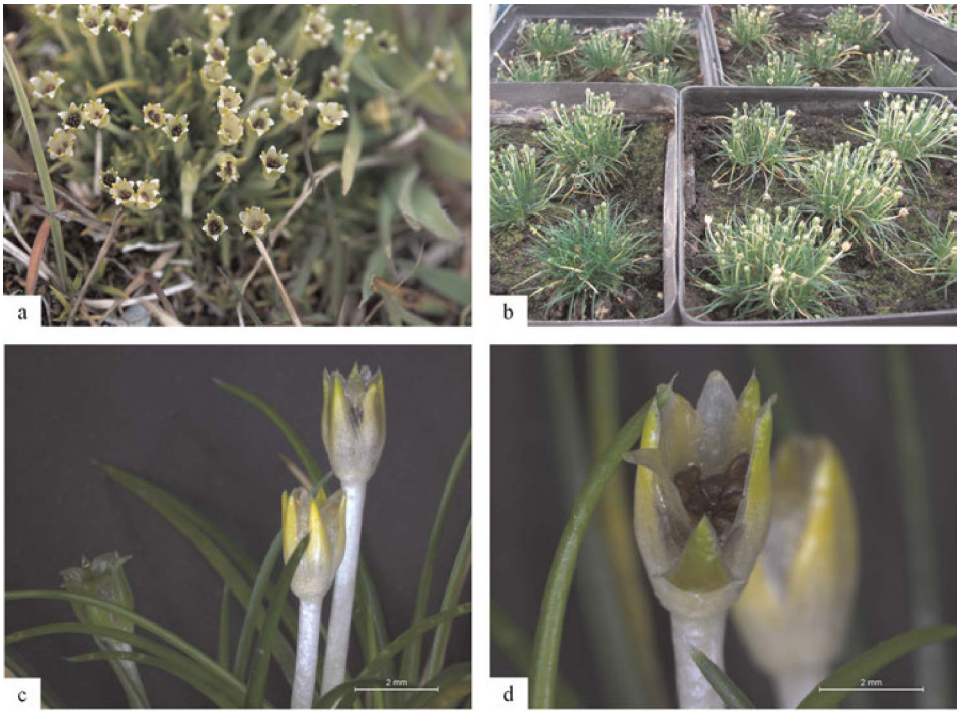

Fig. 1. Morphological features of *Colobanthus apetalus* plants. a. Specimens in natural environmental condition. b. Plants in a greenhouse cultivation. c. Developed flowers with a white-green perianth. d. Mature brown seeds in the open capsule.

thickened, strongly shortened stems in the leaf axils. Numerous flowers developed on shoots within a few (6–8) weeks and grow on pedicels 3-3.5 cm long (Fig. 1c, d). Individual *C. apetalus* flowers were surrounded by green, usually 5-, less often 6- or 4-element perianth, undifferentiated into petals and sepals.

Microscopic observations of the *C. apetalus* flower bud showed that inside the ovary chamber formed by 5 (less often 4 or 6) carpels, there are numerous (from several to several dozens) anatropous ovules with two integuments (Fig. 2a, b). The observed ovules were inverted, which means that the ovule bends 180° during development, which in effect causes the ovule micropyle to be located just at the junction of the ovule and the placenta tissue. At some point a megasporocyte developed in the micropylar part of the nucellus. As a result of the first meiotic division, the megasporocyte divided into two cells. One cell of the dyad was visible in the micropylar part of nucellus (Fig. 2b). After the second meiotic division a linear tetrad of megaspores was formed (Fig. 2c, d). The chalazal megaspore became a functional megaspore and continued development. It developed into a female gametophyte — an embryo sac, and the other megaspores degenerated (Fig. 2e). The embryo sac developed in almost every ovule. In the micropylar part of the mature embryo sac, an egg cell with a visible cell nucleus and two synergids were observed (Fig. 2f).

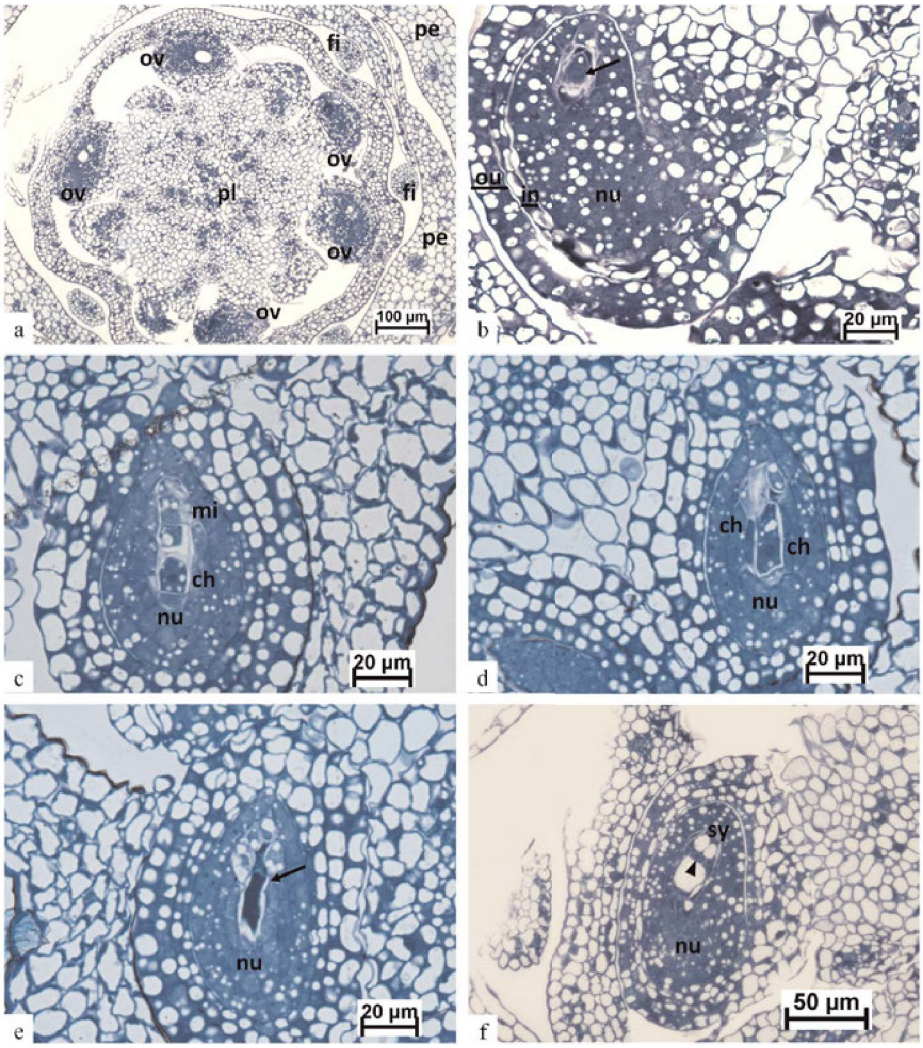

Fig. 2. Cross-section of *Colobanthus apetalus* flower bud and female embryological processes. Semi-thin sections stained with toluidine blue and azure B. a. Ovary with numerous ovules (ov) on a centrally positioned placenta (pl), ovary shielded by free sepals of a perianth (pe). Crosswise cut stamen filaments (fi) are visible under perianth's leaves. b. Anatropous, crassinucellar ovule in the ovary chamber. Nucellus (nu) is protected by two integuments - inner (in) and outer (ou); dyad of megaspore cells (arrow) is visible in the micropylar region. c-d. Tetrads of megaspores; micropylar (mi) and chalazal (ch) megaspores are visible. e. Ovule in the stage of functional megaspore, arrow indicates the degenerating megaspore cells. f. Mature embryo sac with an egg apparatus on the micropylar pole. Two synergids (sy) and an egg cell (arrowhead) are visible.

Under the perianth leaves, androecium differentiated, forming 4–6 stamens (most often 5). On the cross-section through the heads of the stamens, two microsporangia (Fig. 3a, b) that were regularly circular in shape in cross section were visible. The photographs clearly showed the individual wall layers of the

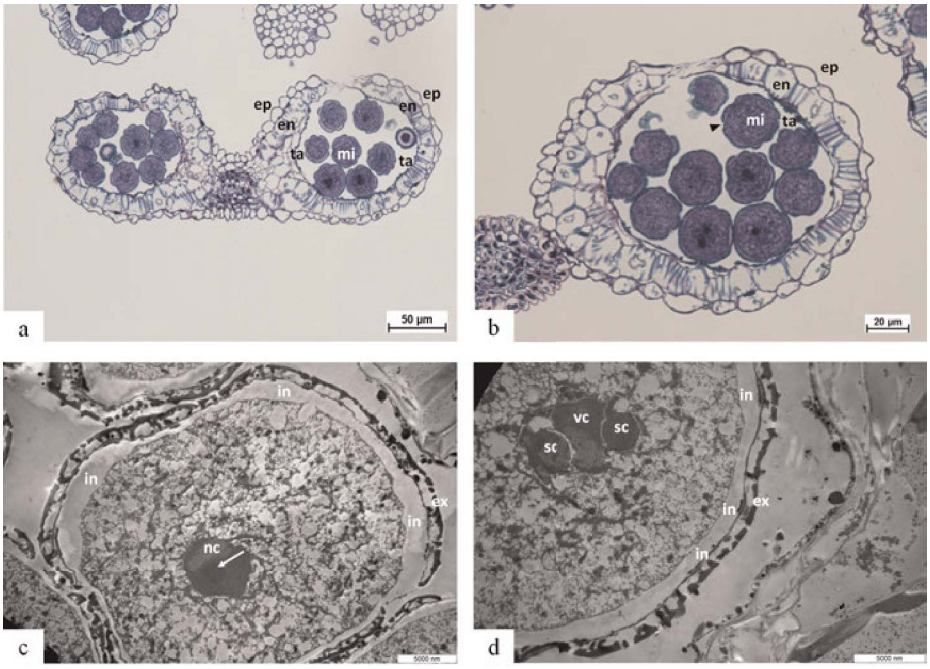

Fig. 3. a-b. The structure of the microsporangium *Colobanthus apetalus* during pollen development. Semi-thin cross sections stained with toluidine blue and azure B. Layers of the microsporangium wall: epidermis (ep), endothecium (en), and the residue of tapetum (ta). Microspores (mi) with numerous apertures (arrowhead) are visible inside the microsporangium. c-d. Ultrastructure of microspores and pollen grains of *Colobanthus apetalus*. c. Microspore surrounded by two-layer sporoderm - outer exine (ex) and inner intine (in); visible nucleus (nc) with a nucleolus (arrow). d. Mature male gametophyte showing two sperm cells (sc) and a vegetative cell nucleus (vc).

microsporangium — epidermis, endothecium and tapetum. Numerous microspores developed in microsporangia. Microspores — stem cells of male gametophytes with a single nucleus arranged in the central part of the protoplast of the cell were visible on the electronograms (Fig. 3c, d). Three-celled male gametophyte made of two sperm cells and a vegetative cell were also observed. The microspore wall was formed by a double-layered sporoderm. Its outer layer — exine and the inner, relatively thick, polysaccharide intine. Exine was visible in the form of a dark, osmophilic layer, while intine was a lighter, less osmophilic layer. Numerous apertures were visible in the sporoderm, through which the pollen tube can germinate. The microspore cytoplasm contained numerous small vacuoles and drops of material of varying density and varying levels of osmophilicity. There were about a dozen pollen grains in every microsporangium. Pollen grains had a diameter of 25–35 µm. In the transmission electron microscope, an ultrastructure of pollen grains with numerous, distinct apertures was observed.

A dozen or so seeds most often developed in the ovary of *C. apetalus*. Seeds were very light and small, reached dimensions of about 0.6 x 0.4 x 0.2 mm

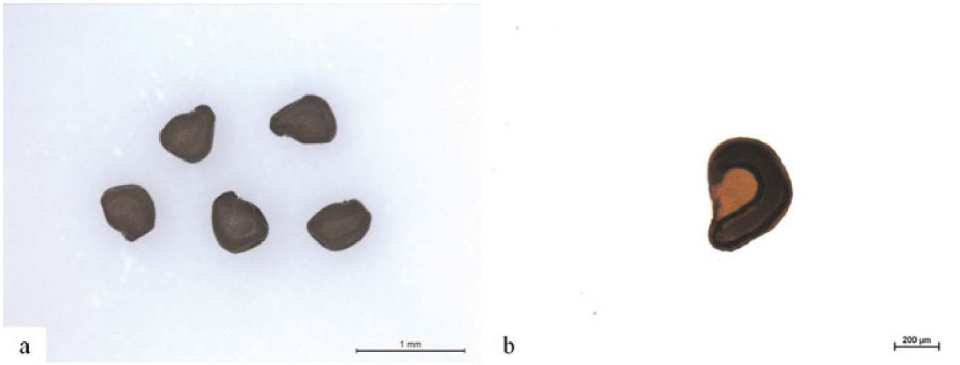

Fig. 4. a-b. Seeds of *Colobanthus apetalus* collected from plants growing in the greenhouse of the University of Warmia and Mazury in Olsztyn (Poland).

(Tab. 1). Mature seeds were brown, flattened laterally and had a triangular or quadrangular shape (Fig. 4a). A large part of the seed was occupied by a curved, peripherally located embryo, visible macroscopically under the smooth surface of the seed coat (Fig. 4b).

During the study in *C. apetalus* the phenomenon of vivipary was observed. However, this phenomenon was observed only in laboratory conditions – in the incubator. Plants in the incubator bloomed profusely, as in natural and greenhouse conditions. Vivipary appeared in 100% of the buds. From 79 to 100% of the seeds germinated in every flower bud. In buds with germinating seeds, the perianth remained green, unlike perianth and pericarp elements in which the seeds began to rest. Flower buds under the weight of seedlings bent towards the ground or seedlings fell out of the flower bud and took root (Fig. 5a, b). Our studies revealed that seedlings' roots did not grow into the receptacle. The vivipary was observed in plants growing in the incubator when the humidity exceeded 75%. Moving these plants to a room with air humidity of around 15–20% caused inhibition of seeds germination in capsules. Our observations over several years allowed us to

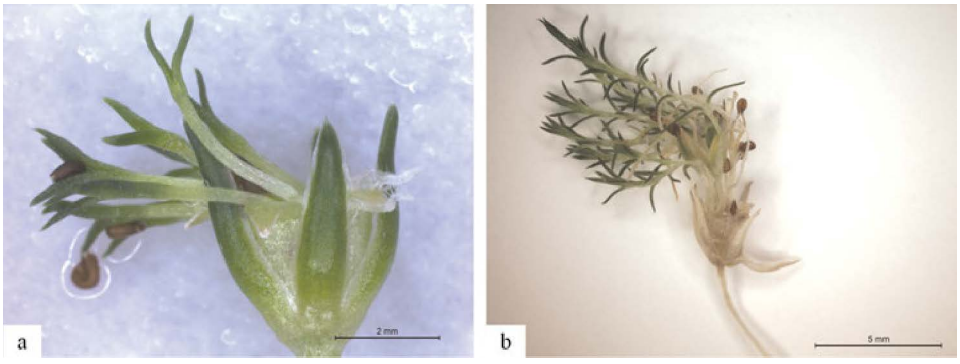

Fig. 5. a-b. Vivipary in *Colobanthus apetalus*. a. Young seedlings in a still green capsule. b. Older seedlings.

conclude that the occurrence of the vivipary phenomenon depends on the level of air humidity. In natural conditions, numerous representatives of this species with open capsules and mature seeds were observed. However, no cases of seed germination were found yet within the capsule.

Discussion

The occurrence of flowering plants in the Antarctic and Subantarctic regions is very limited and depends primarily on the availability of nutrients and water (Alberdi *et al*. 2002). According to many authors (Alberdi *et al.* 2002; Block *et al.* 2009; Convey 2012; Cavieres *et al.* 2016), specific environmental conditions, in particular low temperature, salinity, limited water availability, as well as large fluctuations in these factors have a negative influence on the plant development. Only a few species of flowering plants are able to grow and reproduce in extremely harsh environmental conditions in these regions. In the Maritime (Western) Antarctic area there are two native species of flowering plants — *Colobanthus quitensis* and *Deschampsia antarctica* (Lewis Smith 1984; Komárková *et al.* 1985; Alberdi *et al.* 2002; Giełwanowska 2005; Parnikoza *et al.* 2007). Subantarctic flora, due to the milder climate, is characterized by richer vegetation (Lewis Smith 1984; Block 1994). There are many species of mosses, liverworts, algae and lichens as well as more species of flowering plants (Rakusa-Suszczewski *et al.* 1998; Alberdi *et al.* 2002; Rakusa-Suszczewski 2012), including *Colobanthus apetalus* which became the object of the current study.

The reproductive strategies of polar flowering plants have been widely discussed in the literature. For a long time, plants from the polar regions — the Arctic and the Antarctic — were thought to reproduce mainly in a vegetative way (Bliss 1958). Very good example for this strategy could be *Deschampsia antarctica*, which reproduces mainly by stolons (Parnikoza *et al.* 2012). However, there are reports that Antarctic plants reproduce also generatively and undergo a full development cycle, which leads to viable seeds formation (Lewis Smith 1984; Convey 1996; Zúñiga *et al.* 1996). According to King (1994), Kellmann-Sopyła *et al.* (2011) and Cavieres *et al.* (2016) intensive climate change, primarily warming, which is observed over the past few decades, are beneficial for generative reproduction and is likely to favor this phenomenon.

Flowering plants of the southern polar region produce small bisexual flowers. Flowers of native Antarctic species — *C. quitensis* (Giełwanowska 2005) and *D. antarctica* (Parodi 1949) are usually closed (cleistogamic). Observations by Giełwanowska (2005) performed in the vicinity of the Polish *H. Arctowski* Antarctic Station have shown that the majority of *C. quitensis* flowers were closed. Only a few plants growing in ground niches or sheltered by rocks had open flowers. Therefore, the cleistogamy among plants in polar regions is most

likely caused by low temperature, high humidity and strong winds (Giełwanowska 2005; Giełwanowska *et al.* 2011). *C. apetalus* flowers observed in natural condition and in the greenhouse of the University of Warmia and Mazury in Olsztyn were open and developed in typical way. According to the authors, open (chasmogamic) flowers facilitate cross-pollination and fertilization (Giełwanowska *et al.* 2007; Parnikoza *et al.* 2011; Giełwanowska 2013). Cross--fertilization is a desirable phenomenon from the point of view of evolution and adaptation of species to changing environmental conditions (Rodkiewicz *et al.* 1996).

Ovules of *C. apetalus* are anatropous and crassinucellar, like in majority of representatives of family Caryophyllaceae. During the development of the ovule, two integuments made up of two layers of cells undergo differentiation, which was shown in *C. apetalus* analyzed in this paper, as well as in *C. quitensis* and *Cerastium alpinum* L. (Giełwanowska 2005; Kellmann-Sopyła *et al.* 2017). A monosporic embryo sac of the Polygonum type differentiated in the ovule (Bednara 2003; Giełwanowska 2005; Domaciuk *et al.* 2016). This type of development is most common in flowering plants — it affects about 95% of flowering plant species (Bednara 2003). The entire mature *C. apetalus* female gametophyte, including the egg apparatus, is organized similarly to *C. quitensis*. The egg apparatus consists of two typically polarized synergids and an egg cell. In the synergids of the *C. apetalus* embryo sac a very extensive filiform apparatus develops, similar to that described in *C. quitensis* (Giełwanowska 2005; Giełwanowska *et al.* 2011), through which a pollen tube with sperm cells penetrates. Studies on the embryo sac of various species of flowering plants show that for some of them, one of the synergids contains higher amounts of actin and this one takes the pollen tube (Bednara 2003).

In *C. apetalus* flowers, analogically to *C. quitensis*, usually five stamens develop, and two microsporangia differentiated in each stamen head. The microsporangium wall is made of three layers of cells. A mature male gametophyte in the studied *C. apetalus* is three-celled. A similar structure of the male gametophyte was previously observed by Giełwanowska (2005) in two species of Antarctic flowering plants – *C. quitensis* and *D. antarctica*. Three-celled male gametophytes have been proved to be better adapted to harsh environmental conditions, because they germinate faster than two-celled gametophytes (Mascarenhas 1989). Mature three-celled pollen grains also accumulate higher quantities of mRNA, which allows the synthesis of large amounts of protein products used during germination and pollen tube growth (Linskens 1988).

A self-pollination occurs in the natural environment of *C. quitensis*, however, cross-pollination cannot be excluded due to the opening of flowers under favorable conditions. In *Colobanthus* flowers after the anther wall break-down, the pollen reaches the stigma and the process of pollination and double fertilization takes place, which involves the entering of the two sperm cells into

the embryo sac via the pollen tube. The nuclei of sperm cells enter the egg and the central cell. From the combination of the sperm cell and the egg cell, a zygote is formed, which then develops into the embryo of the plant, while from the fertilized central cell, endosperm is formed. Further development of the fertilized ovules leads to the formation of seeds (Giełwanowska 2005).

C. apetalus plants develop numerous flower buds and seeds in greenhouse cultivation. These seeds are very small, brown, have a triangular or quadrangular shape and are flattened laterally. The size and shape of seeds appeared to be a part of a plant adaptation strategy to the local environment. Observations by Tilman (1988) indicate that the production of numerous small seeds characterizes poor habitat species, which include polar and subpolar regions, and seed size is correlated with the degree of competition for local resources. A second possibility is that small seeds are one of adaptations to a spatial or pioneering succession (Tilman 1982; Pacala and Rees 1998; Bolker and Pacala 1999); in that case small-seeded species should possess additional physiological adaptations for rapid growth (Tilman 1982; Pacala *et al*. 1996; Davies 2001). The research by Thompson and Grime (1979) shows that persistent seed banks are usually formed by species that develop small seeds. The formation of seed banks was observed for plants native to Antarctica – *Colobanthus quitensis* and *Deschampsia antarctica* (McGraw and Day 1997; Ruhland and Day 2001) and for introduced species – *Poa annua* (Wódkiewicz *et al.* 2013; Chwedorzewska *et al.* 2014). According to Convey (1996) low temperatures and a short summer period cause death of many seeds produced by plants. Research by Edwards (1974) showed that fertile seeds develop from flower buds formed at the beginning of the growing season, whereas flowers formed at the end of the season do not produce seeds in most cases. *Colobanthus apetalus* plants produced viable seeds in greenhouse cultivation. The seeds of *C. apetalus* plants growing in the greenhouse are very small and light. Their length and width did not exceed 1 mm, and 1000 seed weight was very low (about 60 mg). The seeds of *C. apetalus* are similar in size to the seeds of the other Caryophyllaceae species – *Colobanthus quitensis* (Kellmann-Sopyła *et al.* 2017).

The phenomenon of vivipary was also significant. Vivipary in flowering plants is defined as germination of seeds without a resting period, and continuous growth of the offspring when still attached to the mother plant (Goebel 1905; Elmqvist and Cox 1996). The vivipary is particularly widespread within the Poaceae family, where it is found among many crop species (Beetle 1980; Lee and Harmer 1980; Heide 1994; Vega and Rúgolo de Agrasar 2006). According to the literature there are many causes of vivipary, among others hybridization, polyploidy, malformation and adverse environmental factors (Beetle 1980). Vivipary in *Poa alpina* L. depends on both photoperiod and temperature. As with *Poa bulbosa* L. and *Festuca vivipara* (L.) Sm., short days and low temperatures induced viviparous proliferation in *Poa alpina* L., suggesting that vivipary is acclimative, i.e., phenotypic and not genotypic

(Heide 1989; Keller and Körner 2003). The view that vivipary might result from hybridization and consequent sterility was advanced by Flovik (1938). In contrast to the Arctic, vivipary occurs sporadically in the Subantarctic – the phenomenon observed in *Acaena magellanica* (Lam.) Vahl, *Phleum alpinum* L. and *Poa flabellata* (Lam.) Raspail growing in wet habitats or during long spells of wet weather (Lewis Smith 1984). According to our observations also increased humidity belongs to the factors which may induce vivipary – as it was observed in our experiment. *Colobanthus apetalus* seeds began to germinate in conditions of high air humidity, whereas moving plants to a room with lower humidity caused inhibition of that process.

Conclusions

Our observations indicate that in greenhouse conditions (similarly to natural circumstances), *Colobanthus apetalus* develops intensely branched cushion forms, reproduces generatively and undergoes a full development cycle, including viable seed production.

1. *Colobanthus apetalus* blooms profusely, producing small, bisexual flowers, usually surrounded by a 5-element undifferentiated into petals and sepals.

2. Flowers usually form 4–6 stamens.

3. Numerous anatropous, crassinucellar ovules are formed in the ovary. Embryo sacs are monosporic and develop according to the Polygonum type.

4. Vivipary occurs in *C. apetalus*. An increase in air humidity above 75% causes germination of seeds, immediately after their formation, while there are still in green, closed capsule.

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