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A new species of succulent plants from the Muko-jima group of the Bonin Islands, Japan: *Sedum mukojimense* (Crassulaceae)

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Abstract

A taxonomic re-examination of *Sedum boninense*, which is endemic to the Muko-jima and Chichi-jima groups of the Bonin Islands, Japan, was carried out. Morphological and physiological comparisons revealed differences between plants from the Muko-jima and Chichi-jima groups in the shape and size of leaves and underground bulb scale leaves, plant habit, habitat and flowering season. Molecular phylogenetic analysis using the ITS region revealed that the plants from respective island groups formed sister clades. Therefore, the plant from Muko-jima group is described as a new species of *S. mukojimense*.

Keywords: Bulbs, East Asia, Eudicots, Evolution, Oceanic island, Stone crop

Introduction

The genus *Sedum* Linnaeus (1753: 430) is the largest genus in the family Crassulaceae, comprising approximately 420 species, distributed mainly in the Mediterranean Sea, Central America, the Himalayas, and East Asia (Stephenson 1994, Thiede & Eggl 2007). The genus *Sedum* generally prefers bright, arid environments and comprises herbs with succulent leaves and stems (Stephenson 1994). A previous phylogenetic study reported that *Sedum* is polyphyletic within its seven American genera (Carrillo-Reyes *et al.* 2009), whereas Eurasian *Sedum* members form a monophyletic or paraphyletic group (Mayuzumi & Ohba 2004, Carrillo-Reyes *et al.* 2009, Nikulin *et al.* 2016).

The Bonin (Ogasawara) Islands are located in the northwestern Pacific Ocean, approximately 1,000 km south of the Japanese archipelago; they were designated as a United Nations Educational, Scientific and Cultural Organization (UNESCO) Natural World Heritage Site in 2011. The Bonin Islands consist of approximately 30 small islands, divided into the Muko-jima, Chichi-jima, and Haha-jima groups, from north to south (Fig. 1). The Bonin Islands formed during the Paleocene and appeared above sea level before the middle Pleistocene (Kaizuka 1977, Imaizumi & Tamura 1984). Due to the relatively long history of these islands, endemism is high among vascular plants of the Bonin Islands, at approximately 43%, which is almost equal to the rate for plants of the Galapagos Islands (Porter 1978, Ito 1998). Most of these endemic species originated from the surrounding regions, including Southeast Asia, Taiwan, mainland Japan, the Ryukyu Archipelago, and Polynesia (Yamazaki 1981, Shimizu 1991).

Only one native *Sedum* species, *S. boninense* Yamam. ex Tuyama (1936: 428), is distributed in the Bonin Islands. This species is a perennial herb that occurs sparsely on barren rocks along hilltops and has unusual morphological and physiological features compared with other *Sedum* species, such as summer dormancy and the formation of underground bulbs (Ohba 2001). *Sedum boninense* is currently thought to be endemic to the Muko-jima and Chichi-jima island groups (Tuyama 1936, Ohba 2001) and is treated as a threatened species (EN) in Japan due to its scarcity and limited occurrence (Japanese Ministry of the Environment 2019). *Sedum boninense* was described as an independent species based on a type specimen collected from Chichi-jima Island (Tuyama 1936) but has since been treated as *S. japonicum*

Siebold ex Miquel (1866: 156) subsp. *boninense* (Yamam. ex Tuyama) Ohba (2003: 300). However, the findings from a comprehensive molecular phylogenetic study using East Asian section *Sedum* species (Ito *et al.* 2017, 2018) suggested that *S. boninense* is an independent species, which was in agreement with Tuyama (1936). Furthermore, *S. boninense* was deemed to be sister to *S. uniflorum* Hooker & Arnott (1838: 263), which is endemic to the Ryukyu Archipelago of Japan (Ito *et al.* 2017, 2018).

The Muko-jima group mainly comprises the uninhabited Kitano-shima, Muko-jima, Nakoudo-jima, and Yome-shima Islands, which are located approximately 70 km north of the Chichi-jima group (Fig. 1). Islands of the Muko-jima group are normally inaccessible and therefore well protected. In 2019, the Tokyo Metropolitan Government conducted wildlife conservation field surveys on the Muko-jima islands; during this survey, the second author of the present study collected plants treated as *S. boninense*, but with a non-typical morphology, from the Muko-jima islands. In this study, we conducted morphological and physiological comparisons in living materials and performed molecular phylogenetic analyses to clarify the taxonomic status of these plants.

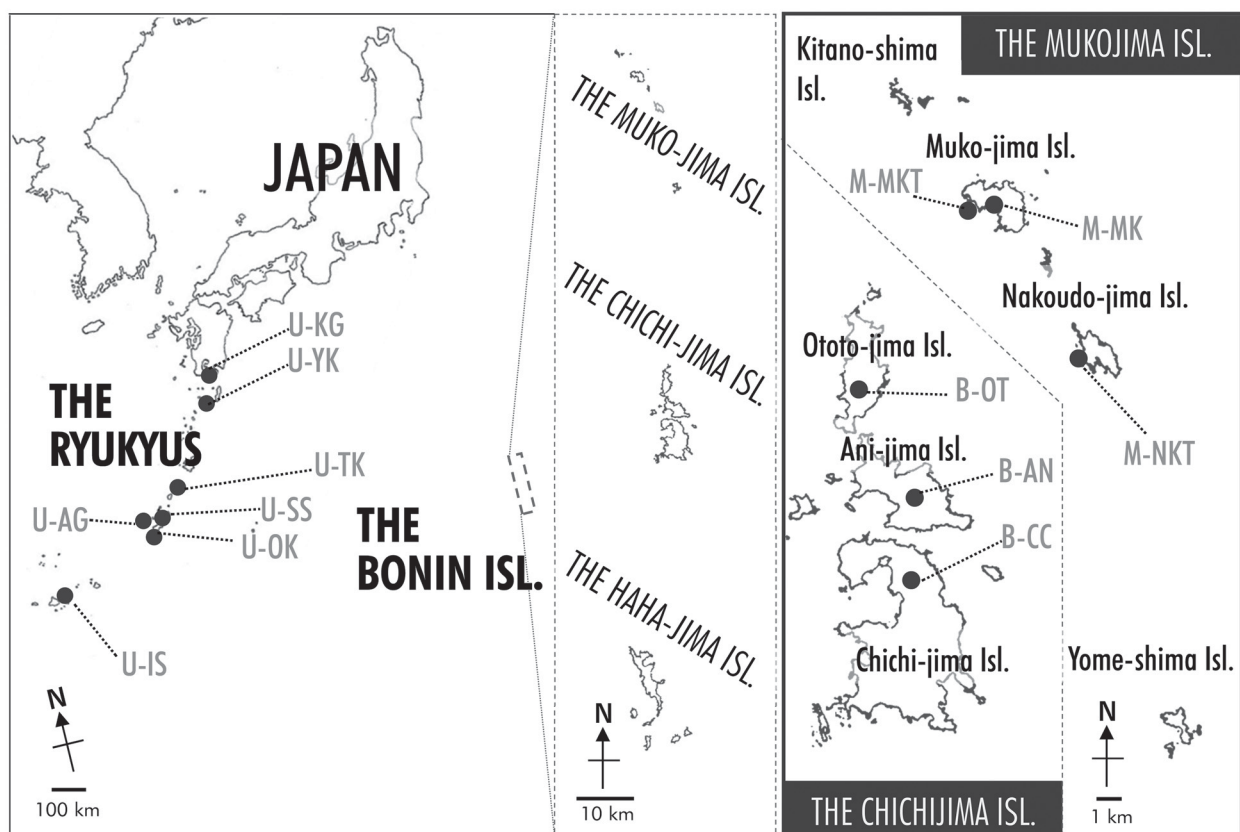


FIGURE 1. Map showing the location of the Muko-jima Group and the adjacent area. (see Tables 1 for abbreviations for collection localities).

Material and methods

Plants materials

For morphological and physiological comparison, we conducted a comprehensive field survey and sampling of *S. boninense* including type locality, and *S. uniflorum* in the Ryukyus and the Bonin Islands shown in Fig. 1. Additionally we used plants of *S. boninense* and *S. uniflorum* cultivated in Tsukuba Botanical Garden and Botanical Garden of University of Tokyo (Koishikawa Botanical Garden) besides the above-mentioned samples, and also herbarium specimens deposited in herbaria of Kagoshima University Museum (KAG), The University Museum, The University of Tokyo (TI) and National Museum of Nature and Science (TNS).

For molecular phylogenetic analysis, 10 accessions of *S. boninense* including the Muko-jima group populations collected by the second author from Muko-jima, Muko-jima-tori-shima, Nakoudo-jima-tori-shima Island and also four

accessions of *S. uniflorum* from the Kyushu and the Ryukyus were used (Table 1). For molecular study, we additionally included internal transcribed spacer (ITS) sequences one *S. boninense* accession and five *S. uniflorum* accessions in the samples, which were reported in recent molecular studies by Ito *et al.* (2018)(Table 1). In total, 20 operational taxonomic units (OTUs) were included in our molecular phylogenetic analysis (Table 1). Voucher specimens for the materials were deposited in the TNS herbarium for the analyses.

TABLE 1. List of plant material collected *Sedum* taxa for sequencing in the present study and ITS sequences of *Sedum* registered in the DDBJ/ENA/NCBI database with their respective locality, abbreviation, voucher and DDBJ Accession number.

Taxon	Source locality	Abbreviation*	Voucher (herbarium)	Accession no.**	
<i>S. boninense</i> Yamam. ex Tuyama	Japan: Tokyo, the Chichi-jima Isl. Ani-jima Isl.	B-AN1	<i>T. Ito 5625</i> (TNS)	LC530815	
		B-AN2	<i>T. Ito 5626</i> (TNS)	LC530816	
		B-AN3	<i>T. Ito 5627</i> (TNS)	LC530817	
	Japan: Tokyo, the Chichi-jima Isl. Chichi-jima Isl.	B-CC1	<i>T. Ito 2371</i> (TNS)	LC2292423 ¹	
		B-CC2	<i>T. Ito 2372</i> (TNS)	LC530818	
		B-CC3	<i>T. Ito 3924</i> (TNS)	LC530819	
		B-CC4	<i>T. Ito 5628</i> (TNS)	LC530820	
	Japan: Tokyo, the Chichi-jima Isl. Ototo-jima Isl.	B-OT	<i>T. Ito 5708</i> (TNS)	LC530821	
	Japan: Tokyo, the Muko-jima Isl. Muko-jima Isl.	M-MK	<i>T. Ito 5704</i> (TNS)	LC530822	
	Japan: Tokyo, the Muko-jima Isl. Muko-jima-tori-shima Isl.	M-MKT	<i>T. Ito 5706</i> (TNS)	LC530823	
	Japan: Tokyo, the Muko-jima Isl. Nakoudo-jima-tori-shima Isl.	M-NKT	<i>T. Ito 5707</i> (TNS)	LC530824	
	<i>S. uniflorum</i> Hook. & Arn.	Japan: Kyushu, Kagoshima	U-KG1	<i>T. Ito 3244</i> (TNS)	LC530829 ²
			U-KG2	<i>T. Ito 3483</i> (TNS)	LC530830 ²
Japan: Ryukyu, Kagoshima, Toku-no-shima Isl.		U-TK	<i>T. Ito 962</i> (TNS)	LC530825	
Japan: Ryukyu, Kagoshima, Yaku-shima Isl.		U-YK	<i>T. Ito 2639</i> (TNS)	LC530831 ²	
Japan: Ryukyu, Okinawa, Aguni Isl.		U-AG	<i>T. Ito 2531</i> (TNS)	LC530826	
Japan: Ryukyu, Okinawa, Ishigaki Isl.		U-IS	<i>T. Ito 5453</i> (TNS)	LC53082	
Japan: Ryukyu, Okinawa, Okinawa Isl.		U-OK1	<i>T. Ito 447</i> (TNS)	LC2292412 ¹	
		U-OK2	<i>T. Ito 861</i> (TNS)	LC530828	
Japan: Ryukyu, Okinawa, Sesoko Isl.		U-SS	<i>T. Ito 3856</i> (TNS)	LC530832 ²	

*Abbreviation are used for Figs. 1 & 4.

**Reported by ¹Ito *et al.* (2017) and ² Ito *et al.* (2018).

DNA extraction, amplification, and sequencing

DNA was extracted from dried leaves using a DNeasy Kit (QIAGEN, Valencia, CA, USA) following the manufacturer's protocol. The ITS region (ITS1, 5.8S rDNA, and ITS2) was amplified by polymerase chain reaction (PCR) amplification with an iCycler (Bio-Rad, Hercules, CA, USA) using the forward primer ITS1 and the reverse primer ITS4 (White *et al.* 1990). Amplifications were performed using EmeraldAmp PCR Master Mix dye (Takara, Otsu, Japan). After an initial 3 min denaturing at 94°C, the PCR profile comprised 35 cycles of 30 s at 94°C, 30 s at 50°C, and 1.5 min at 72°C. The PCR products were purified with an ExoStar clean-up kit (USB, Cleveland, OH, USA). Cycle sequencing was performed using a BigDye Terminator Cycle Sequencing Kit ver. 3.1 (Applied Biosystems, Foster City, CA) and the abovementioned PCR primers. The samples were purified by ethanol precipitation, and then electrophoresed on an Applied Biosystems 3130xl Genetic Analyzer. The electropherograms were assembled using ATGC ver. 6 software (GENETYX, Tokyo, Japan). Sequence data from this study were deposited in the DNA Data Bank of Japan (DDBJ; extant since 1983).

Phylogenetic analysis

The ITS sequences obtained by PCR were aligned using ClustalW 1.8 (Thompson *et al.* 1994) and then adjusted manually. Phylogenetic analyses were based on maximum-likelihood (ML) phylogenetic analysis using RAxML (Stamatakis 2014). The ML phylogenetic analyses were implemented in RAxML 8 (Stamatakis 2014) with a GTRGAMMA substitution model. The ML bootstrap proportions (BPs) and trees were obtained by simultaneously running rapid bootstrapping with 10,000 iterations followed by a search for the most likely tree. The output tree file was generated using FigTree ver. 1.3.1 (Rambaut 2009).

Results

Morphological and physiological comparisons

Field and herbarium surveys revealed that *S. boninense* from the Muko-jima group (Muko-jima, Muko-jima-tori-shima, Nakoudo-jima, and Nakoudo-jima-tori-shima Islands) and the Chichi-jima group (Ani-jima, Chichi-jima, and Ototo-jima Islands) share similar morphological and physiological characteristics including flower morphology, flower number per inflorescence (1–12), underground bulb formation, and summer dormancy (Figs. 2 and 3, Table 2). However, plants from the Muko-jima group differ from those from the Chichi-jima group in leaf shape and size (flat, spatulate to obovate, 6–14 × 2–5 mm vs. thick, elliptic to oblanceolate, 2–7 × 1–2 mm), shape of underground bulb scale leaves (flabelate vs. widely obovate), length of flowering stem (7–20 cm vs. 5–10 cm), plant habit (gregarious vs. ungregarious), habitat (rocky slopes on seashores vs. barren rocks on hilltops), and main flowering season (February–April vs. November–February) (Table 2, Figs. 2 and 3). Muko-jima group populations also share several flower morphological traits and plant habit, with *S. uniflorum* (Table 2). However, the former differ from the latter in underground bulb formation (presence vs. absence), leaf shape (flat, spatulate to obovate, 6–14 × 2–5 mm vs. thick, elliptic to oblanceolate, 3–5 × 1.5–2.5 mm), flower number per inflorescence (1 vs. 1–12), and flowering season (February–April vs. May–June) (Table 2). These populations share similar habitats, i.e., rocky slopes on seashores; however, *S. uniflorum* also occurs on sandy beaches (Table 2).

TABLE 2. Comparison of morphological and physiological features of *Sedum boninense* from the Chichi-jima group and the Muko-jima group, and *S. uniflorum*.

TAXON	<i>S. boninense</i> (the Muko-jima group)	<i>S. boninense</i> (the Chichi-jima group)	<i>S. uniflorum</i>
Habit	Gregarious	Ungregarious	Gregarious
Flower number	1–12	1–12	1
Flowering stem	7–20 cm	5–10 cm	4–10 cm
Leaves	Flat, spatulate to obovate 6–14 × 2–5 mm	Thick, elliptic to oblanceolate 2–7 × 1–2 mm	Thick, elliptic to oblanceolate 3–5 × 1.5–2.5 mm
Underground bulb	Presence	Presence	Absence
Scale leaf	Flabelate	Widely obovate	-
Flowering Season	February–April	November–February	May–June
Habitat	Rocky slopes in seashores	Barren rocks on hill top	Rocky slopes and sandy beach in seashores

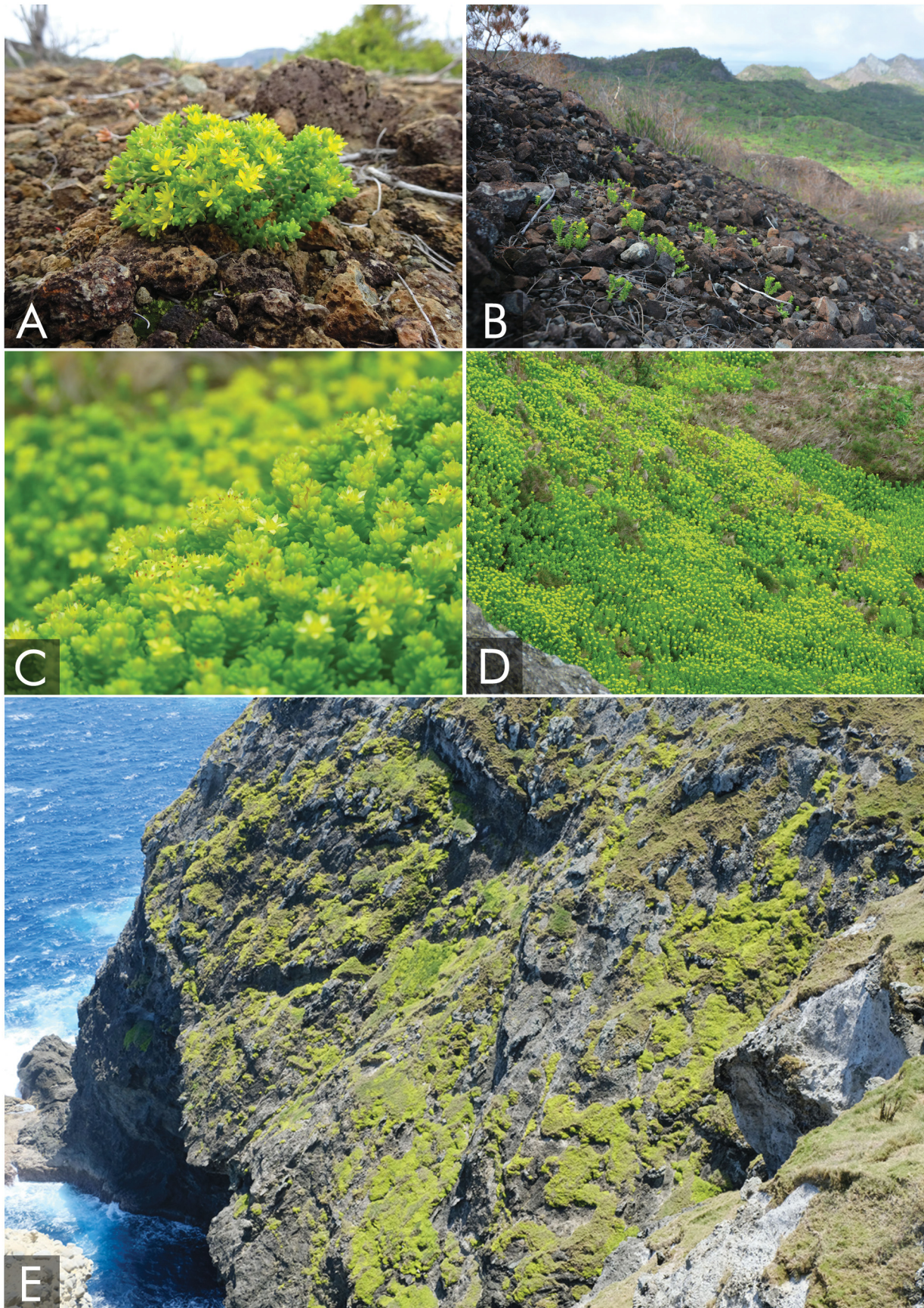


FIGURE 2. *Sedum boninense* from the Chichi-jima Group (A & B) and from the Muko-jima Group (*S. mukojimense*) (C–E). A & C. Habit. B, D & E. Habitat. [A. Ani-jima island of the Chichi-jima Group in Dec. 2013; B. Ototo-jima island of the Chichi-jima Group in Dec. 2019; C, D & E. Nakoudo-jima island of the Muko-jima Group in Mar. 2016 and Apr. 2018]

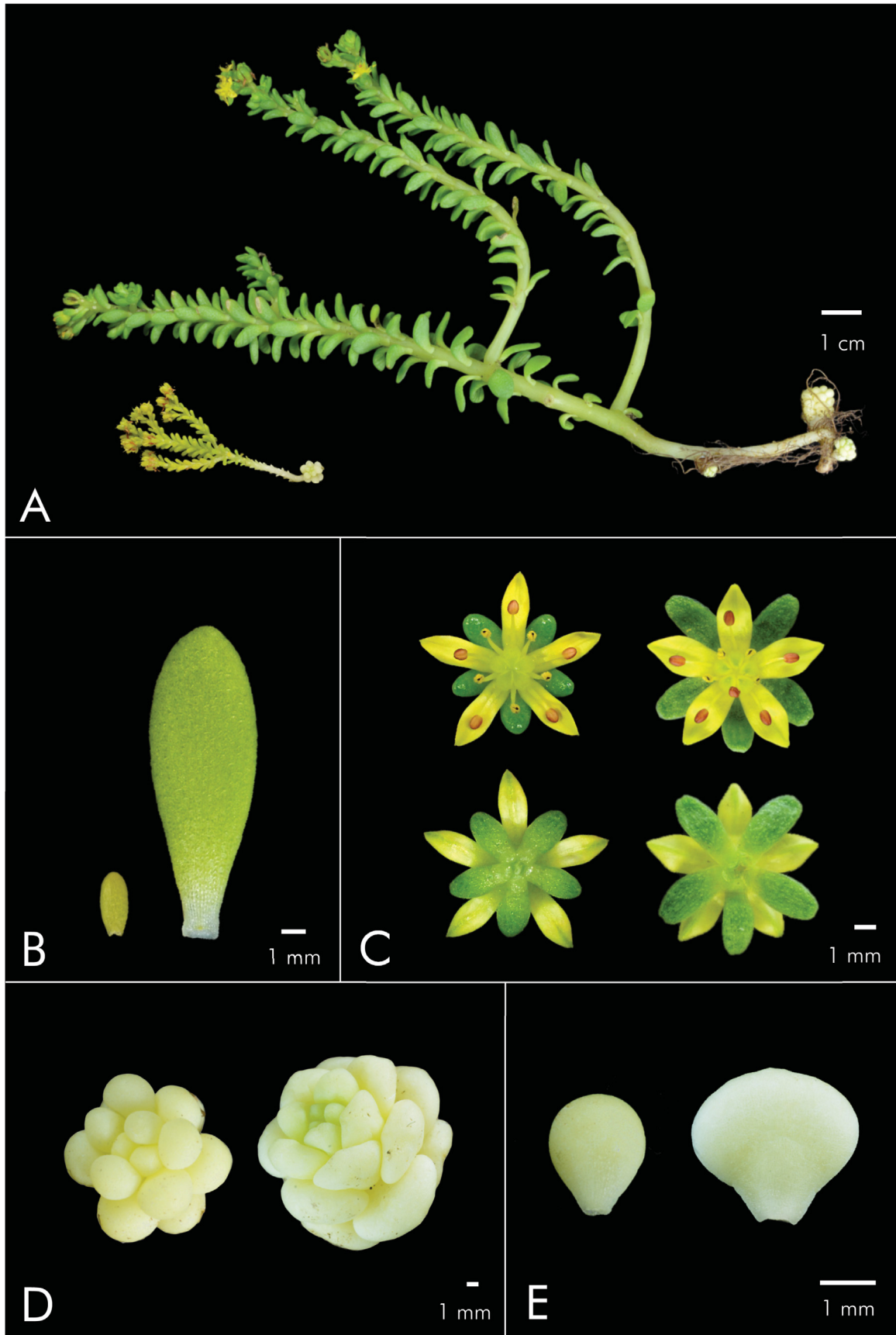


FIGURE 3. *Sedum boninense* from the Chichi-jima Group (A–E: Left) and from the Muko-jima Group (*S. mukojimense*) (A–E: Right). A. Habit. B. Leaf. C. Flower. D. Underground bulb. E. Underground bulb scale leaf. Scale bars are 1 cm for A, 1 mm for B–E.

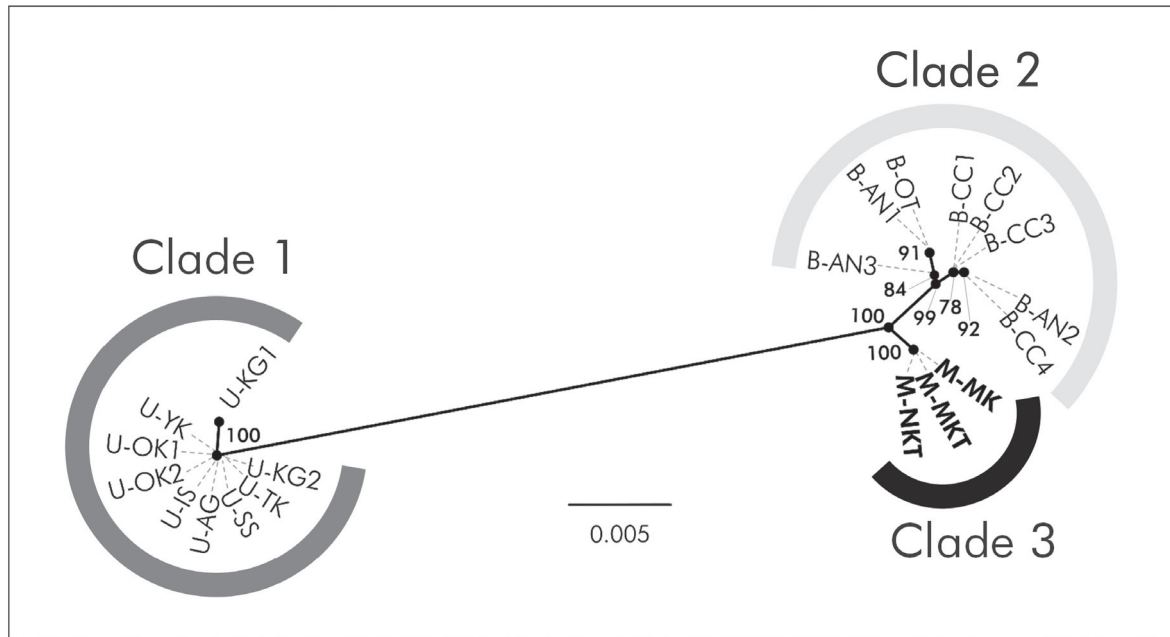


FIGURE 4. Maximum likelihood tree of *Sedum boninense* and *S. uniflorum* based on ITS sequence. Bootstrap percentages are shown at the nodes (See Tables 1 for the abbreviations of localities)

Phylogenetic relationships based on the internal transcribed spacer region

For maximum likelihood phylogenetic analyses, we obtained 20 operational taxonomic units, including six accessions obtained from GenBank (Table 1). After alignment, we obtained a matrix of 635 base pairs (bp). Bootstrap replicates (10,000) were plotted on the generated maximum likelihood tree, which showed that *S. uniflorum* and *S. boninense* each formed a well-supported clade (bootstrap replicates = 100, Clade 1; 100, Clade 2 + Clade 3). *Sedum boninense* was divided into two subclades, which comprising the Chichi-jima and Muko-jima group populations respectively. (99, Clade 2; 100, Clade 3) (Fig. 4).

Discussions

Taxonomic reconsideration of S. boninense

In the description of *S. boninense* (Tuyama 1936), specimens collected from the Muko-jima group (Muko-jima and Nakoudo-jima Islands) were used as paratypes for the species. However, our morphological comparisons clearly distinguished the Muko-jima group plants from *S. boninense* in the Chichi-jima group and *S. uniflorum* according to morphological and physiological differences (Table 2, Figs. 3 and 4). Molecular phylogenetic analysis showed that the Muko-jima group and the Chichi-jima group, including the type locality, formed a distinct clade, consistent with the morphological and physiological differences mentioned above.

Therefore, we conclude that the plants from the Muko-jima group, which have historically been treated as *S. boninense*, should be considered a different taxon endemic to the Muko-jima group among the Bonin Islands. This is the first report to identify an endemic plant taxon in the Muko-jima group. This new species is described below.

Taxonomic treatment

Sedum mukojimense Takuro Ito, *sp. nov.* (Figs. 2C–E & 3)

Type:—JAPAN. The Bonin Islands, Muko-jima group, Muko-jima Island, 17 March 2019, *Takuro Ito* 5704. (holotype TNS!).

Diagnosis:—*Sedum mukojimense* differs from its close relative *S. boninense* Yamam. ex Tuyama (1936: 428), in that it has a larger and flatter leaf, a flabelate scale leaf of underground bulb, a longer flowering stem, gregarious habit and later main flowering period from February to April.

Description:—Perennial herb, gregarious, sometimes branched, erect, fleshy, glabrous. Bulbs form underground after flowering, globose or cylindrical, 0.8–1 cm. Scale leaves numerous, white, thick, flabelate, 2.8–3.9 mm long, 1.7–3.3 mm wide, apex rounded, base attenuate, margins entire. Roots fibrous. Leaves alternate, densely arranged, ascending, fleshy, terete, flat, sessile, spatulate to obovate, 6–14 mm long, 2–5 mm wide, apex rounded, base attenuate, margins entire. Flowering stems fleshy, 7–20 cm tall, arising from bulbs, base 3 mm broad, greenish or yellowish, erect. Inflorescences with terminal cymes, flowers usually 1–12. Sepals 5–7, free, greenish–yellowish, fleshy, equal in size, narrowly elliptic or oblanceolate, 2–4 mm long, 0.8–1.2 mm wide, apex round or obtuse. Petals 5–7, blight yellow, lanceolate 3.9–5.8 mm long, 1.7–2.4 mm wide, apex acuminate, base slightly connate. Stamens 10–14, shorter than petals, 3.8–5 mm long, erect at flowering, 2-whorled; anthers oblong, approximately 0.5 mm long, red before dehiscence. Carpels 5–7, free, horizontal, connate at base, gibbous ventrally, 3.2–4.6 mm long. Fruits (follicles) star-shaped, spreading, 4.5–7 mm long. Flowering in February to April. Categorized in sect. *Sedum* due to presence of adaxially gibbous carpels (Fu & Ohba 2001) (Fig. 3).

Etymology:—Epithet refers to the Japanese name of type locality in the Muko-jima island group.

Distribution and habitat:—Endemic to the Muko-jima group of the Ogasawara (Bonin) Islands (Japan), on sunny, coastal, rocky slopes exposed to direct sunlight. It is unclear whether this species is distributed on the other islands of the Muko-jima groups, such as Kitano-shima or Yome-shima Island, which were not surveyed in the present study.

Phenological note:—Note that the flowering season of *S. boninense* was not mentioned in the species description, whereas previous studies have reported a flowering season from April to May (Ohba 2001). We confirmed that *S. boninense* blooms from November to February in the Chichi-jima group and from February to April in the Muko-jima group.

Japanese common name:—Muko-jima-mannen-gusa (nov.).

Additional specimens examined:—JAPAN. TOKYO: Muko-jima Island, *T. Tuyama 034424* (KAG), *T. Tuyama 1413, 1417, 1418* (TI), Muko-jima-Tori-shima Island, *T. Ito 5706* (TNS), Nakoudo-jima Island, *T. Tuyama 034425, 034426* (KAG), *T. Tuyama 1415, 1421, 1422, 1423, 1425, 1427* (TI), *T. Ito 5705* (TNS), Nakoudo-jima and Tori-shima Islands, *T. Ito 5707* (TNS).

In situ conservation:—According to IUCN red list criteria (IUCN 2016), *S. mukojimense* should be categorized as Vulnerable, because it occurs currently only on small islands of the Muko-jima group. But the habitat of this species is relatively stable because landing is effectively prohibited, and feral goats which heavily damaged the vegetation on these islands were eradicated in 1999 (Hata *et al.* 2007). Presently, a relatively large number of individuals of the species broadly covers sheer cliff coastlines and sandy slopes in the group. However, it should be noted that the vegetation is undergoing recovery (Shimizu 1993, Hata *et al.* 2007). Vegetation recovery is generally desirable; however, the sudden thriving of other plant species could lead to a reduced *S. mukojimense* population size because the genus *Sedum* is a weaker competitor compared with other plants and is also sensitive to changes in the light environment in general. Therefore, it is necessary to carefully monitor the effects of vegetation recovery on *S. mukojimense* population size.

Diagnostic key of *S. mukojimense* and related species

1. Solitary flowers, underground bulbs absent, shoots persists throughout the year.....*S. uniflorum*
– 1–12 flowers per inflorescence, underground bulbs present, shoots withers during summer.....2
2. Scale leaf widely obovate; leaf thick, elliptic to oblanceolate, 2–7 × 1–2 mm; flowering stems, 5–10 cm tall; habit ungregarious; main flowering season from November to February..... *S. boninense*
– Scale leaf flabelate; leaf flat, spatulate to obovate, 6–14 × 2–5 mm; flowering stems 7–20 cm tall; habit gregarious; main flowering season from February to April.....*S. mukojimense*

Biogeographical and evolutionary history of *Sedum mukojimense*

Biogeographically, the flora of the Bonin Islands mainly originated from surrounding regions including Southeast Asia, Taiwan, mainland Japan, the Ryukyu Archipelago, and Polynesia (Yamazaki 1981, Shimizu 1991). Previous reports have shown that *S. boninense* is sisters to *S. uniflorum*, which is endemic to the Ryukyus (Ito *et al.* 2017, Ito *et al.* 2018). This finding suggests that the ancestors of *Sedum* species endemic to the Bonin Islands could be originated from continental islands of the Ryukyu Archipelago, far approximately 1,500 km. In general, plants distributed on the

Bonin Islands and their close relatives must have experienced long-distance dispersal by wind, birds, or sea currents (Ito *et al.* 1998, Takayama *et al.* 2005). However, seeds of extant *Sedum* species are dispersed mainly by gravity and wind and are thought to be incapable of long-distance dispersal, because they are much larger and heavier than typical anemochorous seeds (Thiede & Eggli 2007). Therefore, only a few *Sedum* species are distributed among oceanic islands far from continents (Stephenson 1994), and it is unclear how it migrated. Further biogeographical and ecological studies may reveal the biogeographical history of *S. mukojimense* and related species.

One evolutionary mode of plants on oceanic islands is a habitat shift from coastal to inland, accompanied by loss of dispersal mechanisms (Carlquist 1974, Takayama *et al.* 2005). The dispersal mechanisms of the two Bonin Islands species examined in this study remain unclear, but their habitats are distinct: coast and inland, respectively. Plant habit differences (e.g., gregarious vs. ungregarious) between *S. mukojimense* and *S. boninense* may reflect differences in dispersal mode and reproductive ecology. Further ecological studies focusing on the dispersal and reproductive ecology of these species would allow generalization of their evolutionary dynamics in terms of their habitat shift on oceanic islands.

Alternatively, *Sedum* species experienced unique morphological evolution on the Bonin Islands, including the formation of underground bulbs (the anatomy of which has not been studied in detail) and summer dormancy. Generally, underground bulb formation and summer dormancy are adaptive traits for long and dry summer periods (Volaire & Norton 2006, Phillips 2010). Underground bulbs are particularly prominent among monocotyledons, e.g., Alliaceae, Amaryllidaceae, Hyacinthaceae, and Liliaceae (Goldblatt & Manning 2000), whereas bulbous plants are extremely rare among eudicots, recognized only in genus *Oxalis* (Oxalidaceae) (Oberlander *et al.* 2009). The development of underground bulbs in *Sedum* may support parallel evolution among multiple unrelated families at the order level.

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