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Emended description and new localities of *Oxygyne shinzatoi* (Burmanniaceae/ Thismiaceae), with discussion of phylogenetic relationships of *Oxygyne* from Japan and Africa

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Abstract

During a recent survey, *Oxygyne* specimens were discovered in three lowland evergreen forests on Okinawa Island, Japan. After morphological investigation, we identified the specimens as *O. shinzatoi*. Intriguingly, the colour of the specimens from one of the localities was significantly different from that of specimens collected from both the type and two of the new localities. Furthermore, morphological analysis also revealed clear differences between specimens collected from the type locality, including the type specimen, and previous descriptions of *O. shinzatoi*. Therefore, an amended description of *O. shinzatoi* is provided, based on the type and newly collected specimens. Phylogenetic relationships of *Oxygyne* from Japan and western Central Africa are also discussed, with consideration of the characteristics of newly discovered colour variation.

Keywords: Burmanniaceae, Dioscoreales, colour variation, mycoheterotrophy, *Saionia,* Saioniinae, Thismiaceae

Introduction

Oxygyne Schlechter (1906: 140) is a poorly known genus of achlorophyllous, mycoheterotrophic, perennial herbs in Thismiaceae (Cheek *et al.* 2018) or a broadly circumscribed Burmanniaceae in the monocot order Dioscoreales (APG IV, 2016). The morphology of *Oxygyne* clearly differs from that of other related taxa (Yokoyama *et al.* 2008, Suetsugu *et al.* 2018). *Oxygyne* species possess a morphologically unspecialized perianth, more specifically, identical inner and outer perianth whorls and three stamens that are basally enlarged and curved inwards (Woodward *et al.* 2007, Cheek *et al.* 2018).

During a recent botanical survey, *Oxygyne* specimens were discovered in three lowland evergreen forests on Okinawa Island, Japan, and morphological investigation identified the specimens as *O. shinzatoi* (Hatusima 2015: 115) Tsukaya (2016: 195), which has also been reported to occur on Okinawa Island, Ryukyu, Japan (Hatusima 1975, 1976, Abe & Akasawa 1989, Yahara & Tsukaya 2008, Tsukaya 2016). Although surveys have been conducted elsewhere, the species thus far has been known to occur only at the type locality. In addition, its occurrence there has been documented only in 1972, 1974, 2004, 2008 and 2011 (Cheek *et al.* 2018), although investigations have been conducted in some other years (Cheek *et al.* 2018). The three new localities were located ca. 13.5 km from the *O. shinzatoi* type locality. Analysis of the newly discovered *Oxygyne* specimens revealed previously undocumented variation. For example, the coloration of one of the *O. shinzatoi* populations was clearly distinct from that of specimens collected from the type and the other two localities. Morphological analysis also revealed clear differences even between specimens collected from the type locality, including the type specimen and previous descriptions of *O. shinzatoi*. Therefore, an emended description of *O. shinzatoi* is provided based on specimens collected from all localities. Phylogenetic relationships of *Oxygyne* species from Japan and western Central Africa are also discussed, with consideration of morphological characteristics and, especially, the newly discovered colour variant.

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Taxonomic treatment

Oxygyne shinzatoi (Hatus.) Tsukaya (2016: 195)

Type:—Japan, Ryukyu Islands, Okinawa Prefecture, Okinawa Island, Kunigami-son, Yona, 18 September 1974, *Shinzato s.n*. (holotype RYU!, spirit collection).

Homotypic synonyms: *Saionia shinzatoi* Hatusima (2015: 115).

Saionia shinzatoi Hatusima (1975: 909), nom. invalid.

Oxygyne shinzatoi (Hatus.) Abe & Akasawa (1989: 163), comb. invalid.

Achlorophyllous mycoheterotrophic herbs. Roots unbranched, vermiform, radiating from the base of the rhizome, 2–5 cm long. Stem simple or branched at base, erect, glabrous, 0.5–1.5 cm tall. Inflorescence racemose, 1–5-flowered, pedunculate; peduncle ca. 1.0 mm in diameter. Scale leaves inserted spirally on the upper half of the rhizome, translucent white, lanceolate, 2–3 mm long. Bracts at base of flowers (3–)5, 3–5 mm long, ovate-lanceolate to lanceolate, translucent white. Flowers 4.8–6.2 mm long, 7–12 mm in diameter, bluish green. Perianth tube campanulate, 4.8–6.2 mm long, 2.7–3.8 mm in diameter, 6-lobed, glabrous; perianth lobes patent or ascending, narrowly triangular to filiform, 3.0–9.0 × 0.6 mm basally, translucent white, with callus-like cluster of round cells on adaxial surface at base; callus cluster ca. 0.5 mm long; each perianth lobe with a lamella at throat; lamella convex, inflexed, forming an annular corona with a hole in its centre; lamella of each inner perianth lobe with a slit that connects to the central hole, lamella of each inner perianth 1.0 × 0.7–1.1 mm, trapezoid, with 2(–4) apical teeth, curved downward from throat of perianth tube, forming 3 narrow slits and a small opening at centre of throat; teeth on free apical part mostly 2, triangular and similar in shape and size, rarely 3, with middle teeth shallow and ambiguous and lateral teeth larger and similar in shape and size. Stamens 3, extending from base of inner perianth lobes, each filament curved downward into a slit formed by the lamella of an inner perianth lobe, with two projections at the base, and bearing a single anther. Anthers pale yellow, bithecal, 1.2–1.6 mm long. Ovary ca. 3 mm long, white. Style 1, 1.0–1.5 mm long, bilateral, pale yellow, surrounded by (2–)3 bluish green appendages, with (2–)3 stigmas; stigmas less than ca. 0.4 × 0.2 mm, pale yellow. Tip of stylar appendages ball-like, ca. 0.3 mm in diameter, ca. 0.5 mm long including stalk. Ovary white, campanulate, ca. 2 ×1 mm wide basally, ca. 2 mm wide apically, unilocular, placentae 3, attached distally near the junction with the perianth floor. Seeds numerous.

Additional specimens examined:—Japan, Ryukyu Islands, Okinawa Prefecture, Okinawa Island, Kunigami-son, Yona, 20 September 2004, *Yokota* & *Ishii s.n.* (RYU, spirit collection), loc. cit., 8 October 2006, *Tsukaya 061008.* (TI, spirit collection, TNS, spirit collection), Ogimi-son, site A, 1 September 2018, *Sugimoto TSP021* (TNS, spirit collection), loc. cit., 1 September 2018, *Sugimoto TSP023* (TNS, spirit collection), loc. cit., 17 September 2019, *Suetsugu KS545* (TNS, spirit collection), Ogimi-son, site B, 1 September 2018, *Sugimoto TSP038* (TNS, spirit collection), loc. cit., 17 September 2019, *Suetsugu KS546* (TNS, spirit collection), Ogimi-son, site C, *Sugimoto TSP019* (TNS, spirit collection), loc. cit., 1 September 2018, *Sugimoto TSP035* (TNS, spirit collection), loc. cit., 17 September 2019, *Suetsugu KS547* (TNS, spirit collection).

Distribution and phenology:—The greenish brown colour of specimens at one of the three newly discovered localities of *O. shinzatoi*, was clearly distinct from that of specimens collected from the type and other two localities (deep greenish blue; Figs 1–5). The colour variants are not completely sympatric with the other localities of *O. shinzatoi*, and the other two localities of *O. shinzatoi* are ca. 50 m and ca. 1 km away. In addition, the distance between the type locality of *O. shinzatoi* and the three new localities of *O. shinzatoi* is ca. 13.5 km. These populations harbour dozens of flowering plants under humid evergreen broadleaf forest dominated by *Neolitsea sericea* (Blume) Koidzumi (1926: 343), *Cinnamomum yabunikkei* Ohba (2006: 243; both Lauraaceae) and *Psychotria asiatica* Linnaeus (1759: 929; Rubiaceae). *Oxygyne shinzatoi* flowers in late August to mid-October in both the type locality and these three new localities.

Nomenclatural notes:—*Oxygyne shinzatoi* is the best studied of the *Oxygyne* species and is the only one for which cytological and molecular phylogenetic studies have been conducted (Tsukaya *et al.* 2007, Yokoyama *et al.* 2008). Despite this, the specific name was invalidly published after its discovery in 1972 because, contrary to the *International Code* (ICN), two specimens were designated as holotypes in Hatusima (1976). Furthermore, Abe & Akasawa (1989), evidently unaware of this problem, later transferred the species to *Oxygyne*, where it was also invalid. Ohashi (2015) rectified the matter by selecting a single holotype, and finally, both *Saionia* and the type of the species *Saionia shinzatoi* were validly published. In addition, Tsukaya (2016) later treated the species as *O. shinzatoi* (H.Ohashi) Tsukaya. However, because Ohashi (2015) ascribed the name to Hatusima and provided a full and direct

reference to a validating description that is unequivocally associated with Hatusima, Art. 46.10 notwithstanding, the name is therefore attributed to Hatusima, not "Hatusima ex H.Ohashi" or "H.Ohashi", based on ICN Art. 46.3. Note. 4. (Turland *et al.* 2018). Therefore, the species should be referred to as *O. shinzatoi* (Hatusima) Tsukaya because errors in citation of the basionym, including incorrect author citation, do not preclude valid publication of a new combination based on ICN Art. 41.6. (Turland *et al.* 2018).

FIGURE 1. *Oxygyne shinzatoi* from the type locality. A–B. Flowering plants. C. Flower. Arrows point to a pair of projections at the base of a filament. Photograph by Tazuko Watanabe.

Taxonomic notes:—The combination of characters observed in the newly discovered specimens (i.e., three stamens attached to the perianth and presence of lamellae at the mouth of the perianth tube) indicates that the specimens belonged to the genus *Oxygyne*. In particular, the new specimens were characterized by a style surrounded by three rounded appendages and filiform perianth lobes with a callus-like cluster of round cells on their adaxial surfaces (Figs. 2–5). Because these characteristics generally coincide with the description of *O. shinzatoi*, the specimens were identified as *O. shinzatoi* and were considered to represent the first record of the species outside the type locality. Despite the similarities, a few minor differences between the newly discovered specimens and *O. shinzatoi* specimens from the type locality were observed, especially the shape of the perianth lobes (4.0–9.0 mm in length, often ascending *vs*. 3.0–5.0 mm long, often patent; Figs. 1–5). However, the angle of the perianth lobes was observed to vary, depending on floral conditions, in both the type and new localities, with those of older flowers generally patent and those of fresh flowers generally erect. In addition, there was sometimes an overlap in the lengths of perianth lobes from the type

locality and new localities. Given the absence of differences in inner floral characteristics, such as the shape of the style or stigma, which are crucial for the identification of *Oxygyne* species, the minor difference should be regarded as the intraspecific variation.

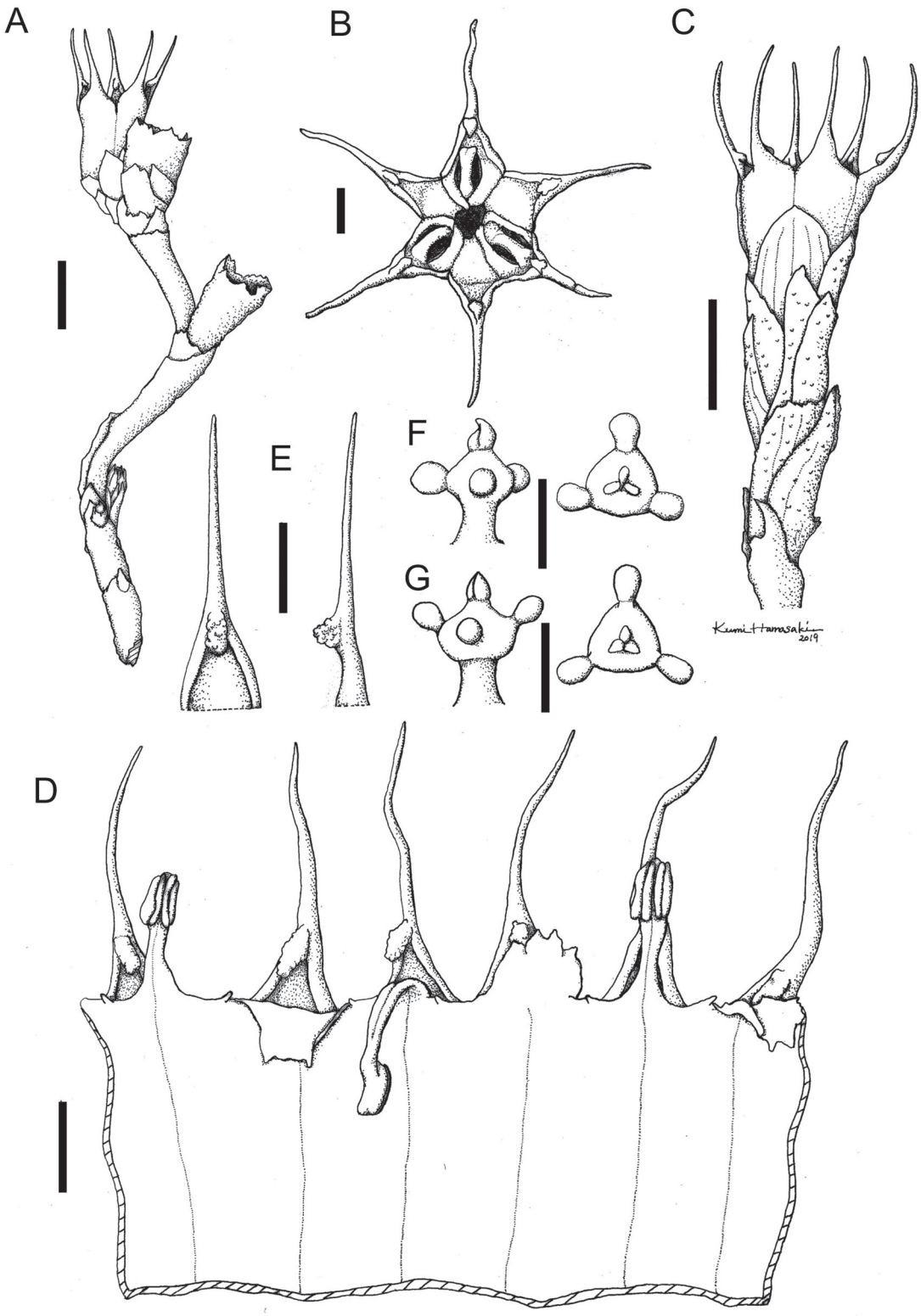

FIGURE 2. *Oxygyne shinzatoi* from the type locality. A. Habit. B–C. Flower. D. Flattened perianth tube. E. Perianth lobes. F–G. Style and stigmas. A, C. Bar = 3 mm. B, D–G. Bar = 1 mm. Drawn by Kumi Hamasaki. A–F. Based on *Tsukaya 061008* (TI). G. Based on *Yokota & Ishii s.n.* (RYU).

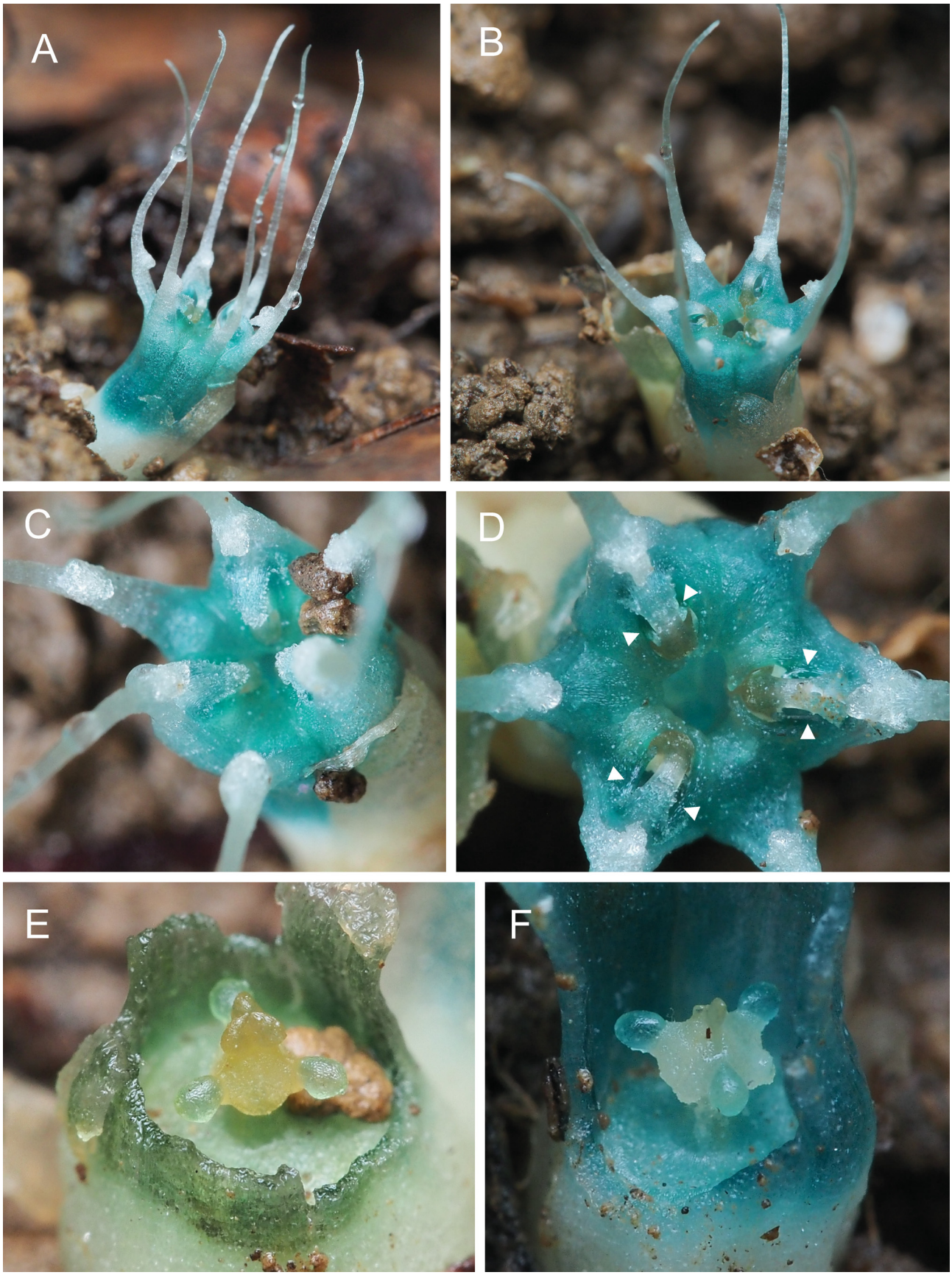

FIGURE 3. *Oxygyne shinzatoi* from a new locality (deep greenish blue; *Sugimoto TSP023*, TNS). A–B. Flowering plant. C–D. Flower. E–F. Style and stigmas. Arrowheads point to a pair of projections at base of a filament.

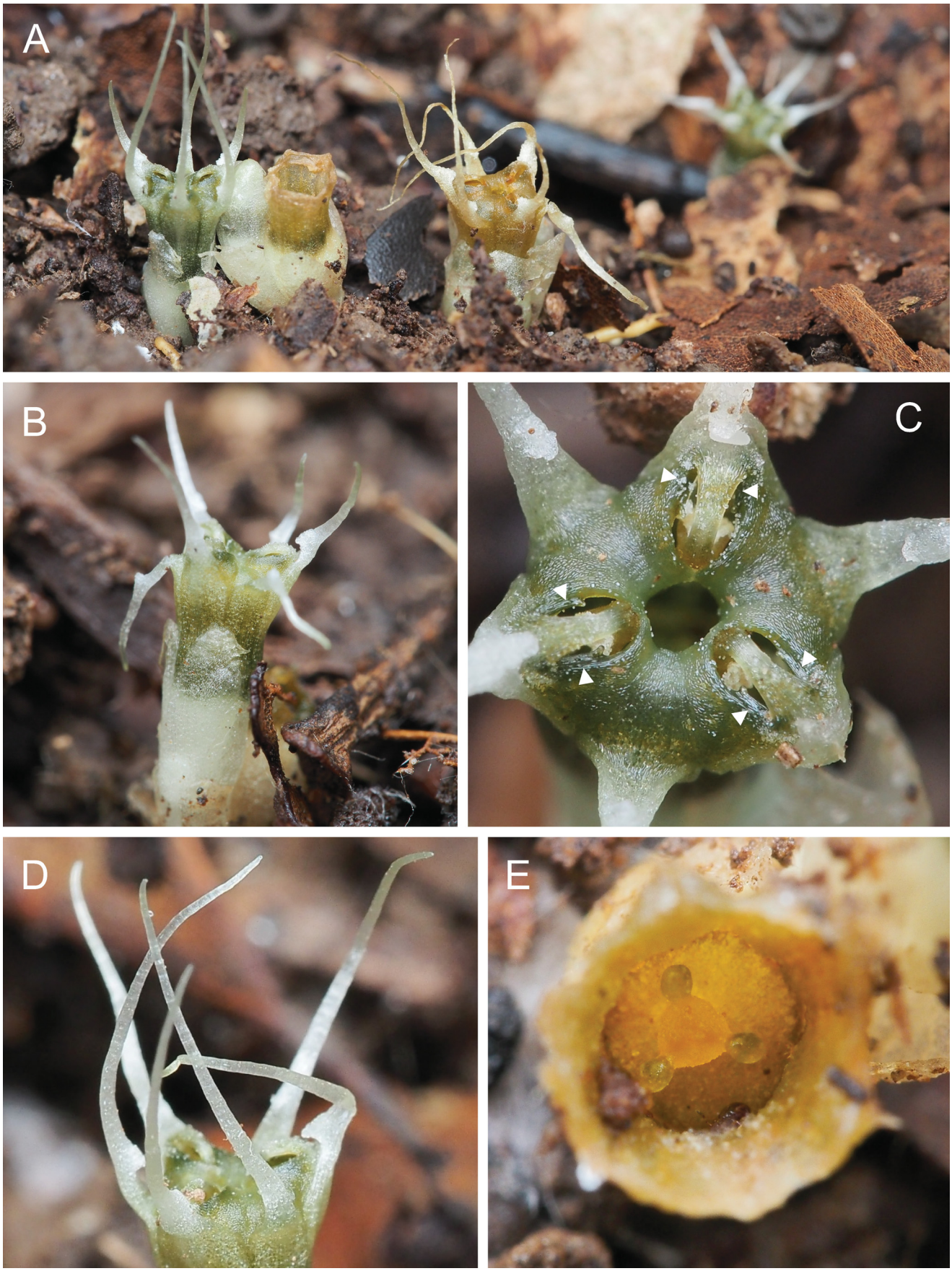

FIGURE 4. *Oxygyne shinzatoi* from a new locality (greenish brown). A–B. Flowering plants. C. Flower. D. Perianth lobes. E. Style and stigmas. Arrowheads point to a pair of projections at the base of a filament.

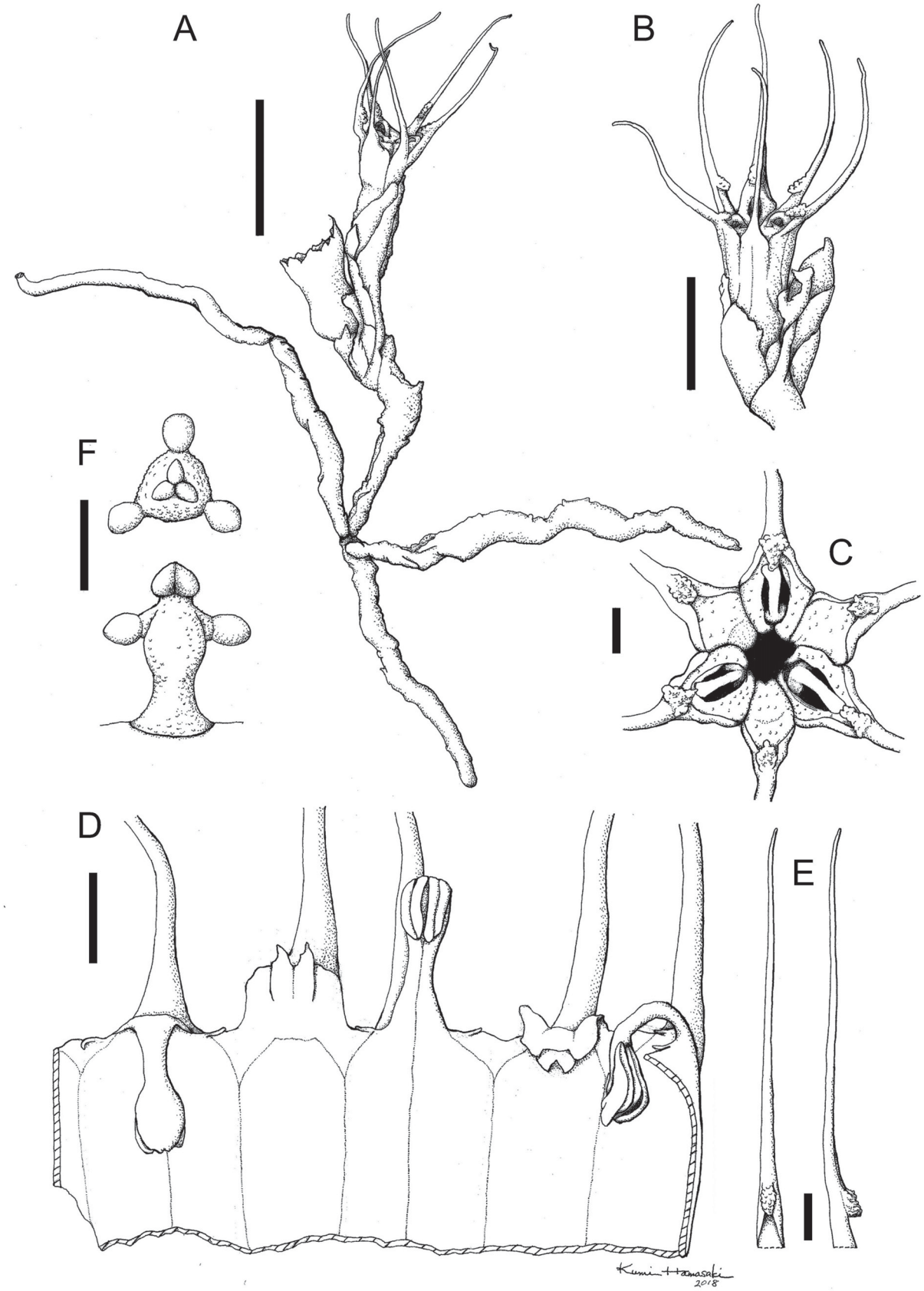

FIGURE 5. *Oxygyne shinzatoi* from a new locality (greenish brown; *Sugimoto TSP019*, TSN) A. Habit. B–C. Flower. D. Flattened perianth tube. E. Perianth lobes. F. Style and stigmas. A, C. Bar = 3 mm. B, D–G. Bar = 1 mm. Drawn by Kumi Hamasaki.

Our morphological investigation also revealed differences between specimens collected from the type locality, including the type specimen, and previous descriptions of *O. shinzatoi*. The most notable difference was the status of the lamella in the throat of the perianth lobe. Hatusima (1976) recognized *O. shinzatoi* (=*Saionia shinzatoi*) as a distinct subtribe (Saioniinae), owing to the absence of an annular band at the throat of the perianth, whereas other authors have generally considered the character to be insufficient to merit its separation from *Oxygyne*, even at the generic rank (Abe & Akasawa 1989, Yahara & Tsukaya 2008, Tsukaya 2016). Nevertheless, even those authors have agreed with Hatusima's argument that *O. shinzatoi* is characterized by poorly developed lamellae (Abe & Akasawa 1989, Yahara & Tsukaya 2008, Tsukaya 2016). In particular, the inner perianth is considered to lack a lamella (Tsukaya 2016, Yahara & Tsukaya 2008). However, our morphological analysis confirmed that both inner and outer perianth lamellae were present and fused to form an annular structure (Figs 1–5). In addition, even though the free lamella of *O. shinzatoi* has been reported to bear small teeth (Yahara & Tsukaya 2008, Tsukaya 2016), the lamellae of the outer perianths of the holotype and other specimens were generally bilobed (Figs 2, 5). Furthermore, Tsukaya (2016) noted that the stigma of *O. shinzatoi* is always unequally sized and sickle shaped, whereas equally sized stigmas can be observed in specimens collected from both the type locality and new localities (Fig. 2F, G; 3E, F). Lastly, a pair of projections at the basal part of each filament has, until now, been overlooked. Since these structures are present in specimens collected from both the type locality and new localities (Figs 1–5), the discrepancy should not be attributed to intraspecific variation among populations but, rather, to faulty earlier description.

The discovery of *O. shinzatoi* at three new localities (particularly the greenish brown colour variants in one locality; Fig. 4) provides us with important insights into the delimitation of *Oxygyne* and *Saionia. Oxygyne shinzatoi* was originally invalidly described as a member of a new genus (i.e., *Saionia*; Hatusima 1976). Abe & Akasawa (1989) rejected the placement of Hatusima (1976) and transferred both *S. shinzatoi* and their new species, *O. hyodoi*, to *Oxygyne*, which was originally established for the Cameroon endemic, *O. triandra* (Schlechter 1906).

Yokoyama *et al.* (2008) noted that the flowers of *Oxygyne* species from Africa are bell shaped and deep brown, with an orange-yellow appendage, whereas the flowers of *Oxygyne* species from Japan are cup shaped and blue-green, which suggests that the two geographically isolated groups are only distantly related. Moreover, Ohashi (2015) proposed that the genus *Saionia* be resurrected for the *Oxygyne* species from Japan because they differ from the type species *O. triandra* in possessing (1) campanulate perianths, (2) bluish perianths, (3) patent perianth lobes, (4) deflexed stamens, in which the anthers are positioned below the base of the filament, and (5) stylar appendages. However, Cheek *et al.* (2018) reported that all these features, except the bluish colour of the perianth, are exhibited by a new Cameroon endemic, *O. duncanii* Cheek in Cheek *et al.* (2018: 16). In fact, *O. duncanii* appears more similar to *Oxygyne* species from Japan than to *O. triandra.* Therefore, considering that flower colour alone is insufficient to support segregation, Cheek *et al.* (2018) rejected the earlier proposal that the species from Japan should be included in *Saionia*.

The newly discovered plants include some that are brownish, thereby representing the first brownish *Oxygyne* accessions in Japan. This is especially significant considering that flower colour was the only character that could be used to clearly distinguish the *Oxygyne* species from Japan and Africa (Cheek *et al.* 2018). Indeed, intraspecific colour polymorphism has been reported to occur in many mycoheterotrophic species (Fukunaga *et al.* 2008, Tsukaya & Okada 2012, Suetsugu & Yagame 2014, Suetsugu 2016a, b) and is likely due to relaxation of selection on photosynthetic and protective pigments.

Finally, even though Ohashi (2015) considered patent perianth lobes to be diagnostic of *Saionia*, the perianth lobes of *O. shinzatoi* specimens from the new localities were often erect. In addition, the angle of the perianth lobes was observed to vary, depending on floral age, even at the type locality, with those of older flowers generally patent and those of fresh flowers generally erect, making this character useless for generic distinction.

Accordingly, despite the unusual and geographically disjunct distribution of *Oxygyne* species in Japan and Africa, our findings provide further support for retention of the Japanese species in *Oxygyne*. However, further phylogenetic investigation of *Oxygyne* species from both Japan and Africa will be needed to elucidate the evolutionary history of this enigmatic genus.

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