The natural hybrid between *Rhodiola amabilis* (H. OHBA)
H. OHBA and *R. Wallichiana* (HOOK.) FU*

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Many botanists have pointed out the tendency towards autogamy and apomixis in arctic plants (e.g. Warming 1888–1920, Mathisen 1921, Mosquin 1966), though the contrary idea has been put forward by Kevan (1972). However, few botanists have said about reproduction in the high altitude plants of the Himalayas. For the purpose of revealing the nature of the high altitude plants of the Himalayas it needs to survey their reproduction.

The present paper deals with a putative interspecific hybrid in the genus *Rhodiola*. *Rhodiola*, specifically concentrated in high altitudes of the region from the Himalayas to S.W. China, is considered to be of entomophily: the flowers offer visual or some olfactory attractants and provide pollen and nectar as food upon which many of high altitude insects depend. During our field surveys we have met few insect visiting the flowers of *Rhodiola*, in spite of its well fruition. The species of *Rhodiola* seem to be independent of insects for reproduction, being autogamous or apomictic. So that the interspecific hybrid is thought to be a strong evidence of insect-mediated cross-pollination. There are two types of flowers in the Himalayan *Rhodiola*: these are hermaphroditic and dioecious monosexual. The dioecism of *Rhodiola*, which is limited within the subgenus *Rhodiola*, is structural and unique in Crassulaceae (OHBA 1978).

The dioecious subgenus, *Rhodiola*, seems to be significantly different from the hermaphroditic subgenus, *Crassipedes*, in seed production. Dioecious *Rhodiola* is functionally in need of outbreeding if they are neither apomixis nor nucellar embryony. Jansson & Rechinger (1970) discussed the occurrence of interspecific hybridization between *Rhodiola heterodonta* (Hook. f. et Thoms.) A. Boriss. and *R. recticaulis* A. Boriss. and also

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R. heterodonta and R. pamiroalaica A. Boriss. However, as far as examined the specimens which are identified as the hybrids by Jansson (& Rechinger) actually fall into the variation range of R. imbricata Edgew. It is insufficient to be regarded that species as hybrid origin. In high altitudes of Nepal, though two or more related species of the subgenus Rhodiola grow together in the same territory, so far as can be determined from field studies they do not hybridize at all. At present the existence of interspecific hybrid is very doubtful in the subgenus Rhodiola.

While in the hermaphroditic subgenus, Grassipes (Ohba 1978), we noticed an intermediate plant between Rhodiola amabilis (H. Ohba) H. Ohba and R. Wallichiana (Hook.) Fu at Beding (alt. ca 3600 m) in Rolwaling Himal in 1983 (Fig. 1). Beding is near the upper limit in the vertical distribution of both species. R. amabilis, endemic to Central and East Nepal, is regarded as a primary invader of the shallow soils on exposed, flat surface of huge rocks or outcrops. R. Wallichiana, ranging from Chitral to Sikkim and Tibet through Kashmir, Kumaun and Nepal (Ohba 1975, 1980), tends to occur among stones in scree or talus. The intermediate plant, growing on moss-covered exposed flat rock surface together with R. amabilis, produces 10 to 12 seemingly functional ovules in each locule and sterile anthers. This is suggested that the intermediate plant is the natural hybrid between the nominated species (Fig. 2). R. amabilis has 20 somatic chromosomes and R. Wallichiana has 22 (Ohba & Wakabayashi unpublished). However, counting of the chromosome number of this hybrid unfortunately resulted in failure.

Fig. 1. Rhodiola amabilis × R. Wallichiana in Beding, Rolwaling Himal.
It is no doubt that this is a circumstantial evidence of (insect-mediated) crosspollination among hermaphroditic species of *Rhodiola*.

The species of the subgenus *Crassipes* have their ranges in rather lower altitudes than those of the subgenus *Rhodiola*: that is, the altitudes growing *Crassipes* are just above the tree line and their flowers seem to be possible visited by insects, particularly...
diptera. However, the number of insects as pollinators is extremely reduced in higher altitudes where the subgenus *Rhodiola* dominates. We suppose that *Rhodiola* gradually becomes independent of insects for seed-set, and that apomixis may result from such difficulties of insect-mediated cross-pollinations in these circumstances. There still remain some questions why *Rhodiola* in higher altitudes is dioecious not hermaphroditic. Because *Rhodiola* usually regenerates by means of vegetative reproduction, dioecism is thought to be economical, producing only stamens or pistils. However, to reply this question it is necessary to make extensive field survey including pollination ecology.

Description

*Rhodiola amabilis* (H. Ohba) H. Ohba × *R. Wallichiana* (Hook.) Fu [Table 1]

A perennial herb with rhizomes 10–15 mm thick, erect or nearly so. Scaly radical-leaves deciduous, triangular-lanceolate, blackish brown or chestnut-brown, 2.5–3 mm long, ca 1 mm wide. Flowering stem 8 to 12 from each of the apex of rhizomes, deciduous, 7–11 cm long, glabrous, nearly smooth, pale green, ca 10 mm thick. Leaves rather densely arranged throughout, widely spreading, sessile, thick herbaceous, linear, acute, entire or nearly so, 8–15 mm long, 0.9–2 mm wide, glabrous, without papillae. Inflorescences terminal, (1–)3–5-flowered, bracteate.

Flowers hermaphroditic, 5-merous, approximately 1 cm wide at anthesis, pedicellate. Calyx 5–6 mm long, fleshy, green, glabrous, the tube ca 0.5 mm long; the lobes 4–5 mm long, 0.9–1.1 mm wide, linear-subulate, round—obtuse at the apex. Petals entirely white, suberect to ascending at anthesis, linear-elliptic, round—obtuse at the apex, 5.7–6 mm long, ca 1.5 mm wide. Stamens distinctly shorter than the petal, erect, filaments white, the epipetalous ones ca 2 mm long, inserted 1.5–1.7 mm from the base, the alternipetalous ones 3.5–4 mm long; anthers ovate, ca 0.5 mm long, without pollen. Nectar-scales broadly oblong, 0.9–1 mm long, ca 0.7 mm wide, yellow. Gynoecium 6–7 mm long, the ovaries ca 1 mm connate ventrally from the base, erect, ca 0.8 mm wide at the middle,

Table 1. Comparison of character states among the hybrid and its putative parents

<table>
<thead>
<tr>
<th>Character</th>
<th><em>R. amabilis</em></th>
<th>The hybrid</th>
<th><em>R. Wallichiana</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of flowering stem (cm)</td>
<td>5–10</td>
<td>7–11</td>
<td>15–30</td>
</tr>
<tr>
<td>Leaf size (mm)</td>
<td>(5–)6–12 × 0.8–1.5</td>
<td>8–15 × 0.9–2</td>
<td>12–30 × 1.2–6</td>
</tr>
<tr>
<td>Shape of calyx-lobe</td>
<td>triangular-lanceolate</td>
<td>linear-subulate</td>
<td>lanceolate—subulate</td>
</tr>
<tr>
<td>Size of calyx-lobe (mm)</td>
<td>4–5</td>
<td>4–5</td>
<td>5.6–8</td>
</tr>
<tr>
<td>Direction of petal</td>
<td>widely spreading</td>
<td>suberect—ascending</td>
<td>ascending—suberect</td>
</tr>
<tr>
<td>Shape of petal</td>
<td>narrowly elliptic</td>
<td>linear-elliptic</td>
<td>narrowly elliptic—linear</td>
</tr>
<tr>
<td>Size of petal (mm)</td>
<td>5–7.5 × 1.7–2</td>
<td>5.7–6 × ca 1.5</td>
<td>7–11 × 1.8–2.5</td>
</tr>
<tr>
<td>Length of alternipetalous filament (mm)</td>
<td>4.2–4.7</td>
<td>3.5–4</td>
<td>7.5–12</td>
</tr>
<tr>
<td>Length of gynoecium (mm)</td>
<td>5–6</td>
<td>6–7</td>
<td>9–14</td>
</tr>
<tr>
<td>Number of ovule</td>
<td>12–18</td>
<td>10–12</td>
<td>28–36</td>
</tr>
</tbody>
</table>
tapering upwards from the middle, the stylar part slightly outcurved, the stigma ± papillate. Ovules 10–12 in each locule, ca. 0.7 mm long.


References


摘要 高山帯を主とする生育地とするペンケイソウ科イワペンケイ属には、両性花と雌雄異株の系統がある。イワペンケイ属の花は、虫媒花と考えられるが、高山帯における野生調査中にはほとんど訪花昆虫が観察されなかった。ところで、両性花のものは、昆虫による花粉の媒介を必要としない自花受粉と無融合生殖の可能性が考えられる。そこで、種間雑種が存在すれば、実際に他家受粉が行われている可能性が強く示唆される。したがって、種間雑種の存否は、単にその形質発現の状態だけでなく、同属での繁殖法を明らかにするうえでも興味深いものがある。

ここに報告するのは1983年中部ネパールのロルワリン・ヒマールのベディン村で見いだされた雑種であり、Rhodiola amabilis (H. OHBA) H. OHBA と R. Wallichiana (HOOK.) Fu がその親と推定される。推定両親種をともに、両性花を生じるモロシパイワペンケイ亜属 (Subgen. Crassipes) に分類され、系統上近縁である。見いだされた個体は、一見したところ両種の中間のかたちをしており、調べた多くの形質において確かに両親種の中間の状態を呈していることが判明した。

今まで、イワペンケイ属では、両性花の系統では雑種に関する報告は皆無であるが、雌雄異株の系統から種間雑種ができるという報告があった。しかし、それらの証拠標本を検討した限りでは種間雑種と見做せるものではなかった。したがって、本報告で記載した個体は、現在のところ同属中雑種と推定される唯一のものである。