Original Article

Comparative characterization of two closely related achlorophyllous orchids, *Gastrodia nipponica* and *G. tokaraensis*

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Received Jun 30, 2006 / Accepted Oct 10, 2006

Abstract

Investigated were characteristics of the two achlorophyllous myco-heterotrophic orchids, *Gastrodia nipponica* and a closely related species *G. tokaraensis*. The latter species was reported as a new species by the authors recently. The two orchids inhabit the bamboo forest on the island of Takeshima, the northernmost island of the Ryukyu Islands of Japan.

There are great differences between the two orchids in morphology and ecology. The conspicuous characteristics of *G. nipponica* are its scattered emergence usually on thickly fallen bamboo leaves, the short lived and simple root system, and the short-lived pubescent rhizomes in the F-layer in soil forming the monopodial or sympodial rhizome system. In contrast, *G. tokaraensis* emerges gregariously in a colony about 70 cm in diameter in open spaces or soil by paths in bamboo forests; it has the perennial and large complex root system, and the perennial smooth rhizomes in the A-layer in soil forming the large rhizome network system in a colony about 70 cm in diameter. In addition, the embryo volume of *G. tokaraensis* is less than half of that of *G. nipponica*. It was also observed that the *G. tokaraensis* plants and the flowers drastically decreased in number only for a two-week period.

Similarities observed in both orchids are as follows: the two orchids flower and fruit from mid-April to the latter half of May, however *G. tokaraensis* emerges at least two weeks later than *G. nipponica*. Both orchids can propagate from the rhizomes.

The habit of the emergence above ground reflects the rhizome system in the ground of the orchid. And it is suggested that there is a close relationship between the rhizome surface and the underground location of the rhizome.

Key Words: *Gastrodia nipponica*, *Gastrodia tokaraensis*, rhizome, rhizome system, root system

Introduction

The genus *Gastrodia* is one of the achlorophyllous, myco-heterotrophic, and terrestrial orchidaceous genera. In the genus, around 40 species have been recognized from temperate and tropical areas of Asia to New Zealand and 12 species of them from Japan and neighboring areas. They inhabit densely shaded forests and spend the greater part of their lives underground; and only their inflorescence emerges from the forest floor after bolting. For these reasons and their rare and ephemeral emergence, they are found only occasionally and are therefore very difficult plants to investigate.

Quite recently, a new *Gastrodia* species, *G. tokaraensis* Yokota et Umata was reported from Japan (Yokota & Umata 2001). This species belongs to the section *Codonanthus* and is most closely related to *G. nipponica* (Honda) Tuyama in systematic, but it differs in that it has many more flowers which are semi-open with wide ovate petals. Moreover this orchid is distinguishable from other species in the section *Codonanthus* from Japan, such as *G. boninensis* Tuyama, *G. confusa* Honda et

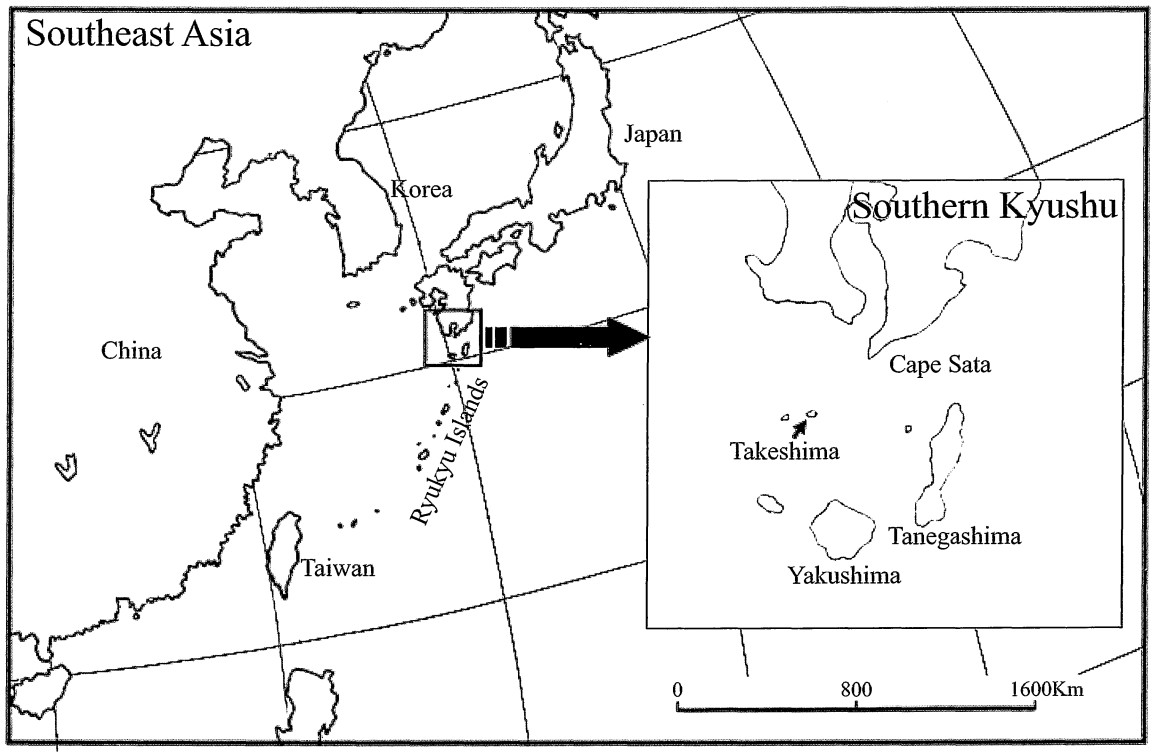

Fig. 1. Location of the island of Takeshima.

Tuyama, *G. pubilabiata* Sawa and *G. shimizuana* Tuyama. Japan and surrounding areas thus appear to be the center of diversity of this section as stated before (Yokota & Umata 2001). However little is known about the ecological and physiological diversity of most species because of the reasons mentioned above.

So far *G. tokaraensis* has been found only on the island of Takeshima, one of the northernmost islands of the Ryukyu Islands of Japan (Fig. 1). We have observed some interesting living habits common to *G. tokaraensis* and *G. nipponica* on the island, that is, both orchids inhabited the bamboo forest, occurred near to each other, and flowered and fruited in the same season from the end of April to the middle of May. We therefore thought that biological diversity between them had to be clarified in detail from various points of view. In this report, we compare and characterize the two orchids based upon their morphological and ecological characteristics, and then discuss the diversity between them.

Materials and Methods

Takeshima, a small and flat volcanic island (approx. 4 km^2), is almost entirely covered with thick bamboos (*Pleioblastus linearis* (Hack.) Nakai). We performed the investigations twice, on 24th April and 8th May, 2002. We searched intensively within a ca. two ha area of the bamboo forest to find the two plants and examined their morphological, anatomical and ecological characteristics. The plants were fixed in FAA or 50% ethyl alcohol until examined.

Results

1. Plant growth and emergence habit

From the 24th April investigation, we obtained the following results. As shown in Fig. 2a, *G. nipponica* developed 1 to 3 flower stalks growing up to 50 cm or higher with a ruptured but not yet opened capsule about 3.5 cm long on each stalk. *G. nipponica* emerged from the thickly fallen leaves mostly a few together or scattered to form a loose colony, though sometimes solitary. In comparison, as shown in Fig. 2c, *G. tokaraensis* developed much shorter stalks less than 20 cm in height with small and immature capsules up to 1.5 cm long, and in rare cases with flowers. *G. tokaraensis* emerged often in the open or spaces formed by paths or from the soil by paths, though sometimes from the fallen leaves. This orchid emerged often gregariously in a colony 70 cm or more in diameter consisting of from 10 to

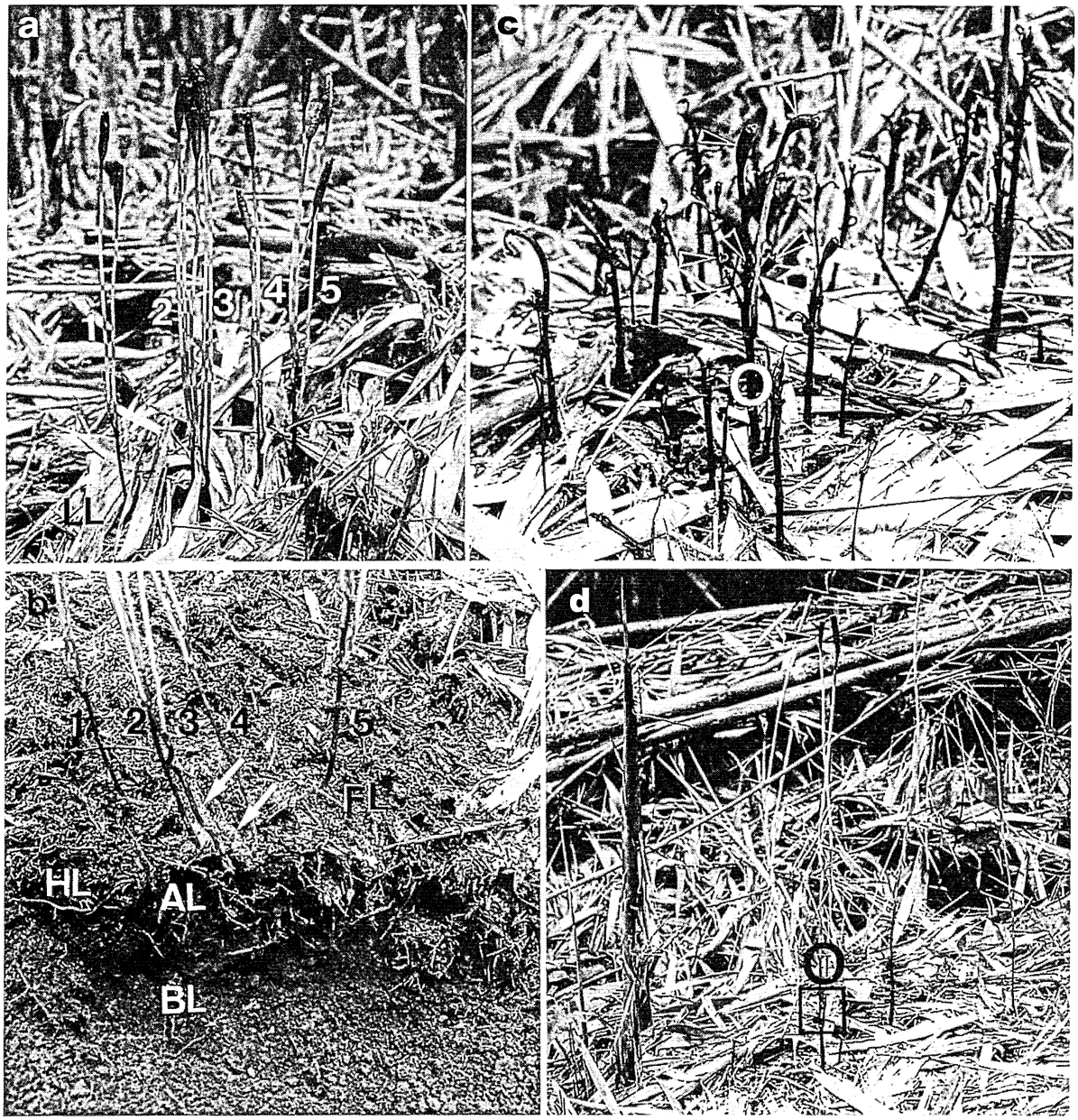

Fig. 2. *Gastrodia nipponica* and *G. tokaraensis* in their natural habitat. (a-b). *Gastrodia nipponica* and their rhizomes underground. The two figures show the same plants. Each of the plant number in (a) corresponds to that in (b). Each of the figures shows a part of the whole colony. (a) Several plants growing together on the thickly fallen bamboo leaves (L-layer) which were rich in air gaps, on 24th April, 2002. (b) Soil profile (L-layer was taken away from around the plants) and locations of the rhizomes. The H-layer is hardly detectable because of its thinness. The rhizomes (arrows) are located among fragments of the decayed leaves (F-layer). (c-d) *Gastrodia tokaraensis* and the drastic decrease in number after a two-week period. The two figures show a part of the same colony. (c) Gregarious emergence in a colony by a path. The colony consists of 40 individuals extending about 70 cm in diameter, on 24th April, 2002. The plant at the center (circle) is 10 cm in height and has six small fruits (arrows). (d) Same location on 8th May, 2002. The decrease in number is drastic from 40 to 8, in just two weeks between 24th April. and 8th May. The plant at the center (circle) is more than 40 cm in height and shows similar growth to *Gastrodia nipponica* in height but was reached in a two-week period (compare with (a).). It only produces two normal fruits (arrows) successfully from six; the rest (square) failed to develop further (compare with (c).).
AL: A-layer, BL: B-layer, HL: H-layer, FL: F-layer, LL: L-layer.

40 individuals, though occasionally several appeared together or solitarily and scattered. We thought that the difference in the habit of the emergence above ground between the two orchids might be due to the spread or construction of the underground rhizomes in each orchid. We therefore examined under the ground and obtained some interesting results as described

below.

From the 8th May investigation, *G. nipponica* bore open and empty capsules from which the seeds had already been scattered, while *G. tokaraensis* (Fig. 2d) reached just a similar growing stage to *G. nipponica* described by the first investigation (Fig. 2a).

Next, two colonies of *G. tokaraensis* were examined for the number of individual plants, and the decrease in number was drastic after only a two-week period. That is, one colony consisted of 37 plants and another contained 40 in the 24th April investigation, and then was found to contain only 8 and 10 respectively by the 8th May investigation (Fig. 2c-d). Moreover, the flowers of *G. tokaraensis* were also examined. This orchid mostly produced several or more flowers, sometimes more than 10, on each stalk. However, only a few flowers successfully developed normal fruits and the rest were sterile, as shown in Fig. 2c-d and Fig. 3b. The peduncles with normal fruits grew long up to 40 cm or more, but those with sterile flowers and fruits did not grow any further at all (Fig. 3b). *G. nipponica* was not examined for the number of individuals and flowers.

2. Rhizome system

As shown in Fig. 2b and 3a, the rhizome of *G. nipponica* occurred singly or occasionally as 2 to 4 joined together in the monopodial or the sympodial rhizome system extending horizontally in the ground. There was mostly one flower stalk on the end of the rhizome, though occasionally there were a few stalks

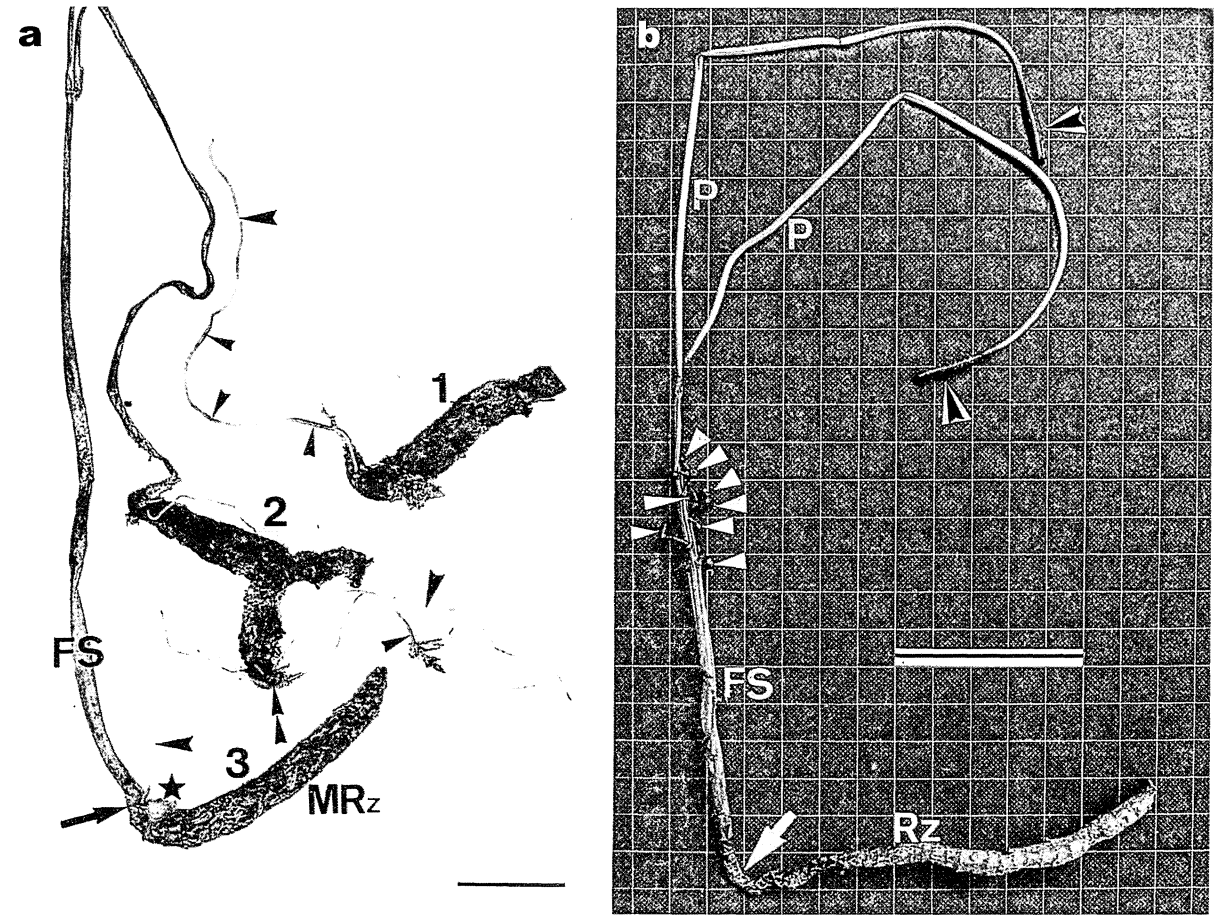

Fig. 3. Morphology of *Gastrodia nipponica* and *G. tokaraensis*. (a) Monopodial (1, 3) and sympodial (2) rhizome system of *Gastrodia nipponica*. The long root (large arrows) and the new daughter rhizome (asterisk) occur at the end of the pubescent mother rhizome, after a one-month culture period. Small arrows show the infected area by a fungal symbiont. Double small arrow shows the base of flower stalk, this indicates that more than one inflorescence bolt if the rhizome system is sympodial. The joint (long arrow) between the rhizome and the flower stalk is sharply distinct, because of the pubescences on the rhizome (compare with (b) and Fig. 6c.). (b) *Gastrodia tokaraensis* producing only two normal and many sterile fruits. The normal fruit (black arrows) is on top of each of the two long elongating peduncles, more than 40cm in length. Whereas eight sterile fruits (white arrows) are on those of small and short peduncles, less than 2 cm in length. The joint (long arrow) between the rhizome and the flower stalk is less distinct compared to that of *Gastrodia nipponica* (a). FS: flower stalk, MRz: mother rhizome, P: peduncle, Rz: rhizome. Bars: 2 cm (a), 10 cm (b).

on a single rhizome if it was a sympodial system.

In contrast, as shown in Fig. 4a-d, *G. tokaraensis* produced numerous rhizomes, more than 20, joined together in a colony larger than 70 cm in diameter extending radially and horizontally; this can be described as a rhizome network system. There were many flower stalks on the rhizomes within the colony (see Fig. 2c, too).

In connection with this, the rhizomes of each orchid having a few lateral buds were embedded in flowerpots in the laboratory. After a one-month culture period, new small rhizomes were observed on each of the embedded rhizomes (Fig. 3a). This result indicates that the lateral buds grow into the small new rhizomes therefore the joined rhizomes observed in nature are suggested to be the daughters produced on the mother. The joint snapped easily between the well-developed rhizomes.

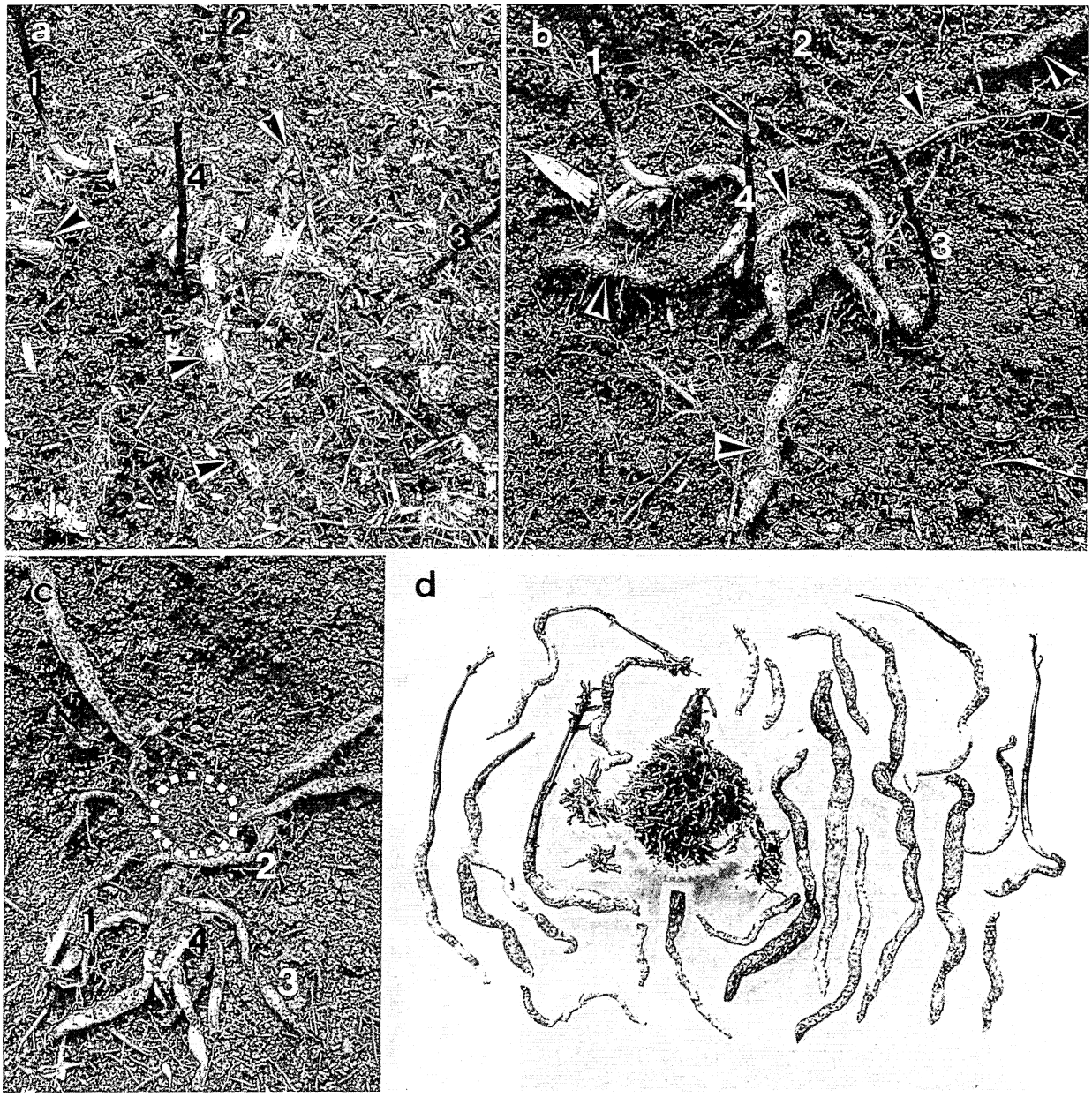

Fig. 4. Rhizome network system of *Gastrodia tokaraensis*, on April 24, 2002. (a), (b), and (c) show a part of the same whole colony. Each of the plant number in (a) corresponds to that in (b) and (c), respectively. (a) Four plants and rhizomes (arrows) being buried in the A-layer, after the removal of the fallen and decayed leaves from around the colony. (b) Network of the rhizome (arrows) spreading horizontally in the A-layer, after digging of soil from around the rhizomes. (c) Root complex (dotted circle) being buried under the center of the rhizome network. (d) Excavated whole colony, consisting of seven rhizomes with flower stalk, 15 rhizomes including broken ones, and one ball-like root complex (center).

3. Root system

From the 24th April investigation of the roots in *G. nipponica,* no roots were observed on the rhizome. However, in the 8th April investigation, a few roots were found on the upper most portion of the rhizome as illustrated by Tuyama (1940). The roots occurred also on the rhizomes embedded in the flowerpots, after a one-month culture period in the laboratory (Fig. 3a). The root system of this orchid was simple, that is, the roots were not branched, and were long, more than 10 cm in length, slender, about 0.7 mm in width, and straight. The lateral short roots were not yet found on the long roots at this time.

In contrast, in the 24th April investigation of the roots in *G. tokaraensis*, a mass of root was found in this orchid immediately beneath the center of the rhizome network (Fig. 4c). As shown in Fig. 4d and 5a-b, the mass of root, 5 cm in height and 4cm in width, was closely associated in a tight complex just like the root ball known in *Monotropastrum globosum* H. Andres (Pyrolaceae). The roots were branched, and were shorter, less than 5 cm, wider, 1.2-1.4 mm, zigzagging, and brittle.

Endomycorrhizal fungi were observed inside the roots in each orchid.

4. Location of the rhizome in the ground and surface of the rhizome

As shown in Fig. 2a-b, the L-layer in the soil was formed from the thickly fallen bamboo leaves and was very rich in air gaps, the F-layer was from the decaying leaves, the H-layer was from humus-like amorphous matter and was very thin, and the A-layer was from dark brown soil and was very firm, respectively. The rhizomes of *G. nipponica* were located in the F-layer on the H-layer (Fig. 2b) and occasionally between the H- and A-layer, while those of *G. tokaraensis* were located in the A-layer (Fig. 4a-c), though occasionally up to the H-layer. The results show that the rhizomes of *G. tokaraensis* are located in deeper ground than those of *G. nipponica.*

The rhizomes of *G. tokaraensis* had deltoid sheaths the same as *G. nipponica* (Fig. 6a-b). Moreover, the rhizome surface of *G. nipponica* was covered densely with pubescence (Fig. 3a, Fig. 6a), as described by Tuyama (1940), while that of *G. tokaraensis* was smooth and hairless (Fig. 3b, Fig. 6b).

We examined the two characteristics of the rhizome, the underground location and the surface of about another 10 species of *Gastrodia* based upon descriptions in the literature and our field observations and summarized them in Table 2. The examined species are *G. callosa* J. J. Smith (Burgeff, 1932), *G. cunninghamii* Hook. f (Campbell, 1964), *G. elata* Blume (Kusano, 1911; Tuyama, 1940), *G. gracilis* Blume (Maekawa, 1971), *G. javanica* (Blume) Lindl. (Tuyama, 1940), *G. minor* Petrie (Campbell, 1963), *G. pubilabiata* Sawa (Kobayashi &

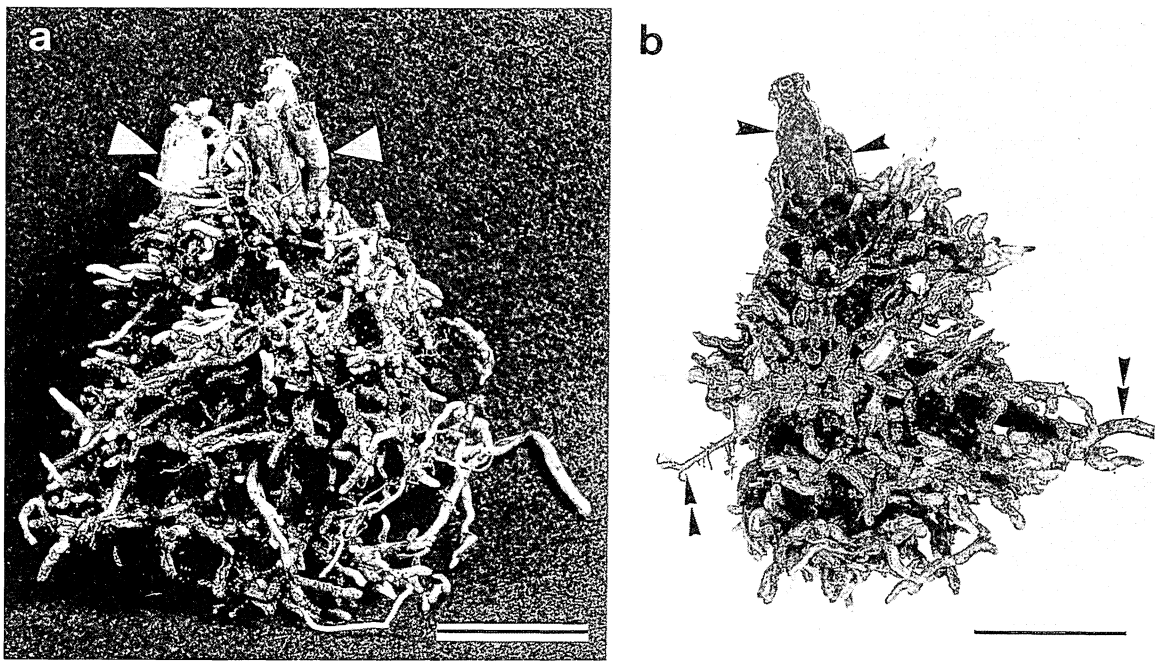

Fig. 5. Root complex system of *Gastrodia tokaraensis,* on April 24, 2002. (a) Surface construction of the root complex, consisting of numerous, ramifying, interwoven and zigzagging roots, and four rhizomes on the top. (b) Vertical section of (a), showing basically the same construction with that of surface. The arrows in (a) and (b) show the rhizomes. Double arrows in (b) show a bamboo root and a tree root. Bars: 2 cm.

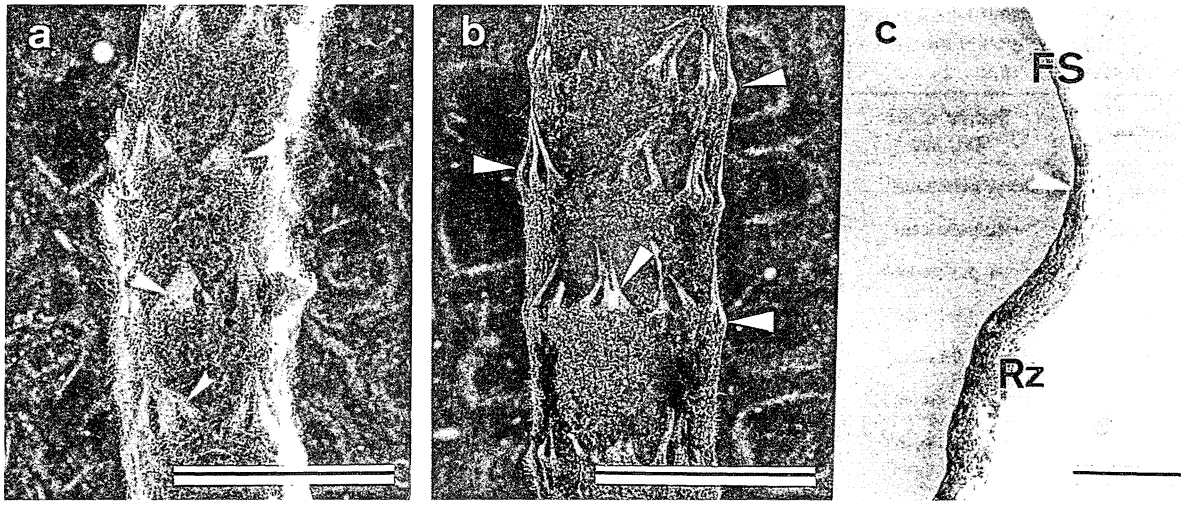

Fig. 6. Surface view of the rhizome of *Gastrodia nipponica* and *G. tokaraensis*. (a) Pubescent surface of the rhizome supplied with deltoid sheaths (arrows) on *G. nipponica*. (b) Smooth surface of the rhizome supplied with deltoid sheaths (arrows) on *G. tokaraensis*. (c) Less distinct joint (arrow) between the flower stalk and the rhizome in *G. tokaraensis*. FS: flower stalk, Rz: rhizome. Bars:1 cm (a, b); 2 cm (c).

Table 1. Diagnostic characteristics of *Gastrodia nipponica* and *G. tokaraensis*, investigated on Takeshima.

	G. nipponica	*G. tokaraensis*
A. Morphology and anatomy		
Dimension of embryo (μm)[1]	(260 ± 28) × (105 ± 10)	(174 ± 14) × (79 ± 7)
Volume of embryo (μm^3)[2]	1,500,135	568,305
Surface of the rhizome	Deltoid sheath and dense pubescence	Deltoid sheath and smooth
Root	Unbranched, straight and long (more than 10 cm), and slender (±0.7 mm in width)	Branched, zigzagging and short (less than 5 cm), wider (1.2-1.4 mm in width), and brittle
B. Ecology		
Flowering and fruiting season	Mid-April to latter half of May. *G. tokaraensis* emerges at least two weeks later than *G. nipponica*.	
Organ for vegetative reproduction	Rhizome	Rhizome
Habit of above ground emergence	Solitary, several together or scattered in a loose colony	Gregarious in a colony 70 cm or more in diameter, sometimes several together
Habitat	On thickly fallen leaves in bamboo forests	On open or ground spaces on path or on the soil by paths in bamboo forests
Underground location of the rhizome	In the F-layer, rarely between the H- and A-layers	In the A-layer, sometimes up to the H-layer
Rhizome system and its life span	Monopodial or sympodial system consisting of one or a few rhizomes. Short-lived, within a few years	Network system consisting of many rhizomes extending horizontally in a colony 70 cm or more in diameter. Perennial
Root system and its life span	Simple system consisting of a few long roots that are produced on top of rhizome in spring. Short-lived,only for a few seasons	Complex system consisting of numerous branches and interwoven short roots beneath the center of the rhizome network. Perennial

1) n = 100

2) The volume of the embryo was calculated by the following equation, proposed by Hadley and Williamson (1971):
$V = \pi B^2 L / 6$
where, V is the volume of the embryo, B is the breadth of the embryo, and L is the length of the embryo.

Table 2. Close relationship between the surface of the rhizome and the underground location of the rhizome in 12 species of *Gastrodia*

Species	Surface of the Rhizome	Underground location of the rhizome
G. callosa	Dense pubescent[1)]	F-layer[1)]
G. nipponica	Dense pubescent[2,3)]	F (to H)-layer[3)]
G. pubilabiata	Dense pubescent[3,6)]	F (to H)-layer[3)]
G. verrucosa	Dense pubescent[2,3)]	F (to H)-layer[3)]
G. gracilis	Dense pubescent[4)]	H-layer[4)]
G. sesamoides	Dense pubescent[2)]	H-layer[5)]
G. shimuzuana	Sparse pubescent[6,7)]	F- to A-layer[7)]
G. elata	Smooth[2)]	H- to A-layer[8,9)]
G. minor	?	H- to A-layer[10)]
G. tokaraensis	Smooth[3)]	A-layer[3)]
G. cunninghamii	Smooth[11)]	A- to B-layer[11)]
G. javanica	Smooth[2)]	?

( ) indicates the occasional occurrence.

1) From the description and illustration by Burgeff (1932). Burgeff describes, "Es handelt sich um eine echte Laubstreupflanze..... Ein in der Horizentalen abgeplattes, raupenförmiges, stark beharrtes Rhizom trägt den aufrechten Blütenstand", therefore we judge the surface of the rhizome to be covered densely with pubescence and the location to be the F-layer.
2) From the description and illustration by Tuyama (1940).
3) Based upon our observations.
4) From the description and illustration by Maekawa (1971). Maekawa describes that this orchid occurs on the thickly fallen leaves being rich in humus; therefore we judge that the rhizome is located in the H-layer.
5) From the description by Campbell (1964). Campbell describes that the rhizome is lying horizontally amongst the brown and organic layer; therefore we judge the location to be the H-layer.
6) From the description and illustration by Kobayashi & Yukawa (2001).
7) From a personal letter from Kobayashi, one of the authors cited in 6).
8) From the description by Kusano (1911). Kusano describes that *G. elata* is found growing in humus soil.
9) Based upon our observations.
10) From the description by Campbell (1963). Campbell describes that the tubers occur at the base of the organic horizon and are readily excavated from the soil (morainic gravel or sandy clay), therefore we judge the location to be between the H- and A-layer.
11) From the description by Campbell (1962). Campbell describes that occasional hairs grow out from the epidermis of the rhizome and that the rhizome lay in clay soil or in the gravel zone. We therefore judge the surface the rhizome to be smooth and the location to be from the A- to B-layer.

Yukawa, 2001), *G. sesamoides* R.Br (Campbell, 1964), *G. shimuzuana* Tuyama (Kobayashi & Yukawa, 2001), and *G. verrucosa* Blume (Tuyama, 1940)

Discussion

There are great differences between *G. nipponica* and *G. tokaraensis* in many items of morphology and ecology as diagnosed in Table 1. The important observations among the items are: (1) root system and its life span, (2) rhizome system, its life span, and the relationship between its system and the emergence habit, (3) the relationship between the surface of the rhizome and underground location of the rhizome, and (4) plant growth and reproduction. Therefore, we will discuss these points in this order below.

1. Root system and its life span

In general, the root system of the terrestrial green orchids is described as being long-lived and simple (Rasmussen 1995). In this investigation, two terrestrial and mycoparasite orchids, *G. nipponica* and *G. tokaraensis*, contrasted markedly in root system and life span, respectively, as follows.

We confirmed in this investigation that the root system of *G. nipponica* was simple, as described by some taxonomists (e.g. Kitamura *et al.* 1977; Tuyama 1940). Moreover, we recognized that the life span of this orchid root was annual and short-lived, only for two or three seasons, because of the following reasons. The timing and the portion of the root formation in *G. nipponica* is the same as those described by taxonomists (e.g. Kitamura *et al.* 1977; Tuyama 1940), who describe the roots as occurring on the top of the rhizome after flowering. In addition, the roots of *G. nipponica* were not observed on 28th April however they were on 8th May, in this investigation. These facts suggest that new roots are produced from the flowering to the fruiting season and are lost until the next spring, probably from the autumn to the winter. This suggestion was confirmed also by the result that the new roots developed on the embedded rhizomes where there were not any roots before culture. On the other hand, concerning the short lateral roots, since they were not observed on the long roots in May, they may occur later.

In contrast, we discovered that the root system of *G. tokaraensis* is large and complex. Moreover, we obtained the following results in the first investigation in April. Firstly, *G. tokaraensis* already had a large root system while *G. nipponica* had no roots. Secondly, *G. tokaraensis* emerges at least two weeks later than *G. nipponica.* From this, we suggest that the root of *G. tokaraensis* is perennial and can consequently establish a large complex system, which is the first discovery in the *Gastrodia* species from Japan and the neighboring areas.

We can therefore recognize that there are at least two kinds of

root system and life span in the *Gastrodia*, that is, a simple root system and a complex one, and an annual root and a perennial one, except for rootless systems in orchids such as *Gastrodia elata* Blume.

2. Rhizome system, its life span, and the relationship between its system and the emergence habit

As described by Rasmussen (1995), the rhizomes of the terrestrial orchids constitute connecting tissue between the old and young ones, though there are variations in development. Many of the rhizomes disappear when the younger one becomes fully developed in many species. However, the rhizomes of some mycoparasite orchids, such as *Corallorhiza* species, can persist for a long time, more than seven years.

The rhizome of *G. nipponica* is characterized by its monopodial or sympodial system consisting of one or a few rhizomes. The number of the rhizomes in the system suggests that the system is renewed every one, two or three years. It follows from this that the life span of the rhizome of *G. nipponica* is short-lived. There are other species that have the short-lived rhizome system in the species of *Gastrodia.* For example, the tuber of *G. elata* is renewed every year (Kitamura *et al.* 1977; Kusano 1940) and the new tubers of *Gastrodia minor* Petrie spread laterally from the old ones and older ones die away in the autumn (Campbell 1963).

On the other hand, the rhizome of *G. tokaraensis* is characterized by a large rhizome network system consisting of many rhizomes, which indicates the system is long-lived. Consequently, *G. tokaraensis* may be able to establish a large rhizome colony of up to 70 cm or more in diameter. Such a rhizome system as *G. tokaraensis* has been unknown in the species belonging to the section *Codonanthus* from Japan and the surrounding areas. However, Campbell (1962) reported from New Zealand that *Gastrodia cunninghamii* Hook. f. has a similar rhizome system to *G. tokaraensis.* According to Campbell, four flowering stems of this orchid lying on the circumference of a circle 1.2 m in diameter, were attached to the one original rhizome, and new rhizomes arise laterally on any of the old rhizomes and these may in their turn give rise to flowering stems. We think that *G. cunninghamii* establishes the rhizome network system but might take a lot of time to develop up to a circle 1.2 m in diameter.

From a comparison with the results, we conclude that the rhizome system of an orchid reflects the habit of the emergence above ground of the orchid. However, we cannot conclude that there is a relationship between the life span of the root and that of the rhizome, because in spite of having a long-lived rhizome system, *G. cunninghamii* is a rootless orchid.

3. The relationship between the surface of the rhizome and its underground location

Table 2 shows that there are two kinds of rhizome in *Gastrodia* species: one is the pubescent rhizome and another is from the sparse pubescent to the smooth one. Moreover, the underground location of the smooth rhizome is deeper than that of the pubescent one, in many species. Since the air gap becomes narrower and soil moisture increases the deeper you go, the F-layer is probably always considerably dry compared to the A-layer. From this, we propose that there is a close relationship between the surface construction of the rhizome and the underground location of the rhizome, that is, the dry conditions in the soil is an important factor of occurrence of pubescences on *Gastrodia* species. Burgeff (1932) suggests that pubescence on the rhizomes is the important organ for water and water-soluble nutrients absorption through the mycobiont that colonizes inside pubescence and extends mycelia outside. In the case of *Gastrodia* species, mycobionts colonizing pubescences also may fulfill such roles.

4. Plant growth and reproduction

From the two investigations of the growth in the two orchids, it can be stated that the plant of *G. tokaraensis*, from flowering to fruiting, emerges on the forest floor at least two weeks later than that of *G. nipponica.* It has been reported that *G. pubilabiata*, *G. shimizuana*, and *G. verrucosa*, produce 1-7 flowers, but *G. nipponica* produces two flowers in most cases (e.g. Tuyama 1940; Kitamura *et al.* 1977; Kobayashi & Yukawa 2001). However, it has been unknown in those *Gastrodia* species how many plants grow normally and how many normal fruits are produced successfully. It was noteworthy in *G. tokaraensis* that the drastic decrease in the numbers of the individuals and the flowers only for two weeks. We think for the moment that this decrease was caused probably by the undersupply of nutrients through mycobionts and rhizomes, because aboveground plants linked to each other may require a large a mount of nutrients in order to finish flowering to fruiting within a short term, probably only three to four weeks.

In *G. nipponica*, the vegetative organs to produce new individuals have been misunderstood for a long time probably because of its rare emergence. For example, there is a description that the new individuals occur on the long roots developing from the uppermost of the rhizomes (e.g. Satomi 1982). In the present study, it became obvious that the new rhizomes occurred on the old rhizomes in each orchid as described above. This fact leads

to the conclusion that a daughter *G. nipponica* is born from the mother rhizome. This conclusion is naturally applicable to *G. tokaraensis*. Although the buds occurring on roots, which can give rise to new plants, have been observed in many species (e.g. Rasmussen 1995), the products on the long roots of *G. nipponica* may be the short lateral roots where the orchid and a fungus establish the symbiotic association, as described by Kitamura *et al.* (1977).

The two orchids successfully produce normal fruits, and the embryo volume of *G. tokaraensis* is less than half of that of *G. nipponica* (Table 1). According to our unpublished data, the seeds of *G. nipponica* germinated to develop to rhizomes with roots successfully in the absence of mycobionts, while those of *G. tokaraensis* were not observed to germinate. Because the embryos of achlorophyllous orchids contain only minimal nutritional reserves within them (Leake, 1994), difficulty to germinate in *G. tokaraensis* is likely due to its small volume of embryo.

Acknowledgments

We thank Dr. Cha Joo Young, Faculty of Agriculture, Hokkaido University and Dr. S. Kobayashi, Kochi Prefectural Makino Botanical Garden for supplying useful information on the underground location of the rhizomes of *Gastrodia elata* and *G. shimuzuana*, and also Mr. S. Ashihara and Mr. H. Uchihara, Faculty of Agriculture, Kagoshima University, for their kind help in the two investigations on Takeshima.

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無葉緑蘭ハツザキヤツシロランとその近縁種トカラヤツシロランとの特質の比較

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要　旨

無葉緑蘭で菌寄生植物のハルザキヤツシロランとその近縁種トカラヤツシロランの特質について研究を行った。トカラヤツシロランは新種として最近筆者らによって報告された種である。両種とも琉球列島の最北に位置する竹島ではタケ林に生息している。

両種は後述するように形態的にまた生態的に大きく異なっている。ハルザキヤツシロランの顕著な特徴は，発生様式が散生で厚く堆積したタケの落葉上に発生すること，根系は短命で単純システムであること，塊茎は細毛を帯び土壌層のF層に位置し，短命で単軸または仮軸システムを形成することである。トカラヤツシロランの場合は，発生様式は群生で直径70cmほどのコロニーを作りタケ林内を通じる歩道脇などの開けたところや裸地上に発生すること，根系は永年生の複雑なシステムを形成すること，塊茎は無毛で土壌層位のA層に位置し，永年生でネットワーク状の塊茎システムを作り直径70cmほどのコロニーとなることである。さらに，トカラヤツシロランの胚の大きさは容積にしてハルザキヤツシロランの半分以下である。また，トカラヤツシロランではわずか2週間の間に個体数も花数も劇的に減少することが観察された。

両者の類似性は以下の通りである。両種とも4月中旬から5月下旬にかけて開花・結実する。しかし，ハルザキヤツシロランの方がトカラヤツシロランより少なくとも2週間は発生が早い。また，両者とも塊茎によって栄養繁殖を行うことが出来る。

地上での発生様式は地下の塊茎組織の存在様式を反映したものと思われる。また，塊茎表面と塊茎が存在する土壌層との間には密接な関係があるものと思われる。

キーワード：ハルザキヤツシロラン，トカラヤツシロラン，塊茎，塊茎システム，根系