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# Seed surface morphology in some representatives of the Genus *Rhodiola* sect. *Rhodiola* (*Crassulaceae*) in the Russian Far East

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## Abstract

The seed coat morphology and anatomy of *Rhodiola angusta*, *Rh. alsia*, *Rh. integrifolia*, *Rh. ishidae*, *R. rosea* subsp. *arctica*, *Rh. rosea* subsp. *rosea* and *Rh. rosea* subsp. *sachalinensis* were examined comparatively using scanning and light microscopy methods in order to evaluate their characteristics for use in systematic studies. Based on the features of the arrangement of cells and cell outline, three morphological types of seed coats were identified – laticostate (*Rh. rosea* subsp. *rosea*), tenuicostate (*Rh. integrifolia*, *Rh. rosea* subsp. *rosea R. rosea* subsp. *arctica* and *Rh. rosea* subsp. *sachalinensis*) and colliculate (*Rh. alsia*, *Rh. angusta*, *Rh. ishidae*). Exotesta sculpture features are stable across a range of habitats in all taxa except *Rh. rosea* subsp. *rosea.* Considerable variability of seed coat morphology is reported in the latter species and its possible implication for species taxonomy is discussed.


***Keywords:*** Anatomy; *Rhodiola* sect. *Rhodiola*; Seed coat morphology

## Introduction

The genus *Rhodiola* L., based on one species, *Rh. rosea* L., was described in the first edition of "Species Plantarum" (Linnaeus, 1753). Although there is a 250-year history for the genus *Rhodiola*, its taxonomy and particularly some features of its species delimitation remain in question. This problem is illustrated by a wide disparity in the number of *Rhodiola* species estimates. Ohba (2005) accounted for ca. 60 sp. in the whole genus, while Fu and Ohba (2001) reported ca. 90 species in China alone. Variability in morphological characters traditionally used for species delimitation resulted in the description of many ambiguous taxa, afterwards synonymised by other students. For example, the type species of the genus, *Rh. rosea*, accounts for as many as 50 synonyms and *Rh. integrifolia* Raf., another widely distributed member of the genus, for ca. 30 (Ohba, 1981). These two taxa, along with 20 other, mostly confined to the Himalayan region species, are classified in the section *Rhodiola* of the subgenus *Rhodiola* (Ohba, 1981). In the Russian Far East, the section is represented by six species and infraspecific taxa (Gontcharova, 2000). Other authors, however, consider at least three of them to be conspecific with *Rh. rosea* (Ohba, 1981, 2005).

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Seed morphology provides a number of characters potentially useful for species identification, phylogenetic inference and character-state evolution (Attar et al., 2007; Johnson et al., 2004; Moazzeni et al., 2007). Observations in many plant groups have shown that seed morphology and anatomic features are rather conservative, which makes them taxonomically important (Barthlott, 1984; Esau, 1977; Werker, 1997).

Data on the seed morphology of representatives of *Rhodiola* are rather limited and mostly confined to papers on *Crassulaceae* systematics (Clausen, 1984; Ohba, 1981). Knapp (1994) described seed micromorphology in four *Rhodiola* species and classified it along with *Orostachys* Fisch., *Pseudosedum* A. Berger and *Adromischus* Lem. as a «Netzförmige Structur» *Orostachys*-type. However, further studies have demonstrated that at least some of the Far-Eastern representatives of the genus *Rhodiola* differ from *Orostachys* in seed coat sculpture, stressing the need for a more detailed investigation (Gontcharova, 1999).

The aim of the present study is to characterize seed coat structure and anatomy in some species of the *Rhodiola* section *Rhodiola* distributed in the Russian Far East and to search for micromorphological diagnostic characters that may help to elucidate species relationships in the section.

## Material and methods

Thirty-five specimens representing five species and subspecies of the section *Rhodiola* that are found in the Russian Far East were studied – *Rhodiola angusta* Nakai (1 specimen), *Rh. integrifolia* (5 specimens), *Rh. ishidae* (Miyabe et Kudo) H. Hara (6 specimens), *Rh. rosea* subsp. *rosea* (21 specimens), *Rh. rosea* subsp. *sachalinensis* (Boriss.) S. Gontch. (2 specimens). Seed morphology of *Rh. alsia* (Fröd.) Fu (1 specimen), occurring in China, and *Rh. rosea* subsp. *arctica* (Boriss.) A. et D. Löve (1 specimen), distributed in the Arctic, was also studied for comparison. Seeds were collected from their natural habitats in the Russian Far East and Japan or were obtained from the Botanical Garden-Institute FEB RAS, other botanical gardens and herbaria (Appendix A).

Seed coats were studied and photographed with a JEOL S 5800 SEM at 15 KV and Axiolab LM. The seeds were photographed at a magnification of × 10–20, × 55–100, × 850 and × 4500. Seed coat morphology was described in the middle section opposite the raphe side.

For this anatomical investigation, seeds were dehydrated with acetone and embedded in plastic. Cross-sections were attached to glass slides and stained with Schiff's reagent and toluidin blue (Weng and Kuo-Huang, 1998).

The terminology of seed coat sculpturing and anatomy follows Barthlott (1981), Corner (1976) and Stearn (1992). Sensu Barthlott (1981), we distinguish primary and secondary sculptures. The primary sculpture characterizes the macromorphology of the seed and is determined by several characters. The most important characters are (1) outline of epidermal cells (isodiametric or elongated); (2) curvature of the outer periclinal wall

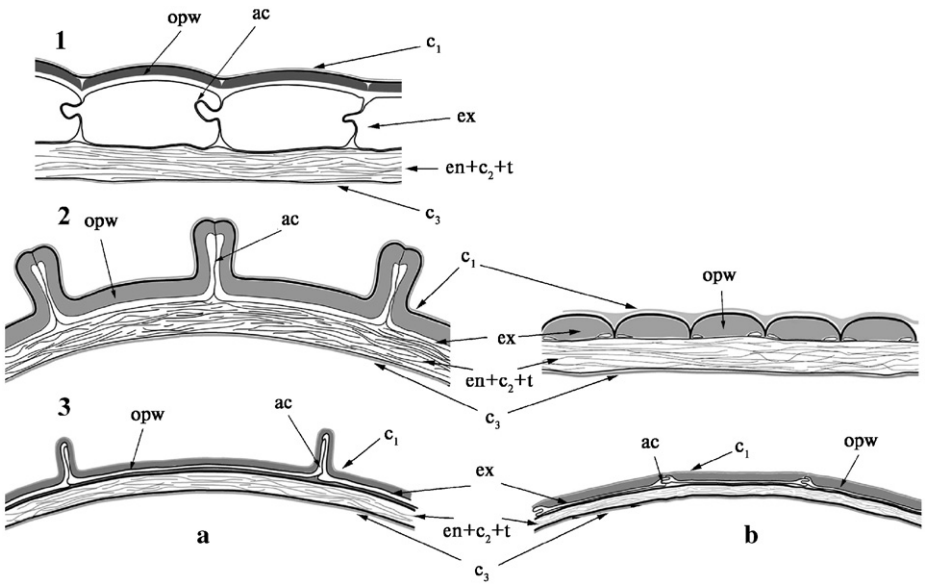


**Fig. 1.** Schematic anatomical structure of the seed coat in *Rhodiola* sect. *Rhodiola* representatives. (1) Colliculate seed coat; (2) laticostate seed coat, (a) longitudinal section, (b) transverse section; (3) tenuicostate seed coat, (a) longitudinal section, (b) transverse section. ex – exotesta; en – endotesta; $c_1$ – outer cuticle; $c_2$ – intermediate cuticle; $c_3$ – inner cuticle; t – tegmen; ac – anticlinal cell wall; opw – outer periclinal wall.

**Table 1.** Seed morphological characteristics in *Rhodiola* sect. *Rhodiola*

| Taxon | Shape and size (μm) | Wing-like projection/ folds | Raphe | Seed coat architecture type | Cell shape | Cell boundaries | | Anticlinal walls | Periclinal walls shape/ thickness | Wall microsculpture |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Proximal | Distal | | | |
| ***Rh. alsia*** | O to EEL, 1800–2000 × 600–700 | Large projection | Weakly defined | Colliculate | Q to H (L/W ratio ⩾2) | Well-defined, concave and straight | | Not defined | Weakly convex, thickened | Finely wrinkled |
| ***Rh. angusta*** | EEL, 2800–3000 × 600–900 | Large folds | Weakly defined | Colliculate | Nearly isodiametric | Well-defined, concave and straight | | Not defined | Convex, thickened | Smooth |
| ***Rh. ishidae*** | EEL, 2000–3000 × 500–900 | Large projection or folds | Weakly defined | Colliculate | Q to polygonal, isodiametric to transversely extended | Well-defined, concave, slightly curved | | Not defined | Convex, thickened | Smooth |
| ***Rh. rosea* subsp. *rosea*** | EEL, 1200–1700 × 400–600 | Small folds | Well-defined | Laticostate | Q to H, transversely extended (L/W >2) | Well-defined, concave, straight | Weakly noticeable, slightly curved | Distal raised, tight-adjoining, proximal not raised | Concave, thickened | Smooth to granulate |
| | | | | Tenuicostate | | | | Distal raised, tight-adjoining, proximal raised or not | Concave, not thickened | |
| ***Rh. rosea* subsp. *arctica*** | EEL, 1700–2000 × 500-600 | Small projection and folds | Defined | Tenuicostate | Q, transversely extended, L/W⩾3 | Not noticeable | | Distal weakly raised, tight-adjoining | Concave, not thickened | Smooth to granulate |
| ***Rh. rosea* subsp. *sachalinensis*** | EEL, 1700–2000 × 500-600 | Small projection and folds | Defined | Tenuicostate | Q, transversely extended, L/W⩾3 | Well-defined, | Weakly noticeable, slightly curved | Distal raised (up to 10 μm), tight-adjoining | Concave, slightly thickened | Nearly smooth |
| ***Rh. integrifolia*** | EEL, 2300–2500 × 600–700 | Folds | Well-defined | Tenuicostate | Q to H, transversely extended | Well-defined, straight | Weakly noticeable, slightly curved | Distal raised (up to 25 μm), tight-adjoining | Concave, slightly thickened | Smooth to finely granular |

O – oviform, EEL – elongate-elliptic, Q – -quadrangular, H – -hexagonal.

(convex, concave or straight); (3) shape and relief of anticlinal walls (straight, curved, thickened or not thickened); and (4) relief of the cell boundaries. Depending on the height, arrangement, degree of fusion and cuticle thickness of anticlinal cell walls, the boundary can be either defined or not, straight or curved, concave or flat. A secondary sculpture characterizes seed micromorphology and is determined by the cuticle sculpture (Barthlott, 1981).

## Results and discussion

Among the members of the section *Rhodiola* that were studied, seed shape was rather uniform, elongate–elliptic to egg-shaped, and often with attenuate obtuse ends (Table 1). The raphe could be either well defined (as a narrow straight comb) or not. The size of the seeds examined was in the range 1200–3000 μm × 400–900 μm. A wing-like projection at the chalazal end (Fig. 2: 3; Fig. 4: 3) or folds on either ends (Fig. 2: 5; Fig. 3: 1) formed by the seed coat were typical of most specimens studied. The testa cells are morphologically uniform or with little shape variation, more or less regularly arranged in longitudinal rows that become less regular near raphe. The cells were nearly isodiametric (Fig. 2: 4) or extended transversely up to three times and were quadrangular to polygonal. Outer periclinal exotesta cell walls are flat, weakly concave or convex. Anticlinal walls are thickened or not, entirely fused or not defined.

Based on the pronounced outer cell morphology and seed coat anatomy, we have identified three types of seed surface sculpture.

### Colliculate seed surface (*Rhodiola alsia*, *Rh. angusta* and *Rh. ishidae*)

Cells are quadrangular to polygonal, isodiametric or extended transversely (length to width ratio ⩾2) and are arranged in regular longitudinal rows (Fig. 2: 1–6). Cell boundaries are well defined, concave, straight to curved. The outer periclinal cell wall is convex. The cuticle is smooth or weakly wrinkled.

The seed coat has an anatomical structure typical for the family representatives (Corner, 1976; Netolitzky, 1926).

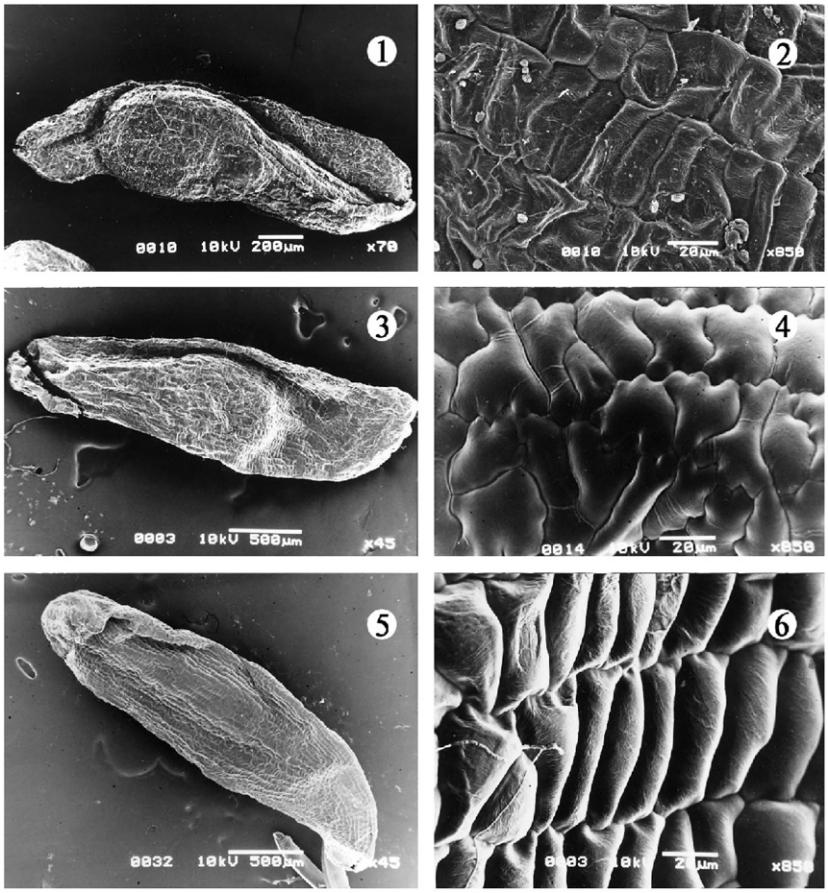


**Fig. 2.** Scanning electron micrographs of *Rhodiola* seeds. 1–6: colliculate seed coat sculpture: *Rh. alsia* (1, 2), *Rh. angusta* (3, 4), *Rh. ishidae* (5, 6).

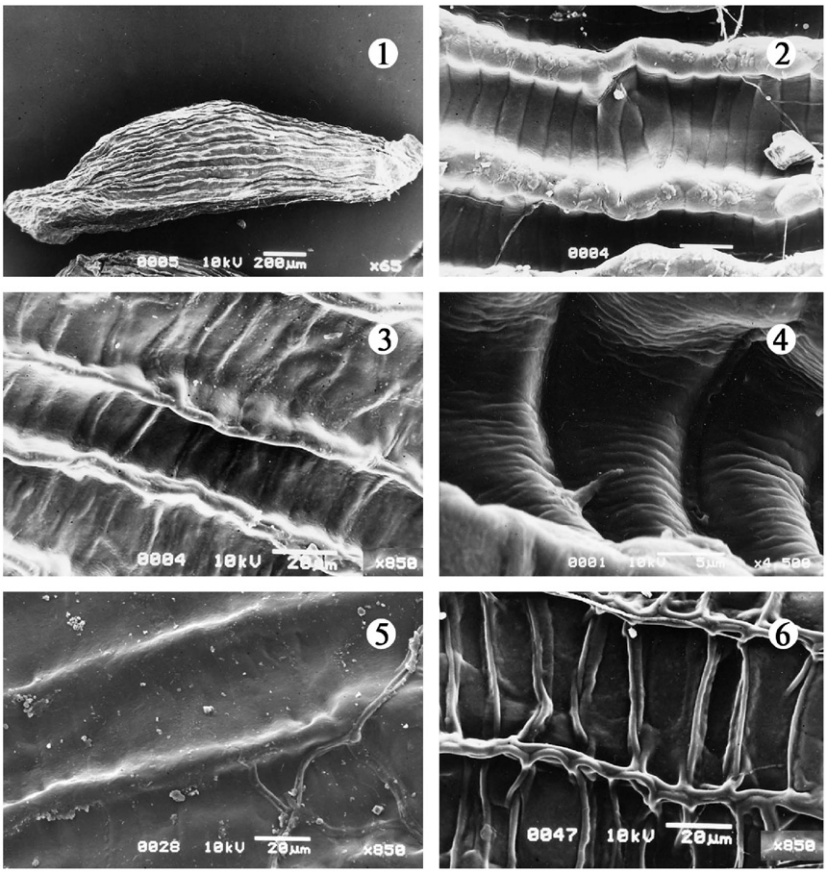


**Fig. 3.** Scanning electron micrographs of *Rhodiola rosea* subsp. *rosea* seeds; laticostate sculpture (2, 4), tenuicostate (3, 5, 6).

Transverse and longitudinal sections are identical (Fig. 1: 1). Only the exotesta has a well-defined layer. A convex thickened outer periclinal cell wall causes a characteristic colliculate surface appearance, while all other parts of the cell wall remain thin. The cell lumen is narrow and at times contains the remnants of protoplasm. The endotesta has thin dark-colored walls with indistinguishable individual cells. The number of layers in the inner integument (tegmen) is also not distinguishable. Endotesta, tegmen and intermediate cuticle are compressed to form one pigmented layer. The tegmen at the endosperm side is covered with a colorless cuticle. Exotestas form large wing-like projections or fold at the seed chalazal end.

## Laticostate seed surface (*Rh. rosea* subsp. *rosea*)

In this type long cell boundaries are well defined, concave or slightly convex and have straight, short boundaries that are weakly defined and slightly curved. The outer periclinal wall is convex. The distal cell ends have rounded apices, are raised and thickened. The raised parts of the outer periclinal wall form regular longitudinal undulate ribs. Distal anticlinal cell walls are somewhat raised and are entirely fused. Proximal anticlinal cell walls are not defined, are concave and straight. The cuticle ranges from nearly smooth to granular (Fig. 3: 2, 4).

The anatomical structure of the seed coat in seeds with a laticostate surface is similar to that in *Rh. alsia*, *Rh. angusta*, *Rh. ishidae* in general but that in this instance shows a difference with raised anticlinal cell walls (Fig. 1: 2).

## Tenuicostate seed surface (*Rh. rosea* subsp. *rosea*, *Rh. rosea* subsp. *sachalinensis*, *Rh. rosea* subsp. *arctica*, *Rh. integrifolia*)

The distal anticlinal cell walls are raised (twice higher then proximal) and are entirely fused (tenuicostate surface; Fig. 3: 3, 5; Fig. 4: 3–6). The proximal anticlinal cell walls show weakly defined ribs or are flashed. The cell boundaries are weakly defined or not defined at all. Sometimes the distal and proximal anticlinal cell walls are of equal thickness and heights (Fig. 3: 6). Specimens combining both types are also observed. Some proximal anticlinal walls are as high as the distal walls, but some are not defined (Fig. 4: 1). Secondary sculpture varies.

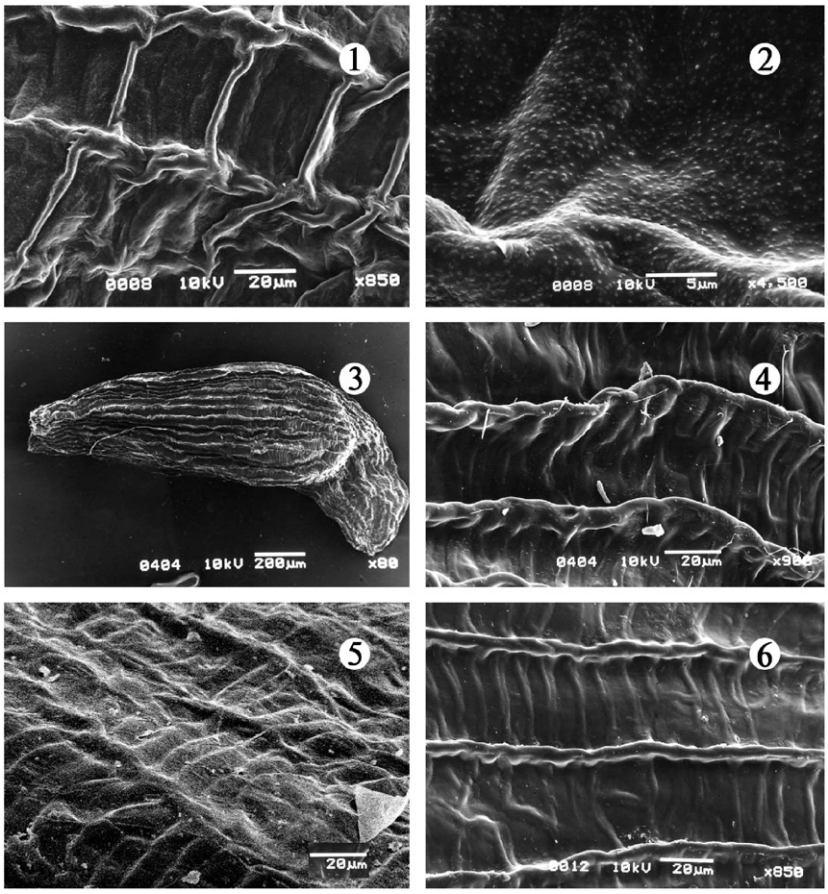


**Fig. 4.** Scanning electron micrographs of *Rhodiola* seeds. 1–6 tenuicostate surface: *Rh. rosea* subsp. *rosea* (1, 2), *Rh. integrifolia* (3, 4); *R. rosea* subsp. *arctica* (5); *Rh. rosea* subsp. *sachalinensis* (6).

Seeds with nearly smooth cuticle were most common, some specimens had a helical or granular surface (Fig. 3: 4; Fig. 4: 2).

Cross-sections clearly show that the exotesta anticlinal walls are raised, S-shaped, and they form folds that appear to thicken, while the periclinal wall is concave and nearly aligned with the inner wall (Fig. 1: 3, 4).

Thus, the study of the seed characters in seven taxa of predominantly Far-Eastern *Rhodiola* section *Rhodiola* representatives revealed a heterogeneous seed surface sculpturing in the section. This observation contradicts data on other Crassulaceae genera, *Hylotelephium*, *Aizopsis* and *Orostachys*, traditionally considered to be closely related to *Rhodiola*. It has been shown that their intrageneric taxa (section and series) are characterized by a uniform set of seed coat features that could be used to discriminate these entities (Gontcharova, 1999; Hart and Berendsen, 1980; Knapp, 1994; Koldaeva and Gontcharova, 2005). Here we report three distinct types of seed coat sculpture, each characterized by a specific anatomical structure (Table 1, Figs. 1–4). Variability of this character in the section under discussion is not in agreement with the stability of this character in many other plant genera (Barthlott, 1984; Esau, 1977). This may be indicative of the section's artificial nature. Indeed, a recent molecular study on phylogenetic relationships in Sedoideae could not define *Rhodiola* sections and series as monophyletic entities (Mayuzumi and Ohba, 2004). The current taxonomic structure of the genus remains therefore in question, and taxon sampling in both molecular and seed micromorphology analyses is still too limited to draw any conclusion from seed coat features in order to characterize *Rhodiola* supraspecific taxa.

It is also evident that the significance of seed coat sculpturing at the lower taxonomic levels is not uniform in the genus *Rhodiola*. The characteristics of seed coat sculpturing are nearly identical in the three taxa that are characterized by a colliculate seed surface, *Rh. alsia*, *Rh. angusta* and *Rh. ishidae*, with the consequence of little value in species distinction. The close relationship of these taxa, based on their similar vegetative morphology, has already been stressed by Ohba (1981). The common seed coat sculpture type and the presence of large wing-like projection or folds in all of them emphasize this as well. The common seed coat features are known only in these three species, differentiating them from other members of the sect.

*Rhodiola*. Therefore, we believe that these species can be grouped into one sect. *Algida* (Boriss.) S. B. Gontch. (Gontcharova, 2006).

In contrast, the morphological characters are more diverse in seeds with a tenuicostate surface type and their patterns clearly differentiate taxa having seeds of this type (e.g. *Rh. rosea* and its subspecies). Discrimination of these subspecies based on vegetative morphology alone is somewhat problematic, and some specialists reject them as synonyms of the type variety (Ohba, 1981, 2005). However, the data presented here put such a treatment in question.

The broad variability of the seed surface sculpture revealed in *Rh. rosea* subsp. *rosea* contradicts a generally accepted notion that morphological features of the seed coats show little plasticity and thus the variation among individuals most likely reflects genetic differences (Barthlott, 1981; Buss et al., 2001). Seed coat feature diversity in one taxon (e.g. *Rh. rosea* subsp. *rosea*) suggests either ambiguous identification of some specimens or the artificial nature of the taxon. We were unable to establish firm relationships between seed coat morphology and specimen origin. However, plants from Europe have a laticostate seed surface, while those from Asia are observed to have two types of seed coats (laticostate and tenuicostate), with the tenuicostate type the more common. This pattern tentatively suggests that at least some populations of this widely distributed species may, in fact, represent a cryptic subspecies or even taxa of a higher rank otherwise weakly differentiated morphologically from *Rh. rosea* subsp. *rosea*.

In conclusion, seed morphology and anatomical characters of the Far-Eastern representatives of *Rhodiola* sect. *Rhodiola* show considerable variation that may reflect non-monophyly of the section, suggested by molecular phylogeny data. At the species level, the seed coat characters correspond to the features of gross morphology and they identify at least three morphotypes in the section. Diversity of seed coat sculptures in widely distributed *Rh. rosea* subsp. *rosea* possibly suggests the presence of cryptic species and requires further studies.

## Acknowledgement

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## Appendix A. Specimens examined

***Rhodiola alsia*** TNS 103785;
***Rh. angusta*** TNS 67793;
***Rh. arctica*** obtained from the Polar-Alpine Botanical Garden-Institute of the KSC RAS;
***Rh. integrifolia*** Kamchatka, Bistrynskiy Distr., 5 km from village Esso 850 m alt. 29.08.1998, V. V. Yakubov; Kamchatka, Bystrinsky Distr., Sredinniy Ridge, 4 km east from village Esso, 1000 m alt. 01.09.1998, V. V. Yakubov; Kamchatka, Bystrinsky Distr., Sredinniy Ridge, 800 m alt. 30.08.2000, V. V. Yakubov; Central Kamchatka, south slopes of vulcano Tolbachik, 22.08.2000. V. V. Yakubov; TNS 237779;
***Rh. ishidae*** Japan, Honshu, Hayachin, 27.09.98. A. A. Gontcharov; TNS 228917; TNS 303356; TNS 12448; TNS 228917; TI 11547;
***Rh. rosea* ssp. *rosea*** Hokkaido, Shiretoko, Mt. Rausu, 02.09.98, A.A. Gontcharov; Kamchatka, Bystrinsky Distr., foots of vulcano Anaun, 820 m alt. 11.09. 1998.V. V. Yakubov; Central Kamchatka, south slopes of vulcano Ostri Tolbachik, 26.08.2000. V. V. Yakubov; Japan, Honshu, Mt. Hayachine, 27.09.98. A. A. Gontcharov, TNS 107450 (USA); TNS 209962 (Switzerland), TNS 198310 (Scotland), TNS 246341 (Japan, Honshu), TNS 603276 (Japan, Hokkaido), TNS 107450 (USA), TI 90800 (Japan, Honshu), TI 908005 (Japan, Honshu), TI 867092 (Japan, Hokkaido), TI 758154 (Japan, Honshu), TI 5511 (Japan, Hokkaido), TI 177 (Japan, Hokkaido, Isl. Rishiri, 09.05. 1978), TI 909004 (Japan, Honshu), TI 758154 (Japan, Honshu), TNS 107450 (USA), TNS 29776; TNS 209962 (Switzerland, Geneva);
***Rh. rosea* ssp. *sachalinensis*** Sakhalin, Isl. Moneron, 10.09.91, M. N. Abankina, S. B. Gontcharova; Sakhalin, Aniva Bay, near village Yuznoe, 28.08.2001, S. B. Gontcharova.

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