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Lecanorchis moritae (Orchidaceae, Vanilloideae), a new mycoheterotrophic species from Amami-Oshima Island, Japan, based on morphological and molecular data

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Abstract

A new species of the mycoheterotrophic genus *Lecanorchis* Blume (Orchidaceae), *L. moritae,* is described from Amami-Oshima Island, Japan. It is most similar to *L. suginoana* but differs in having a transversely elliptic (slightly contracted at base) midlobe (vs. semiorbicular, not contracted at base), more triangular with almost entire margins (vs. relatively rounded, denticulate margins) and reddish apices (vs. somewhat whitish apices) and a lip with white and purple hairs (vs. white and lemon yellow hairs) and sparse unicellular papillae scattered on the disc (vs. dense unicellular papillae). An illustration and nuclear ribosomal internal transcribed spacer (nrITS) sequence (i.e., DNA barcode) of the new species are also provided.

Keywords: DNA barcodes, Japanese flora, holomycoheterotrophic plants, nrITS, new orchid species, Ryukyu Islands, vanilloid orchids

Introduction

The mycoheterotrophic orchid genus *Lecanorchis* Blume (1856: 188) comprises ca. 30 species that are widely distributed, with endemic taxa reported from many regions of Southeast and Eastern Asia (Seidenfaden 1978, Lin 1987, Hashimoto 1989, 1990, Pearce & Cribb 1999, Szlachetko & Mytnik 2000, Pridgeon *et al.* 2003, Averyanov 2005, 2011 2013, Suddee & Pedersen 2011, Suetsugu & Fukunaga 2016, Suetsugu *et al.* 2018a,c). The genus can be distinguished from other orchid genera by its numerous long, thick, horizontal roots that extend from a short rhizome, a cup-like structure (i.e., calyculus, found in many vanilloid genera) located between the base of the perianth and apex of the ovary and an elongate column with a small lateral, apical wings (Seidenfaden 1978, Hashimoto 1990). However, precise identification of *Lecanorchis* species is often hindered by their overall morphological similarity and brief flowering periods (Suetsugu *et al.* 2016, Suetsugu *et al.* 2017a, Suetsugu *et al.* 2017b, Suetsugu *et al.* 2018b,d,e) and in herbarium specimens by absence of important diagnostic characters; *Lecanorchis* flowers in herbarium material are easily lost or damaged during preservation (Suetsugu *et al.* 2016, Suetsugu *et al.* 2017a,b, Suetsugu *et al.* 2018d, Suetsugu *et al.* 2018e).

Due to the difficulty of identifying *Lecanorchis* specimens, species diversity of the genus is likely to have been underestimated (Suetsugu *et al.* 2016, Suetsugu *et al.* 2018d). Because Japan is known for its great diversity of *Lecanorchis*, harboring ca. 10 species, it is likely that further investigations there could provide more precise data regarding diversity and distribution of the genus. Of particular interest are Ryukyu Islands, which are known to be a hotspot for many endemic mycoheterotrophic plants (e.g. Suetsugu 2017, Suetsugu & Nishioka 2017). During a recent botanical survey on Amami-Oshima Island, in the central Ryukyus, Japan, Hidekazu Morita, a local naturalist, discovered flowering plants of an unknown *Lecanorchis* species. Morita originally considered it an intraspecific variant of *L. suginoana* (Tuyama 1982: 211) Serizawa (2005: 38) or a hybrid between *L. suginoana* and *L. kiusiana* Tuyama (1955: 182). Believing them to be deserving of further study, Morita forwarded samples of these plants to the first author for inclusion in an ongoing systematic revision of the genus that incorporates molecular data. Although the samples were morphologically similar to *L. suginoana*, we found the unknown plants to be genetically fully differentiated from *L. suginoana.* After careful consideration, we concluded that the morphological data also support

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its recognition as a new species. Here we provide a description, illustration, and nuclear ribosomal internal transcribed spacer (nrITS) DNA sequence of the new species.

Materials and Methods

Morphological observation

The morphology of *L. moritae* and previously described *Lecanorchis* species was compared by reviewing the literature, conducting field sampling, and examining both digitized plant specimens from online databases such as JSTOR Global Plants (http://plants.jstor.org/) and specimens from multiple herbaria (KAG, KANA, KPM, KYO, MBK, NTUF, OSA, TAI, TAIF, TI, and TNS; abbreviations follow *Index herbariorum*; Thiers 2017, http://sweetgum.nybg.org/science/ih/).

DNA barcoding

Flowers were collected from *L. moritae* and its putative close relatives, *L. suginoana*, *L. kiusiana*, *L. ohwii* Masamune (1933: 208) and *L. japonica* Blume (1856: 188) and dried in the field using silica gel (Table 1). DNA was then isolated using the CTAB method, and the nuclear ribosomal spacer region (nrITS) was amplified in a 2720 Thermal Cycler (Applied Biosystems, USA) using 20 μL reaction mixtures that contained 2 μL extracted DNA, 10 μL SapphireAmp Fast PCR Master Mix (Takara Bio, Japan), 0.2 μM of each primer (AB101 and AB102; Sun *et al.* 1994), under the following conditions: initial denaturation at 94 °C for 1 min; 30 cycles of 98 °C for 5 s, 55 °C for 5 s, and 72 °C for 15 s; final elongation at 72 °C for 7 min. Finally, the amplified PCR products were purified using EconoSpin columns (Gene Design, Inc., Japan) and sent to Eurofins Genomics (Ebersberg, Germany) to be sequenced using the same primers used for amplification.

The sequence alignment was performed using the neighbor-joining (NJ) method in ClustalW, and the tree was built using MEGAX (Kumar *et al.* 2018). The reliability of each node was assessed using bootstrap analysis (1000 replicates). *Lecanorchis nigricans* (LC315676) was included as the outgroup based on Suetsugu *et al.* (2018d).

TABLE 1. *Lecanorchis* species included in the molecular analysis conducted for the present paper.

Taxon	Location	Collection date	Collection number	GeneBank numbers
L. moritae	JAPAN. Kagoshima Pref., Amami Island	20180510	*H. Morita SL12-01* (KYO)	LC457485
L. moritae	JAPAN. Kagoshima Pref., Amami Island	20180513	*H. Morita N17-01* (TNS)	LC457486
L. moritae	JAPAN. Kagoshima Pref., Amami Island	20180519	*H. Morita N17-17* (KYO)	LC457487
L. japonica	JAPAN. Kagoshima Pref., Amami Island	20180421	*H. Morita M24-003-KS258* (KYO)	LC457488
L. japonica	JAPAN. Kagoshima Pref., Amami Island	20180423	*H. Morita Y13-16-KS259* (KYO)	LC457489
L. japonica	JAPAN. Kumamoto Pref., Chuo-ku, Kurokami-cho	20180521	*A. Kinoshita KS263* (TNS)	LC457490
L. japonica	JAPAN. Osaka Pref., Minamikawachi-gun, Chihayaakasaka Village	20180613	*I. Yamazumi Azumazaka-No.12-KS297* (TNS)	LC457491
L. suginoana	JAPAN. Shiga Pref., Higashiomi City	20160602	*S. Mori s.n.* (KYO)	LC457492
L. suginoana	JAPAN. Niigata Pref., Shibata City	20181011	*R. Fujita KS291-1* (TNS)	LC457493
L. suginoana	JAPAN. Niigata Pref., Shibata City	20181011	*R. Fujita KS291-2* (TNS)	LC457494
L. kiusiana	JAPAN. Kyoto Pref., Kyoutanabe City	20160523	*S. Mitsuta s.n.* (KYO)	LC457495
L. kiusiana	JAPAN. Kagoshima Pref., Yakushima Island, Miyanoura	20160719	*K. Suetsugu s.n.* (KYO)	LC457496
L. kiusiana	JAPAN. Osaka Pref., Kawacinagano City, Teramoto	20180613	*I. Yamazumi Teramoto-No.22-KS295* (TNS)	LC457497
L. ohwii	TAIWAN. New Taipei City, Pinglin	20180413	*T. C. Hsu 10442* (TAIF)	LC457498
L. ohwii	TAIWAN. New Taipei City, Wulai	20180408	*T. C. Hsu 10402* (TAIF)	LC457499
L. ohwii	TAIWAN. Pingtung Co., Shihzi	20050226	*T. C. Hsu 303* (TAIF)	LC457500

Taxonomic Treatment

Lecanorchis moritae Suetsugu & T.C.Hsu, *sp. nov.* (Figs. 1,2).

Type:—JAPAN. Ryukyu Islands: Kagoshima Pref., Amami-Oshima Island, Amami City, Naze, 13 May 2018, *Morita N17-01* (holotype: TNS!, a flower in the spirit collection).

Lecanorchis moritae is closely related and morphologically similar to *L. suginoana*, but differs from the latter in having a transversely elliptic lip midlobe, more triangular, entire margins of the side lobes with reddish apices, white and purple hairs on the lip and sparse unicellular papilla scattered on disc.

Terrestrial, mycoheterotrophic herbs. Roots not seen. Stem erect, 15 cm tall, yellowish brown to purplish brown, 1.5 mm in diam., unbranched with several thin, scale-like sheaths along stem. Rachis 1.0–3.0 cm long, with 5 or less densely arranged flowers. Floral bracts triangular, 3.0–5.0 mm long, apex acute, glabrous. Pedicellate ovary ascending at an acute angle, slightly contorted, inflexed, 17–26 mm long, with a ring-like excrescence below the calyculus; calyculus ca. 1.5 mm high, margin erose-denticulate. Flowers rarely fully opened, facing slightly upwards, brownish yellow to olive-brown except for lip. Dorsal sepal oblanceolate, obtuse, 15.0 × 3.2 mm. Lateral sepals obliquely oblanceolate, subacute, 15.0 × 3.5 mm. Petals obliquely oblanceolate, obtuse, 15.0 × 4.4 mm, slightly reflexed near apex. Lip trilobed, basally adnate for 2/5–1/2 of column length, 15.5 × 7.8 mm when spread out; distal 1/3 of the disc hairy; hairs white or purple, multicellular, ribbon-like, more or less branched in the distal portion, ca. 1 mm long, with scattered unicellular branchlets; posterior portion of the disc except for the base microscopically papillose; side lobes exceeding the column, about 1.5 mm high, triangular and almost entire margin or entire with 1–2 serrations on the distal margins when flattened; midlobe transversely elliptic, slightly contracted at base with an irregularly erose-dentate or erose-undulate and papillate margin, 4.6 × 4.0 mm in natural position, 4.6 × 6.2 mm when spread out. Column 10 mm long, with apical wings; wings with an incision. Anther white, 1.5 mm wide with a depression above, ventrally more or less papillose, pubescent near the slits.

[The measurements above were based on the two populations of this species known thus far and may not be entirely representative of the diversity present in the species when more specimens are found in the future.]

Distribution, phenology and conservation status:—To date, the distribution of *Lecanorchis moritae* appears to be restricted to two localities separated by ca. 13 km. Both populations grow under humid evergreen broadleaf forest dominated by *Castanopsis sieboldii* (Makino 1910: 232) Hatusima (1971: 223; Fagaceae). Each population contains less than ten flowering plants, and currently we are not aware of any other locality where this species exists. Therefore, *L. moritae* should be assigned a risk of extinction of "critically endangered" [CR D1] following the categories of IUCN (2012).

Etymology:—Named for Hirokazu Morita, who collected the type specimens.

Additional specimens examined:—JAPAN. Ryukyu Islands, Kagoshima Pref., Amami-Oshima Island, Amami City, Naze, 19 May 2018, *Morita N17-17* (KYO, a flower in the spirit collection); Ryukyu Islands, Kagoshima Pref., Amami-Oshima Island, Uken Village, 10 May 2018, *Morita SL12-01* (KYO, a flower in the spirit collection).

Taxonomic notes:—*Lecanorchis moritae* is morphologically similar to a group of species including *L. kiusiana*, *L. ohwii* and *L. suginoana* endemic to East Asia; they share two unique characters, i.e. a ring-like excrescence below the calyculus and hairs on disc and midlobe of lip with minute, unicellular papillae on their surfaces (Tuyama 1982, Serizawa 2005). However, *L. moritae* clearly differs from *L. kiusiana* and *L. ohwii* because the midlobe in *L. ohwii* is recurved, and that of *L. moritae* is not. In this respect, *L. moritae* is most similar to *L. suginoana* because of the general similarities in not only gross but also floral morphology. Nonetheless, *L. moritae* can still be distinguished from *L. suginoana* by its transversely elliptic (slightly contracted at base) lip midlobe (vs. semiorbicular, not contracted at base, lip midlobe), more triangular and entire margin of sidelobes (vs. relatively rounded, and denticulate margin of sidelobes), reddish apex of lip sidelobes (vs. somewhat whitish apex of lip sidelobes), white and purple hairs (vs. white and lemon yellow hairs) on the lip and sparse unicellular papillae scattering on lip disc (vs. dense unicellular papillae scattering on lip disc).

It should be noted that *L. moritae* is somewhat similar to the specimens recorded as *L. javanica* from several localities (Comber 1990, O'Byrne & Vermeulen 2002, Suddee *et al.* 2010, Ong 2018). The taxonomic identity of *L. javanica* has remained problematic, mainly due to incompleteness of the original description and poor condition of type specimen. The protologue of *L. javanica* by Blume (1856) is brief and vague: "labello gynostemium inferne amplectente, limbo subimherbi" and cannot be used to distinguish among specimens. Fortunately, we can understand the taxonomic concept that Blume referred to as *L. javanica* thanks to the description and line drawing later published by him (Blume 1858), which includes enough details to identify specimens. This material indicates that the lip is simple,

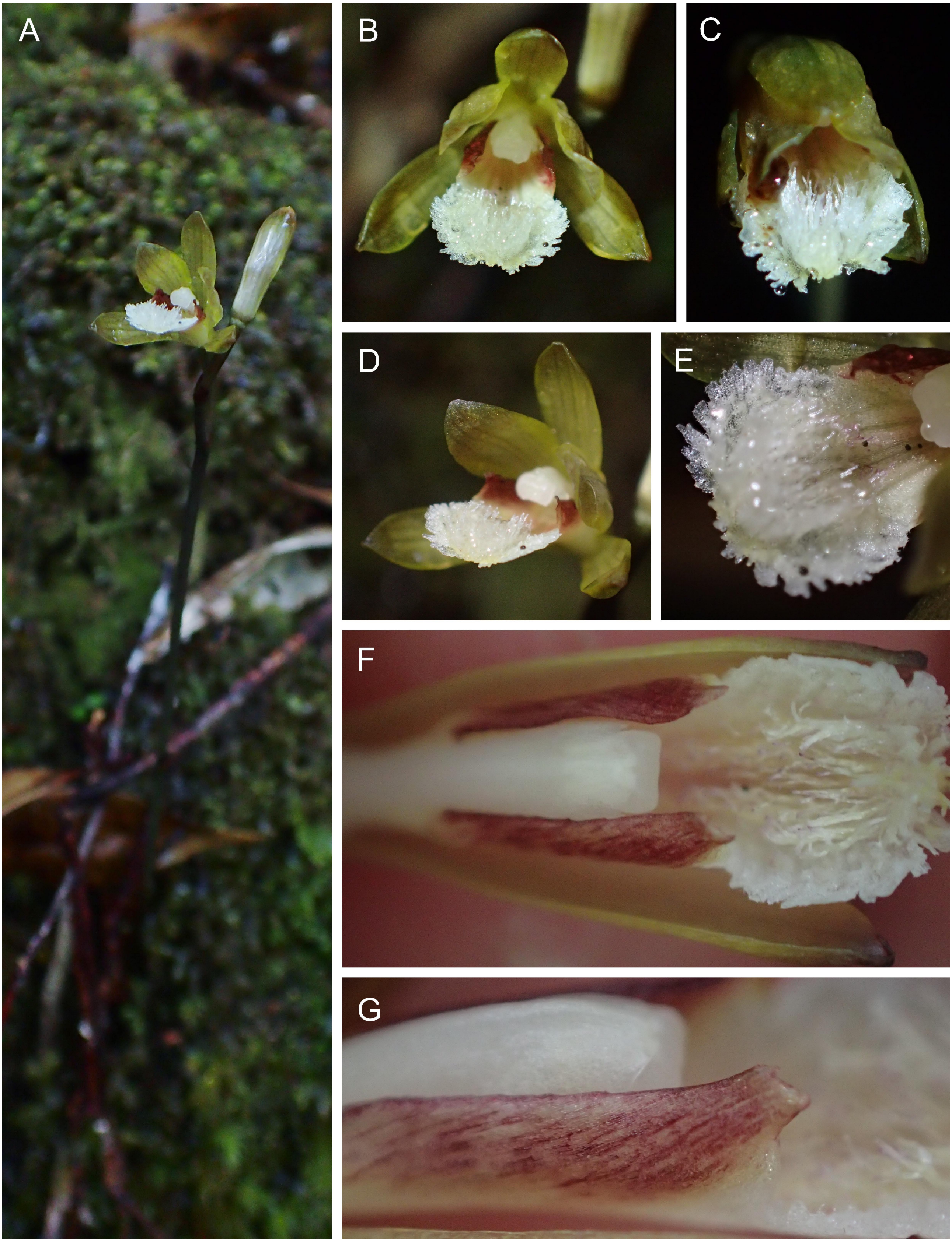

FIGURE 1. *Lecanorchis moritae* from the type locality. A. Flowering plant. B–D. Flower. E. Free portion of midlobe of the lip. F. Lip, column and lateral sepals. G. Close-up of side lobe of the lip and column. Photography by Hidekazu Morita.

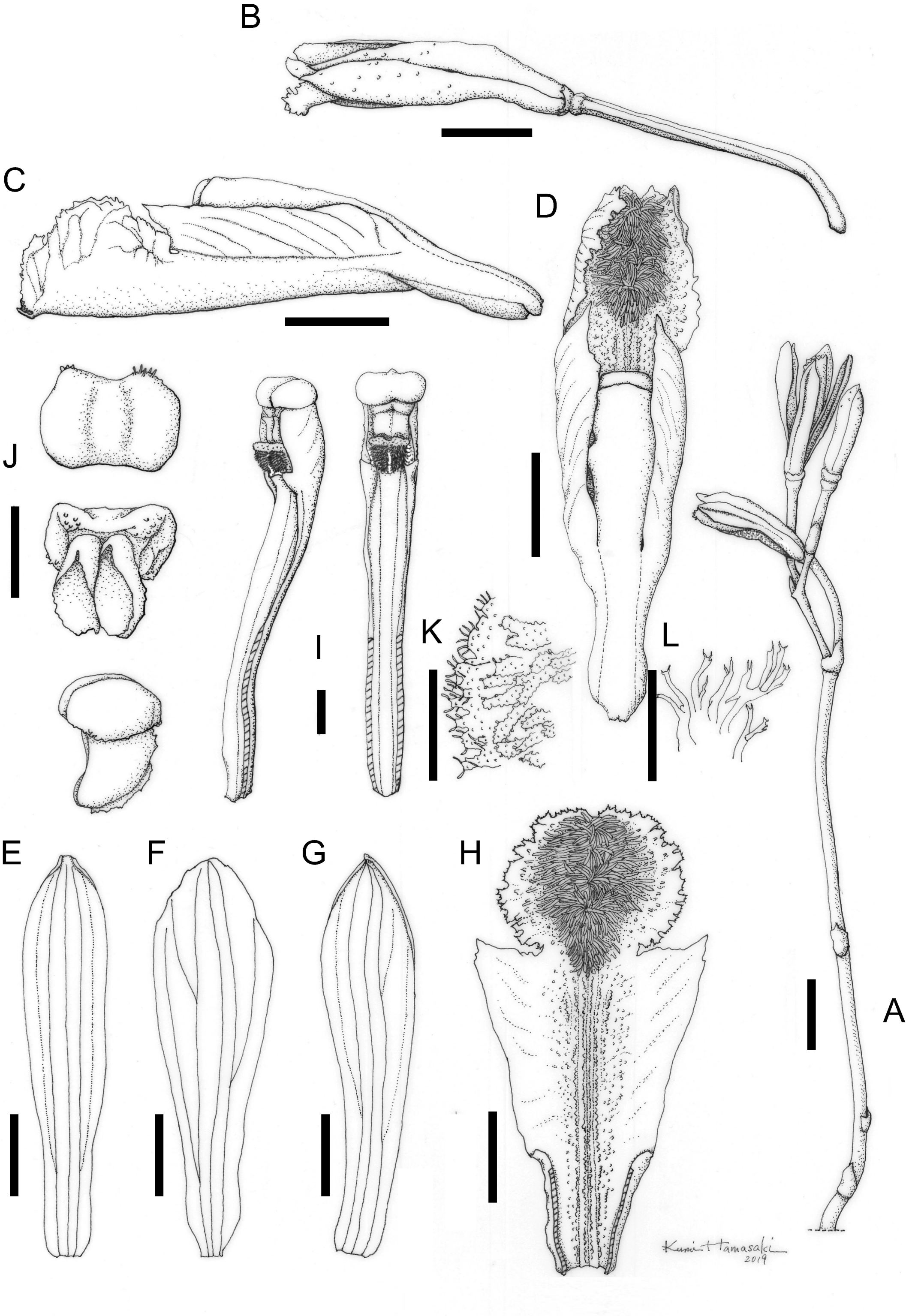

FIGURE 2. *Lecanorchis moritae* (drawn from the holotype). A. Habit. B. Flower and pedicellate ovary. C–D. Lip and column. E. Dorsal sepal. F. Lateral petal. G. Lateral sepal. H. Flattened lip. I. Column. J. Anther cap. K. Adaxial hairs on apical part of midlobe of the lip, showing the papillate apices. L. Adaxial hairs on central part of midlobe of the lip. A–B. Bar = 1 cm. C–H. Bar = 3 mm. I–L. Bar = 1 mm. Drawing by Kumi Hamasaki.

unlobed and sparsely hairy and slightly adnate to the column, suggesting that the specimen shows little differentiation between the lip and tepals, a condition termed peloria (Rudall & Bateman 2002). Most later studies considered *L. javanica* as at least a somewhat peloric form (Smith 1909, 1910, Ames 1911, Comber 1990). For example, Smith (1910) considered that *L. triloba* Smith (1908: 26) should be added to the synonymy of *L. javanica* on the assumption that a peloric form of *L. triloba* must have been described as *L. javanica* by Blume (1856). If Smith (1910) is correct, at species rank, *L. javanica* should have priority over *L. subpelorica* Hsu & Chung (2010: 363), *L. latens* Lin & Lin (2011: 315) and *L. bihuensis* Lin & Wu (2012: 381), which are all peloric forms of *L. triloba* with different degrees of peloria: *L. subpelorica* has a trilobed lip with a sparsely hairy disc; *L. latens* has a trilobed lip with glabrous disc, and; *L. bihuensis* has an entire and glabrous lip (Hsu & Chung 2010, Lin & Lin 2011, Lin & Wu 2012). We also considered *L. betongensis* Suddee & Pedersen (2011: 37) to be a peloric form of *L. triloba*, with a similar condition to that of *L. subpelorica.* Considering that the holotype of *L. javanica* has a lip with small sidelobes and slightly hairy disc (Ong 2018) and subpeloric "*L. triloba*" is widespread (Hsu & Chung 2010, Suddee & Pedersen 2011), *L. javanica sensu* Blume (1856) may be identical with *L. subpelorica* and *L. betongensis*.

Since peloric mutants are often treated as an intraspecific variant (Rudall & Bateman 2002), not only Smith (1910) but also Comber (1990) considered the normal condition should be considered *L. javanica.* However, the normal state of *L. javanica sensu* Comber (1990) without a pair of calli on the disc of lip is completely different from *L. triloba* with a pair of calli on the disc of lip (Smith 1908). It will be somewhat difficult to precisely understand the normal condition of *L. javanica* since the type at Leiden is in poor condition (Ames 1911). Therefore, given that the distant location and lack of detailed morphological data for *L. javanica sensu* Blume (1856), we considered it acceptable to describe the *Lecanorchis* from Amami-Ohshima not as just a new locality for *L. javanica* but rather as a new species.

In addition, *L. moritae* is morphologically similar to *L. pauciflora* Smith (1918: 26), judging from gross floral morphology (Smith 1918, Smith 1922, O'Byrne & Vermeulen 2002, Ong 2018). Although Comber (1990) reduced *L. pauciflora* to synonymy under *L. javanica*, it is possible that *L. javanica sensu* Blume (1856) is different from *L. pauciflora* due to the reasons mentioned above. If not *L. javanica* but rather *L. pauciflora* is conspecific with *L. moritae*, *L. pauciflora* has priority over *L. moritae.* However, it would still be difficult to confirm whether *L. moritae* and *L. pauciflora* are conspecific because the key character of *L. moritae,* scattered papillae on the lip hairs, has not been reported in *L. pauciflora*. In addition, even if scattered papillae on the lip hairs can be detected, it is difficult to judge whether it is synonymous with *L. moritae*, *L. suginoana*, *L. kiusiana* or *L. ohwi* due to the minimal description and old type specimen. Since there are still too few reliable data to clarify the situation for *L. pauciflora*, we could not judge whether these two names should be considered synonyms.

Phylogenetic relationships:—Although Hidekazu Morita originally considered the morphologiy of *L. moritae* to be just an intraspecific variant of *L. suginoana* or a hybrid between *L. suginoana* and *L. kiusiana*, the molecular results indicate an independent specific status for *L. moritae. Lecanorchis moritae* is morphologically similar to *L. suginoana, L. kiusiana* and *L. ohwii.* Molecular results confirmed their close relationships since *L. moritae* seems to be sister to these three species (Fig. 3). However, *L. moritae* is genetically fully differentiated from these species. The molecular divergence between *L. moritae* and other three species (five substitutions) is greater than the molecular divergence among *L. suginoana, L. kiusiana* and *L. ohwii* (zero to two substitutions). Therefore, both morphological (see above) and molecular data are consistent with treating *L. moritae* as distinct species.

In addition, our molecular analysis provides some insight into identities of closely related species. *Lecanorchis suginoana* was first described as the variety of *L. japonica* (Tuyama 1982), whereas Hashimoto (1990) considered it as a variety of *L. kiusiana* due to the similarity of general lip morphology and scattered papillae on the lip. In addition, Serizawa (2015) treated it as independent species based on its distinct column morphology, whereas Serizawa (2005) also considered *L. suginoana* as closer to *L. kiusiana* than *L. japonica*. Indeed, the apex of the column in *L. kiusiana* is significantly trifid due to partially free column wings and clinandrium (Tuyama 1955), whereas the apex of the column in *L. suginoana* is truncate or obscurely trifid. We observed two unique substitutions in the ITS sequence of *L. suginoana*, whereas there is often no genetic divergence in this marker within intraspecific varieties, in spite of their stable morphological characteristics (Suetsugu *et al.* 2018d). This is consistent with independent specific status for both species. Furthermore, we showed greater molecular divergence (six substitutions) between *L. japonica* and *L. suginoana,* confirming that *L. suginoana* is likely more closely related to *L. kiusiana.*

Unexpectedly, we did not detect any molecular divergence between *L. kiusiana* and *L. ohwii.* Recent studies have usually concluded that morphological differences support the independent specific status of *L. ohwii* (Lin *et al.* 2016, Suetsugu *et al.* 2017a), considering that there are distinct differences between its putative closest relative *L. kiusiana* in lip and column morphology that are diagnostic characters for *Lecanorchis* species delimitation. In contrast, *L. ohwiii* has sometimes been considered a variety or a synonym of *L. kiusiana* (Chung 2008, Hsu & Chung 2016) or of

L. japonica (Su 2000, Chen *et al.* 2009). *Lecanorchis ohwii* has priority over *L. kiusiana* if *L. kiusiana* and *L. ohwii* truly represents intraspecific variants. Therefore, although *L. kiusiana* var. *albida* Lin (1987: 147) Hsu (2016: 100) was proposed as substitute name for *L. ohwii*, a new combination is needed for *L. kiusiana* if treated as an intraspecific variant. Further study will be needed to determine if *L. kiusiana* and *L. ohwii* should be treated as synonyms.

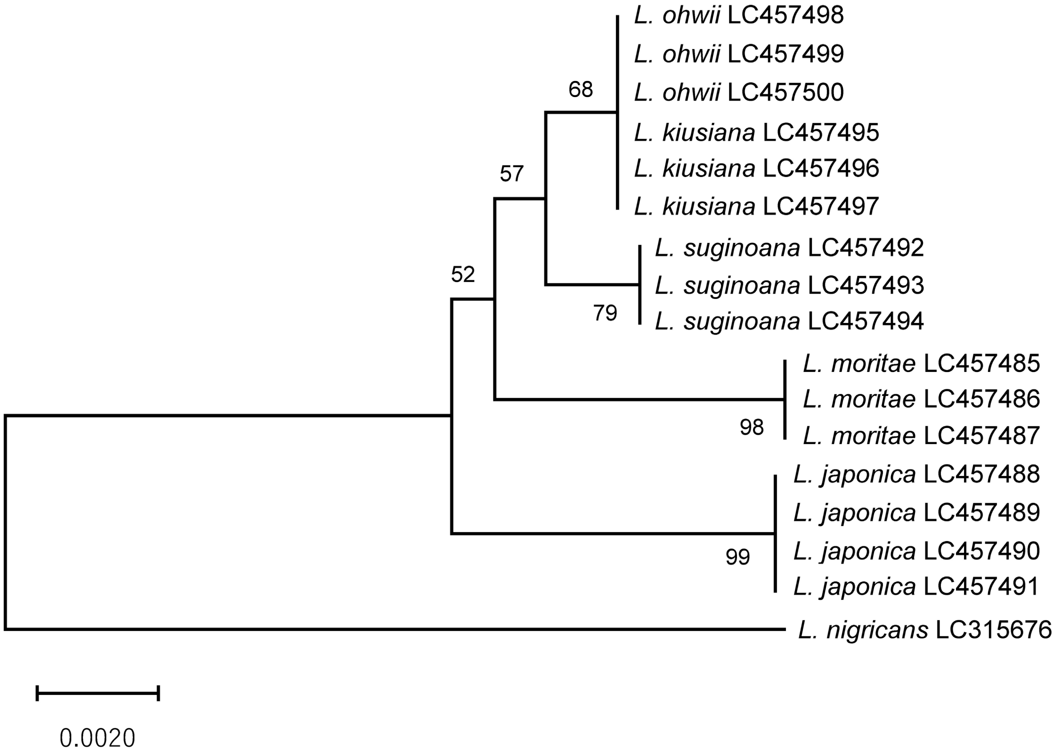

FIGURE 3. NJ tree for *Lecanorchis* based on nrITS sequences. Numbers above branches are bootstrap percentages from 1000 bootstrap replicates. Numbers above the branches represent bootstrap percentages ≥50.

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