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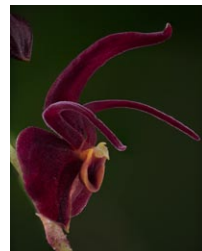
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FRONT COVER

Those massive, frilly lips that we have come to love in complex *Rhyncholaeliocattleya* hybrids (often so-called "brasso-lips") owe their origin to love in complex *Rhyncholaelia digbyana*. This incredible species has proven to be a goldmine for cattleya breeders over the years. Pictured here is *Rl. digbyana* 'Springwater' AM/AOS, photographed by Ernest Walters, was grown by Thanh Nguyen, Springwater Orchids.

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Prepared for download exclusively for Benjamin Crain

Studies on *Oberonia* 7

Ten New Synonyms of *Oberonia equitans* (G. Forst.) Mutel Indicated by Morphology and Molecular Phylogeny

By Daniel L. Geiger, Benjamin J. Crain, Melissa K. McCormick and Dennis F. Whigham

ABSTRACT A combined morphological-molecular investigation identifies ten new synonyms of *Oberonia equitans* (G. Forst.) Mutel: *Oberonia affinis* Ames & C. Schweinf. in O. Ames, *Oberonia aurea* Schltr., *Oberonia ciliolata* Hook. f., *Oberonia enoensis* J.J. Sm., *Oberonia equitans* var. *chaperi* Finet, *Oberonia lampongensis* J.J. Sm., *Oberonia mcgregorii* Ames, *Oberonia murkelensis* J.J. Sm., *Oberonia oxystophyllum* J.J. Sm., and *Oberonia palawensis* Schltr. We designate here as neotype for *Oberonia palawensis* Crain 198 US 3737901. The synonymies are supported by floral characters and habit of each named taxon, ecology and phenological data, and lack of differentiation in a molecular phylogeny. The species is shown to be widely distributed from Malaysia through French Polynesia based on examination of some 300 herbarium specimens. If the magnitude of over-naming in *Oberonia* is indicative of other intrageneric groups that are cryptic and/or difficult to identify in the field or from pressed herbarium specimens, diversity could be over-estimated by a third in such groups.

INTRODUCTION *Oberonia* is a genus of tropical and subtropical orchids ranging from Central Africa eastwards to French Polynesia. On the order of 470 names have been introduced for 200–300 species. The number of currently recognized species is by far too high, with large numbers of synonymies to be addressed (Bunpha et al. 2019; Geiger 2016, 2019a, in press a, unpubl. data).

Difficulties in sorting out identities of names arise from species that lack types and that were never illustrated. Furthermore, verbal descriptions are frequently difficult to match to biological species, particularly from geographic regions that have limited material in herbaria, such as the Republic of Palau in the Caroline Islands of Micronesia.

Fieldwork in Palau provided the impetus for the current study (Crain 2018). While various sources suggest that Palau is home to at least three species of *Oberonia* (Costion 2009, Costion and Lorence 2012, Hillman-Kitalong and Uesugi 2017), herbarium specimens for most of the species are sparse, and some of the type specimens are missing and/or questioned (Fosberg and Oliver 1991, Natural History Museum (NHM) 2014).

Oberonia palawensis Schltr. is a case in point. Ledermann's type specimen for the species (*Ledermann 14475*) is missing and only a few other specimens of the species are known to exist (Fosberg and Oliver 1991). Several specimens are housed in US: *Hosokawa 9100*; *Canfield 367, 666*; *Timberlake 3168*; *Fosberg 25740*; *Bowden-Kerby LR5796*; *Evans 619*. Two recent collecting trips to Palau yielded two additional *Oberonia* specimens that were preliminarily identified as *O. palawensis*. Each of these specimens was examined in

detail to confirm its identity.

While we worked out the identity of the Palau specimens, it became clear that a much more far-reaching taxonomic issue needed to be tackled. We used a combined morphological–molecular approach to demonstrate that multiple described species all refer to one and the same biological species. We identified 10 new synonyms of *Oberonia equitans* (G. Forst.) Mutel in addition to the three already accepted ones.

MATERIALS AND METHODS *Light Microscopy.* Flowers on a herbarium sheet were imaged by applying z-stacking on a Zeiss Discovery V20 stereomicroscope with motorized focus and a 1.5x planapochromatic objective lens. Files of the stack were processed in ZereneStacker using the Pmax algorithm and then further adjusted in AffinityPhoto. For details see Geiger (2013, 2017).

Electron Microscopy. For scanning electron microscopy (SEM), preserved flowers were brought to 100 percent ethanol through three changes of 100 percent ethanol. The flowers were then critical-point dried in a Tousimis Autosamdri 815A (Tousimis, Rockville, Maryland) using default settings, mounted on double-sided carbon tabs (PELCO Image Tabs, Ted Pella, Redding, California) on aluminum stubs and coated with gold in a Cressington 108Auto with rotary planetary stage (Watford, United Kingdom). The flowers were imaged on a Zeiss EVO 40XVP or Zeiss EVO 10 LS SEM in variable pressure (30 Pa) at 20 kV and 50–500 pA depending on magnification and working distance.

Gatherings found in multiple institutions are cited with the most complete data. Standard repository

abbreviations are used: DLG/HOAG indicates Daniel Geiger living collection/ Geiger herbarium and spirit collection, Santa Barbara, California. For elevation and phenology information, data plots with local regression least square fitting were generated with DataGraph 4.3 (Visual Data Tools).

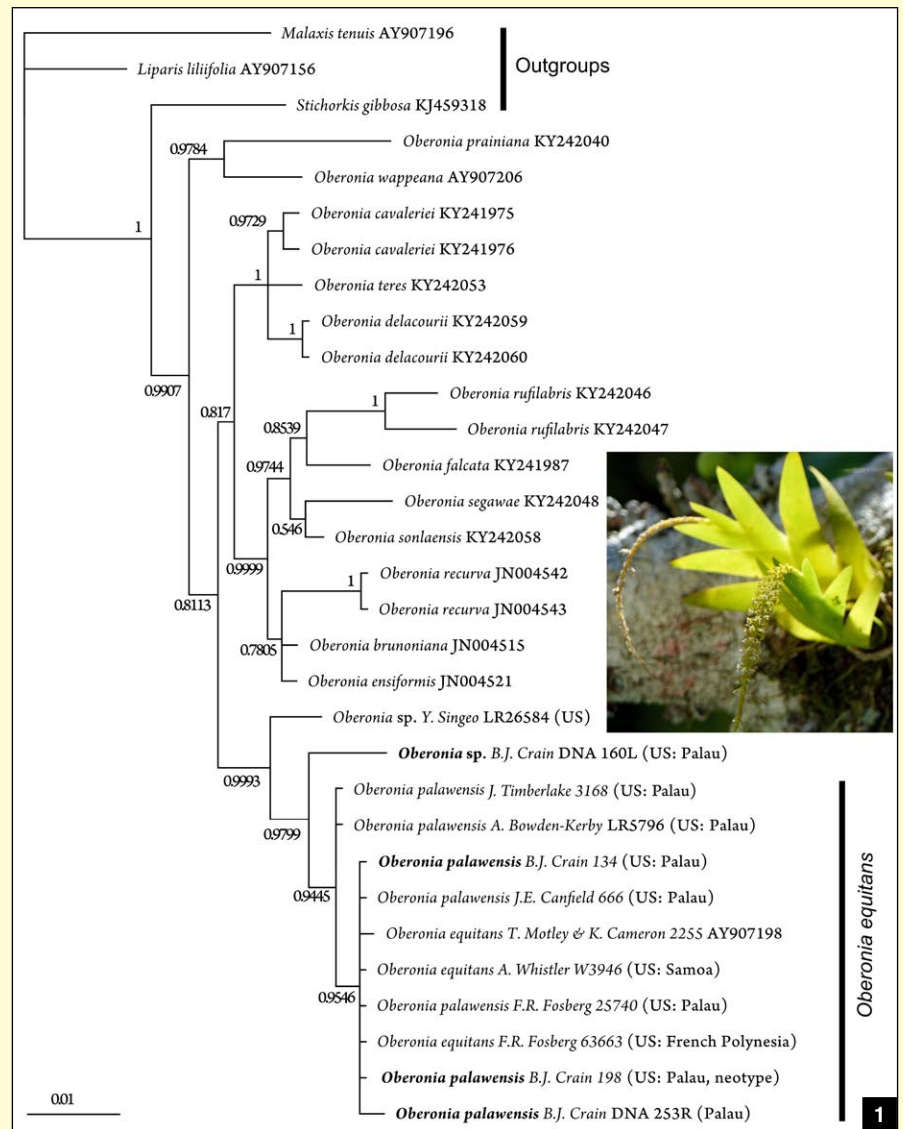
Molecular Analysis. Vegetative tissue samples were collected from four naturally growing individuals of *Oberonia* in the Republic of Palau to facilitate molecular identification. Each leaf and root tissue sample was stored in a sealed 2-ml microcentrifuge tube filled with CTAB buffer solution to preserve DNA, and then frozen at –20 C until processing in the laboratory. For DNA extraction, each tissue sample was removed from the tube with buffer and clipped into small fragments into a well of a 96-sample deep-well plate. For herbarium plant samples, a small (~1 cm²) sample of leaf was similarly clipped into small fragments into a plate well. We extracted DNA from approximately 25 mg of plant tissue using a BioSprint 96 automated DNA extraction workstation with a BioSprint96 Plant DNA kit (Qiagen, Inc., Valencia, California) following the supplied protocol. After DNA extraction, we amplified the *matK* region of the chloroplast using *matK1F/matK1R* (Parveen et al. 2017) in a Bio-Rad C1000 Touch Thermal Cycler (Bio-Rad Laboratories, Inc., Hercules, California). We also amplified the internal transcribed spacer of the nuclear ribosomal repeat (ITS) and chloroplast *trnH/psbA*. These two additional loci amplified poorly from the herbarium specimens and gave similar phylogenetic patterns, so only the *matK* is presented here. We prefer an analysis based on a complete data matrix of fewer

markers to one with more markers but significant missing data.

Polymerase chain reaction (PCR) success was evaluated by electrophoresis on a 1 percent agarose gel, stained using Gel Red, and visualized on a transilluminator. All successful PCR products, defined as those producing a single band, were sequenced using Sanger Sequencing. PCR product was cleaned using ExoSap-IT (Applied Biosystems, Inc., Foster City, California) and subjected to sequencing reactions using BigDye v.3.1 (Applied Biosystems, Inc.) in quarter-strength half reactions, using 1 µl Big Dye 3.1, 2 µl Big Dye buffer, 1 µl 3.2 µmol primer, 5 µl H₂O and 5 µl (50–80 ng DNA) of PCR product, and otherwise followed manufacturer protocols. Sequencing reaction products were cleaned using Sephadex G-50 Fine (GE Healthcare Systems) and dried and analyzed on an ABI 3100 Sanger Sequencer. Sequences were manually checked for quality and trimmed. Forward and reverse sequences were combined into a single contig and discrepancies resolved manually in Sequencher v.5.4.6 (Gene Codes Corp.).

Phylogenetic analysis. We downloaded all *Oberonia matK* sequences from GenBank and aligned our sequences and the downloaded sequences using MUSCLE, implemented in Geneious Prime 2020.0.4 (BioMatters Ltd.) and checked manually. We retained a subset of the downloaded sequences to represent each clade and to demonstrate the amount of variation within a species. We used this approach to allow us to focus on phylogenetic identity of our focal samples, rather than on possible synonymies and identification issues in the genus as a whole. *Malaxis tenuis* (AY907196), *Liparis liliifolia* (AY907156), and *Stichorkis gibbosa* (KJ459318) were used as outgroup taxa. We then estimated phylogenetic trees using MrBayes, implemented in Geneious Prime 2020.0.4 (BioMatters Ltd., Auckland, New Zealand) and using a burn-in of 110,000, sample frequency of 200, total chain length of 1,100,000, four heated chains, a heated chain temperature of 0.2, GTR substitution model and gamma rate variation.

MOLECULAR RESULTS The molecular results support the morphologically derived synonymies (Fig. 1). The Palau specimens are interspersed with those from Samoa and French Polynesia, mostly in a major polytomy with rather short terminal branches. Two samples are separated in a distinct clade. However, the cumulative branch lengths



of less than 0.5 percent within *O. equitans* are as long as or shorter than the terminal branch length in *Oberonia cavaleriei* Finet and *Oberonia rufilabris* Lindl. Those two species are easily identified and distinct. Accordingly, the cumulative branch lengths within *O. equitans* are compatible with a single species. Furthermore, the largest genetic differences are encountered within the rather small islands of the Palauan Archipelago, while the much more distant samples from Samoa and French Polynesia show no phylogenetic patterning at all, as they are found in a large polytomy. The voucher for *O. equitans* from Cameron (2005) *T. Motley & K. Cameron* 2255 was most likely from New Caledonia (K. Cameron, pers. comm.) but the specimen cannot be found at the New York Botanical Garden herbarium (A. Weiss, pers. comm.) and is presumed lost. This sample was also positioned within the same polytomy as the Palauan samples and the more distant samples.

[1] *Oberonia* spp. *matK* phylogenetic tree inferred using MrBayes. The tree shows the relationships between field-collected samples in bold, herbarium specimens, and selected GenBank sequences for references. Values at each node are posterior probabilities. Insert: In situ photograph of *Oberonia equitans* in Palau courtesy of B.J. Crain.

We consider this detail of the topology a random result of limited sampling.

Sample *Oberonia* sp. *B.J. Crain* 160L was conservatively not included under *O. equitans*. The specimen was not in flower, for which reason the identity could not be positively confirmed. Given the extensive vegetative phenotypic plasticity of *Oberonia* spp., the overall rather poor understanding of distributional limits of species in the genus, and the fact that three species of *Oberonia* have been reported from Palau (none of which have molecular data for comparison),

we take the conservative approach of referring to it as *Oberonia* sp. The internal and cumulative branch lengths are compatible with either a single sample of a distinct species, or a further sample of *O. equitans*.

The tree is well supported at the relevant nodes with posterior probabilities >0.94. Some internal nodes are less well supported, with posterior probabilities as low as 0.55, which should be considered unresolved. Those low support values are most likely due to incomplete taxon sampling of a genus with approximately 200 species.

The marker *matK* may be considered of insufficient discriminating power by some who prefer a set consisting of *rbcL* + *matK* + *ITS*. The clean results with samples from the same species forming well-supported clades in every single case (*O. cavaleriei*, *Oberonia delacourii* Gagnep., *O. rufilabris*, *Oberonia recurva* Lindl.) indicate that for the purpose of this investigation *matK* provides the necessary information. Additionally, taking into account within- and between-species branch length and the associated morphological data further supports our conclusion.

Li et al. (2016) found a similar short branch length polytomy for 15 samples of *Oberonia jenkinsiana* Griff. ex Lindl. and its not yet formally recognized synonym *Oberonia austro-yunnanensis* S.C.Chen & Z.H.Tsi in their Bayesian phylogeny based on *matK* + *ITS*, while other species such as the 13 samples of *Oberonia caulescens* showed more structuring. Terminal and internal branch lengths varied in a similar way as in our analysis, and support values were similarly strong. Relative branch lengths were similar in species common to both studies. The terminal and internal branch lengths of *O. rufilabris* were longer than those of *O. cavaleriei*, which were longer than those of *O. delacourii*, suggesting that *matK* is an adequate estimator for the assessment of species boundaries.

As an aside, the spelling of *O. austro-yunnanensis* should retain the hyphen in accordance with ICN Art. 60.11 Ex. 41 (contra World Checklist of Selected Plant Families 2020).

SYSTEMATICS

Oberonia equitans (G. Forst.) Mutel, 1837

Basionym. *Epidendrum equitans* Forster, 1786: 60. Type. *G. Forster 170* lectotype BM (not seen; designated by Kores 1989: 57). *G. Forster 192* isotype/isolectotype BM000084364, P [not seen in 2019, not in P database]. Possible

isotype BM 000082099 *Forster s.n.*, sine loc. Isolectotype Moscow State University Herbarium, fide US herbarium sheet photo. Tahiti.

Oberonia glandulosa: Lindley, 1859: 6. [nomen illeg.]. Type. *Kartalsky (Prescott) s.n.* (K), *Matthews 158* (syntype E00373990, K s.n.), Otaheite [=Tahiti]. No lectotype has been designated (Kores 1991).

Oberonia aurea Schlechter in K. Schumann & Lauterbach, 1905: 109. Type. *Schlechter 14673* (syntype: B lost). Mountain forest near Punam, Neu Mecklenburg, 600 m. Syn. nov.

Oberonia ciliolata Hooker, 1890: 181. *Ridley s.n.*; *Ridley [375]* (syntype K 000943006: basis of Hooker (1895: pl. 2318), SING 0047511); not BM000088559: is lectotype of *O. dissitiflora*, see remarks. Krangi, Singapore. Syn. nov.

Oberonia oxystophyllum J. J. Smith, 1905: 237–238. Type. *Herb. Lugd. Bat. 904, 84–127*, now [*Korthals s.n.*], syntype L 0091768, [*Hallier s.n.*] K 000942986), Gede, near Tjibodas; Patoeba, Java, [Indonesia] [6.788S 106.982E]. Reference by Smith to —128—130? cannot be considered type material, because it was not unambiguously assigned to the taxon. Syn. nov.

Oberonia flexuosa Schlechter, 1906: 62. Type. *Schlechter 15496* (syntype B: lost). On trees along streams in the mountains near Ou Hinna, New Caldeonia.

Oberonia mcgregorii Ames, 1907: 321–322. Type. *R. C. McGregor 291* (syntype AMES 9919/Harvard Barcode 00101991), Balete, Baco River, Mindoro, Philippines. Syn. nov.

Oberonia equitans var. *chaperi* Finet, 1908: 337, pl. 10, figs 29–30. Type. (iconotype), ubi?

Oberonia lampongensis Smith, 1917: 22. Type. *H. A. Gusdorf living Culture In Hort Bogor. sub numero 62 pro parte* (syntype). Lampong near Menggala, Sumatra. Syn. nov. of *O. equitans*.

Oberonia affinis Ames & C. Schweinfurt in Ames, 1920: 79–81, pl. 89, figs. II, 2. Type. *Clemens J. 102* syntypes AMES 16978, 16979; Harvard Bar Code 00101935, 00101936, BM000088335, E00394089, F 493793, K 000942995, MO 68377, MO 6837753, P02291942, SING 0043926, US 1170971, Lobang, Cave, 5,000 feet (= 1,666 m). *Clemens 275*, syntype, Marei Parei Spur. *Clemens 380*, syntype, Kiau. Syn. nov.

Oberonia palawensis Schlechter, 1921: 462–463. Type. *C. Ledermann 14475* (syntype B: lost: Fosberg and Oliver

1991), Palau, near Ngatkip on Babelthaob, Palau, 50 m (7.382N 134.513E). Neotype *Crain 198* US 3737901 here designated. Ngardok Nature Reserve, Melekeok, Babeldaob, Palau. Syn. nov.

Oberonia enoensis Smith, 1928a: 454–455. Type. *Toxopeus 94* syntype L0061740, Boeroe: Wai Eno, 600 m (protologue). Buru, Maluku, Moluccas, Indonesia (type label). Syn. nov.

Oberonia murkelensis Smith, 1928b: 125. Type. *Kornassi ex Ruten 1457*, syntype L 0061788, Goenoeng Moerkele [= Gunung Murkele], Central Seran, [Sumbawa], Moluccas, Indonesia, 1000–1900 m. Syn. nov.

MATERIAL EXAMINED

Thailand. Kerr 610 K 0000596120. Bangkok.

Malaysia. UNESCO 420, 421 SING 0141326. Ulu Kelantan, Gua Musang, Malaya. *UNESCO Limestone expedition 1962 421* K s.n. Gua Muang, Ulu. *Native Collector/Syngé 447* K s.n. Mount Dulit, Dulit Ridge, Sarawak, 1,240 m. *Haviland s.n.* SING 0141407. Sarawak. *Hewitt 15* SING 0141408. Sarawak. *Carr s.n.* SING 0141415. Mount Kinabalu, Koug, Sarawak, 400 m. *Henderson 332* SING 0141327. Kot Glanggi, Pahang. *Henderson 22446a* SING 0141321. Kota Glanggi, Pahang. *Mot Nur s.n.* SING 0141322. Bukit Sagu, Pahang, 300 m. *E Rostado s.n.* SING 0141323. Bundi, Tringganu. *R Denny 313* SING 0141324, 0141328. Sungli Rambai, Malacca. *Ridley 313* BM 000088324. Malacca. *R Derry s.n.* SING 0141326. Sungei Kesang. *Lugas 1489* K s.n. Sabah, Kampung Melangkap Tomis, Sekitar Kampung Melangkap Tomis, 400 m. *Carr 3659, SNF 27982* SING 0141402, SING 0022049 [spirit] Sabah, Bundu Tuhan, 1,400 m. *Carr SFN 26371* SING 0141401 Sabah, Dahobong River on label, Tahubant River in citation, 1,100 m. *Clemens 40924 B* s.n., E 00616203, K s.n. Sabah, Penibukan near Pinokkok Falls, 1,600–2,300 m. *Clemens 40822* BM 000088329, K s.n. Sabah, Penibukan, belos Pinokkok falls, 1,500 m. *Clemens 50240* B. s.n., BM 000088331, K s.n. Sabah, Mount Kinabalu, Tenomopok, 1,650 m. *Clemens 40861* BM 000088330 Sabah, Mount Kinabalu Penibuka, Side Ridge E of camp, 1,350 m.

Papua New Guinea. Carr 10494 CANB 61947, SING 0141467. Lala River, 1,770 m. *Carr 17128* BM 000088388. Kokoda. *Carr 17084* BM 000088410. Kokoda. *Carr 10494* BM 000088415. Lala River, 1,800 m. *Millar NGF 38328* CANB 212585, K s.n., SING 0141492. Watabung, Goroka subdistrict, Eastern Highlands, 2,300

m. *Millar NGF 38328* K s.n. Watabung, Goroka subdistricts, Eastern Highlands, 2,300 m. *Millar & Dockrill 22868* K s.n. Island of Kui Morobe, 15 m.

Singapore. Ridley s.n. BM 000088324. Krangi. *Ridley 2034* BM 000088337, MEL s.n., SING 0010910. Cahn ctran Kang, 23 m. *Ridley 2034a* BM 000088377, K s.n., MEL s.n., SING 0010908. Changi. *JJ Smith s.n.* SING 0010913. Suna Murai?. *JS Goodenough s.n.* SING 0010912. Krangi. *Ridley 10153* SING 0010907. Bukit Tumiak? Road. *Sinclair 5129* E00616464. Seletar forest behind Kee Soon Village.

Indonesia. Balgooy 3669 K s.n. Lake Matano south, between Soroako and Matano, Sulawesi, 400 m. *SBGO 3291* SING 0141504. Sulawesi, Desa Baruppu, Kampong Bubuk, 1,600–1,700 m. *de Vogel 6062* K s.n. Selatan, N shore of Lake Matano, E of Nuha, Sulawesi, 450 m. *Vermeulen & Dustermaat 972* K s.n. interior zone, along trail Long Pa Sia–Long Samado, near crossing with S Malabid, Sabah, 1,300 m. *SBGO 3392* SING 0141501. Lower slopes of E flank Rantepao–Paloppo divide, Sulawesi, 300–400 m. *SGBO 3393* SING 0141503. Lower slopes of E flank Rantepao–Paloppo divide, Sulawesi, 300–400 m. *Alston 13852* BM 000088423. Kambahan, near Lubuksikaping, Sumatra, 300 m. *Haviland 841* K s.n., Borneo. *JJ Smith 22* SING 0141440. Tiibodas?, Java. *Zollinger s.n.* W Reichenbach 12598. Java, 500 m. *S. Darutan 355* BM 000088341. Borneo, 1 mile of Kahung, downstream, 430 m. *Everard Im Thurn 34* P 00310614. [Java] Drake Range, W of Matakina, Colo North, 1,300 m. *Comber 1395* K s.n. Java, Arjuno Weliran, NW above Trawas, 1,370 m. *Comber 1559* K s.n. Java, G Lamongan S of Probolinggo, 510 m. *Comber 1557* K s.n. Java, G Raung S., 1,100 m. *SFN 8155* SING 0141439. Java, Tjibodas on G Godela, 1,500 m. *Chaper s.n.* P 00364386. Borneo. *de Vogel & Vermeulen 7185* K s.n. Celebes, Utara Bolaang Mongondow, Gunung ambang Nature Reserve, Danau Moot area, 1,000 m. Phillipines. *Reillo 16* MO 799956. Luzon, Laguna.

Palau. Canfield 666 US 3293387. Oreor [= Koror]. *Timberlake 3168* US 3293383. Aimeliik, Babeldaob (note: specimen is listed as coming from the island of Oreor [= Koror]; however, the State of Aimeliik is on the island of Babeldaob, which is just north of Koror). *Fosberg 25740* US 3293386. Babelthuap [= Babeldaob], 0–20 m. *Bowden-Kerby Lr 5796* US 3293385. Babelthuap [= Babeldaob], 0–10 m. *Evans 619* US 3293384. Aulupse’el = [Ulebsechel]?, Risong Bay, Koror, 0–50 m. *Canfield*

367 US 3293388. Ngatpang, Babelthuap [= Babeldaob], 5 m. *Hosokawa 9100* US 3726606. Babelthuap [= Babeldaob]. *Crain 134* US 3694789. Ngeruktabel, Koror. *Crain 198* US 3737901. Ngardok Nature Reserve, Melekeok, Babeldaob. *Canfield 366* US 3296687. Ngelobel (Ashakasengu) Island, S Koror Municipality, inlet on NW side of island, 1 m. *Timberlake 3168* US 32993383. Skillang’s Paddock (Tulau), Imutsubech, Aimeliik State.

New Caledonia. Vieillard 3296 P 00081696, 00081697. *Whitmee s.n.* BM 000088469. Loyality Islands Lifu. *MacKee 21978* P 00081685. Oue Koura, haute de Dothio 40 m. *Le Rat s.n.* P 00081684. Sable Unio. *MacKee 26296* P 00081686. Kone, Mount Tandji, 800–900 m. *MacKee 31023* P 00081687. Col d’Amieu, mont Pembai, 800 m. *Hurliman 1163* P 00081683. Paoué valley, south flank, Tipindje, 500 m. *MacKee 33678* P 00081688. Hienghene, Kavatch, 200 m. *MacKee 42529* P 00081680. Noiumea, Haute Amoa, Pomanhou, 500 m. *Veillon 2123* P 00081690. Katrikoin, Launay, 300 m. *Dagostini & Barriere 1281* P 02102974. Tiebahi, 500 m. *Guillaumin 9866* P 00081682. Between Ponerihonen and Honaiton. *McPherson 2562* P 00081701. Mount Panié, 20 air km NW of Hienghénéee, 500 m.

Vanuatu. Macdonald 4 MEL 569474. Aneitum. *HF Moore 277* US 00241464. Maewo. *Morrison s.n.* K s.n. Efate Nudine Bay. *Morrison s.n.* K s.n. Hills between Unum & Anilngkot/Anitzem. *Morrison s.n.* K s.n. Efate Hills Nudum Bay. *Whatley 104* K s.n. Pentecost Village, Ena, 290 m. *Smith 1485* K s.n., P 00310616. Vanua Mbalavu, 0–200 m. *Schmid 3624* P 00310683. Anatom. *Raynal 15994* P 00310684. Ikouroup Tanna.

Wallis and Futuna. Veillon 5108 P 00310685 Futuna, Alofi, north slope 300 m. *Hoff 4053* P 00310687. Futuna, Mount Puke, 450–500 m. *Morat 7084* P 00310686 Mount Lulu.

Niue. Williams 9598 MICH s.n. S of Alofi village, 20 m.

Samoa. Le Guillou s.n. P 00310618. *Sin. coll., s.n.* W 3066. Savaii approx. 100 m. *Palau Whistler W2638* K s.n., US 00241470. Savai’i, W of Mauga Mu 1550 m. *Rechinger 1589* W Reichenbach 3063. Savaii Aopo, 300 m. *Rechinger 16* W Reichenbach 3064. Savaii, Lalatelle. *Rechinger 127* W Reichenbach 3062. Savaii, between Sassina and Aopo. *Graeffe s.n.* W Reichenbach 8372 W68800. Upolu. *HE Parks 16237a* US 00241481. Upolu, near Tiai, 720 m. *WA Whistler W204* US 00241469. Upolu. *F Reinecke 184* US 00241483. Upolu. *WA Whistler 3946*

US 00241456. Namua. *Reinecke 184* E 00616504, WU s.n. Upolu, Vailale ridge. *Whistler 2906* K s.n. Tutuila, Mount Tau, 350 m. *Mansfeld 172* K s.n. Upolu, swamp near Tiavi, 720 m. *K & L. Rechinger s.n.* W Reichenbach 3065. Tutuila, Pago-Pago.

Tonga. Parks 16237 MO 1035159. Eua, Plateau, exposed rocks. *Parks 16237a* BM 000088471, US 00241482. Eua, Plateau. *Yucker 15402* BM 000088470, US 00241473. Eua, above Riechelmann’s Fuai plantation near center of island, 245 m.

Cook Islands. A. Whistler 5825 US 01232921. Mangaia. *Sin. coll., s.n.* Reichenbach 37743 W68916. Mangaia Island. *WA Whistler W5038* US 00447248. Rarotonga, E of Ikurangi. *WR Phillipson 10132* US 00445241. *Luttril 350* K s.n. Rarotonga. *Cheeseman 675* K s.n. Rarotonga, central part of island. *Wilder 8* K s.n. Rarotonga.

Fiji. Seemann 588 MEL s.n., BM 000088468, K s.n., P 00310615, W Reichenbach 37814. Navua and Manar. *Parham 1823* K s.n. Naitasiri, above Wamawaya, 50 m. *Daanu 82* K s.n. Kurovisilou, Serau, 100 m. *AC Smith 7075A* US 00241472. Viti Levu. *AC Smith 7469* US 00241471. Ovalau. *AC Smith 7551* US 00241465, K s.n. Ovalau, Valley of Mbureta and Lovin Rivers, 20–50 m. *AC Smith 8586* US 00241466, K s.n. Viti Levu, Namosi Hill, bordering Winavindrau Creek in vicinity of Wainimakutu, 150–200 m. *AC Smith 1485* US 00241479. Eastern Division, Vanua Balavu (Mbalavu). *AC Smith 5241* US 00241476. Viti Levu, Western Division. *AC Smith 5528* US 00241475, K s.n. Viti Levu, Western Division, Nandroga and Navosa, N portion of Rairaimatuku Plateau, between Nandrau and Nanga, 725–825 m. *AC Smith 5751* US 00241474, K s.n., P 00310613 [top specimen only]. Viti Levu, Central Division, Naitasiri, N portion of Rairaimatuku Plateau between mount Tomanivi/Victoria and Nsasonngo, 870–970 m. *Greenwood 1112* K s.n. Viti Levu, Naitasiri, near Nasinu. *Vaughan 3181* K s.n. Viti Levu, Tamavna Ridge, mile 6, 200 m. *Meebold 16813* K s.n. Suva, 9 miles above Suva. *Greenwood 1155* K s.n. Viti Levu, Lautoka, Mount Evans, 750 m. *Smith 1731* K s.n., P 00310617. Vanua Levu, Mbua Lower Winunu river valley, 0–200 m. *Greenwood 209* K s.n. Mount Lautoka, 260 m. *Tothill & Tothill 511* K s.n. Suva, Central Road. *Tothill & Tothill 883* K s.n. Viti Levu, Suva, Central Road. *Parham 147* K s.n. Viti Levu, Rewa Province, Mount Korobaba, 260 m. *Vaughan 3181* BM 000088472. Tamavua Ridge, Mile 6, 200 m.

French Polynesia. Tahiti. J Banks &

- DC *Solander* 430 US 00241463. *Banks & Solander s.n.* F 694765. *Expedition Novara* 117 W68918. *Sin. coll., s.n.* W Reichenbach 11734 W68802. *Setchell & Parks* 430 P 00310665. *Richard s.n.* P 00310674. *Pancher* 3 P 00310663. *Vieillard* 3 P 00310668. *Vesco s.n.* P 00310667. *Vesco s.n.* P 00310666. *Ribiourt* 82 P 00310676. *Vieillard s.n.* P 00310672. *Vieillard s.n.* P 00402800. *Vieillard s.n.* P 00310673. *Morrenhout s.n.* P 00310677. *Lepine s.n.* P 00310678. *Lay & Collie s.n.* BM 000088474. *Sin. coll. s.n.* BM 000088473. *Shuttleworth s.n.* BM 000088473. *Grandjean s.n.* P 017712107. *WA Setchell & HE Parks* 430 US 00241462. *Florence* 2482 P 00310669. Mount Marau, Sentier du Pic Vert 1,240 m. *Hallé* 6931 P 00310680. Tahiti, route of Mount Marau 700 m. *Hallé* 6937 P 00310679. Riv. Vaihira valley 50–60 m. *Hallé* 6993 P 00310671. Punaahuia, S of Papeete, 300 m. *Raynal & Taureau* 16546 P 00310664. Road of Aorai, between Fare Hamuta and le Belvedere 950 m. *Savatier s.n.* P 00310675, P 00310682. Vallée de la reine. *ML Grant* 3613 US 01104522. Punaauia Diadem district, 491 m. *FR Fosberg* 63613 US 00619673. 5–20 m. *FR Fosberg* 62965 US 00619672. Papeete, headwater of Tipaerui River, 950–1,000 m. *Florence & Sykes* 11342 US 00689598. Papeete, 80 m. *Balgooy* 1677 MO 2228544. Mahina Valley, 700 m. *ML Grant* 3613 P 00310653. Punaauia Diadem district, 491 m.
- Bora Bora. D'Urville* 1061 P 00310645. *D'Urville s.n.* P 00310650. *MMJ Balgooy* 1942 CANB 00583505, K s.n. W slope of Pahia, 100 m. *Florence* 12107 P 00360516. Faanui, Mount Pahia, E flank, 420 m.
- Huahine. L Dunn* 511 US 01076801. *Mouly* 496 P 00592106. Flancs of the Vaiparao valley, 200 m. *J Florence & Tahuaitu* 11583 P 00310656, US 00445241. Fare, Mount Mato Ereere, N crest, 425 m. *Florence & Tahuaitu* 11566 P 00310655. Fare, Pipihaua valley, right flank, 130 m.
- Moorea. HM Smith* 8 US 00241458. *FR Fosberg* 63663 US 00619701. *M-H Sachet* 2542 US 00619665. *FR Fosberg* 60957 P 00310569, US 00619674. Ridge above Le Belvedere, head of Hpunohu Valley. *Cronk et al.* T62 E s.n. SW valleys, Patiri valley, 300 m. *Raynal* 17930 P 00310648. Moo Afaretaitu. *Jolinon* 1334 P 00310654. Vaiare hill summit. *Smith* 8 P 00310660. Opunohu–Roroie District. *Florence* 8318 P 00310661. Haapiti, crest between the high valleys of Vaianae and Atiha, 350 m. *Birnbaum* 75 P 00310657. Afareiatu, Haute Nauroa 700 m.
- Makatea. GP Wilder* 1141 K s.n., US 00241480. 60 m. *Jones* 861 K s.n., P 00310620. 100 m.
- Meetia. St. John* 14198 F 1438060, K s.n., MO 1638487, P 00310643, US 00241478, W Reichenbach 5315 W68919. Fatia-po to Fareura, 200 m.
- Raiatea. GH Gagné* 1786 US 00619667. 475 m. *Welch et al.* 26616 MO 5796911. Trail to Temehani Ute Ute, 450 m. *Welch et al.* 26619 MO 5796913. Trail to Temehani Ute Ute, 400 m. *Moore* 129 MO 2196179. Valley W of Uturoa, 280 m. *Moore* 410 MO 2196301. Opua Valley, 100 m. *Morat* 9683 P 00310649. Temehani ute, 150 m. *Florence* 10351 P 003110658. Uturoa, Mount Tapioi, 230 m. *Mouly* 377 P 00591985. Vaiaou valley, 200 m.
- Funaauia. Florence* 8195 P 00310652. Punaru valley, Fare Anani, 430 m.
- Raupiti. Raynal* 17854 P 003106466, P 003106467. Mount Tiriano, 260 m.
- Tahaa. Florence* 10631 P 00310662. Mount Purauti, SE crest, 245 m.
- Austral Islands. Ruruto. Hallé s.n.* B s.n. N part. *Hallé* 7284 P 00310630. N of Avera. *Florence* 5567 P 00310635. Unaa, N of Tetuanui plateau, high Vaire, 205 m. *Hallé* 7163 P 00310628, US 00241452. Naairoa. *Hallé* 7082 P 00310631. Prise d'eau de Tetuanui. *H St. John* 16741 F 1438056. Arei, 75 m. *N Hallé* 7239 P 00310629, US 00241451. Middle Vaitotai. *Florence* 9240 P 00310623. Rurutu, Rairiri, East, below T Anaeva, 110 m. *Florence* 9180 P 00310622. Tetuanui Plateau, NW sector, 210 m. *Hallé* 6648[b?] K s.n. Middle Saitotai. *Florence* 5703 P 00310636.
- Raivavae. Anatonu*, foot of the cliff below Mount Hiro, 160 m. *Florence & Sykes* 11342 P 00310621. Vaiiuru, Turani valley, 80 m. *N Hallé* 7082 CANB 8602862, K s.n., US 00241453. N of island, spring of Cetuanin.
- Rapa. G Paulay* 85 US 00619675. 200 m. *Hallé* 7694 P 00310632. SSE Pukumia, 185 m. *Hallé* 7619 P 00310633. SSE Pukukia, 200 m. *Sykes* 161 CHR 495761 K s.n. Valley behind Vairua. *John & Fosbert* 15976 K s.n., P 00310634. Pic Rouge, S slope, 80 m.
- Tubuai. SH Shomer* 6761 US 00241468. *SH Shomer* 6692 US 00241467. 300–325 m. *Hallé* 6648 K s.n., P 00310627, US 00241455. Below coffee plantation of Tamatoa, 25–35 m. *Hallé* 6884 P 00310624. N of Mahu, 250 m. *Hallé* 6673 P 00310626, US 00241454. Mahu. *Hallé* 6755 P 00310625. Mont de la Prise d'eau de Mataura, 60–80 m. *St. John* 16349 MO 1638532. Taitaa NE slope, 330 m.
- REMARKS
- In the genus *Oberonia*, the species epithet *equitans* is highly confused because it was introduced by several authors, with subsequent authors creating primary and secondary homonyms:
- *Epidendrum equitans* Forster = *Oberoniaequitans* (Forster) Mutel, correct: Malaya to Western Pacific Islands.
 - *Cymbidium equitans* Thouars = *Oberonia equitans* (Thouars) Lindley, synonym of *Oberonia disticha* (Lam.) Schltr.: East Africa.
 - *Malaxis equitans* Blume = *Oberonia equitans* (Blume) Lindley, junior synonym of *Oberonia padangensis*: Malaya.
- Subsequent authors have not always been aware of those homonyms, commonly adding the wrong authority to the record. The same also applies to identifications on herbarium specimens. This has led to widespread confusion regarding the identity and distribution of *Oberonia equitans*. Sometimes range indications of “*equitans*” were combined from multiple discrete taxa, leading to a cited distribution from East Africa to French Polynesia (e.g., Finet 1908).
- The lectotype of *O. equitans* is labeled *Forster* 170, but in the publication it is erroneously referred to as *Forster* 316 (Kores 1991). The lectotype designated by Kores (1989) at BM and the cited isolectotype at P could not be found in those collections during visits in 2016 and 2019, respectively. They are not recorded in the online databases either. The whereabouts of those specimens is currently unresolved. The only confirmed type known to exist is a *Forster s.n.* sheet at BM, which agrees with the commonly accepted species concept of *O. equitans* (Forster) Mutel.
- Oberonia glandulosa* is a well-established synonym of *O. equitans* (e.g. Cribb and Whistler 1996, 2011) and is not further discussed here.
- Oberonia aurea* is a synonym of *O. equitans*. The common attributes include the habit, the hairy rachis, the hairy pedicelled ovary, the hairs on the external surface of the floral bract and the sepals, the lip with small auricles, constricted mesochile, bilobed and incised epilobe, flower color from pale-green yellow turning to dull orange with maturation (Fig. 2).
- Oberonia ciliolata* is a clear synonym of *O. equitans* (Forster) Mutel. The type of *O. ciliolata* is confusing and requires some clarification. Hooker (1890) designated a specimen collected by Ridley without gathering number (*Ridley*) or repository as type. The specimen cited at Kew is the basis for Hooker's (1895, pl. 2318) figure. Accordingly, this gathering (*Ridley*

375) can be considered the type gathering, with the Kew specimen constituting a syntype. The same gathering number was used twice by Ridley, and that is the type gathering of *Oberonia dissitiflora* Ridley.

The overall caulescent habit, the papillose rachis, papillose pedicelled ovary and papillose back of tepals, the deeply incised acute, acuminate bract, and the identical shape of sepals, petals and bract clearly show conspecificity of *O. ciliolata* and *O. equitans*. *Oberonia equitans* was applied to specimens from the Western Pacific Islands, while *O. ciliolata* was applied to specimens from the Malayan Archipelago.

Oberonia oxystophyllum has the same habit and floral characteristics as *O. equitans*, making the two synonyms. The hairy bracts, hairy column, hairy back of the sepals, the oblong shape of the petals, the lip with moderate auricles, constriction of the mesochile, and bifurcated epichile with incised apical lobes are all shared characters.

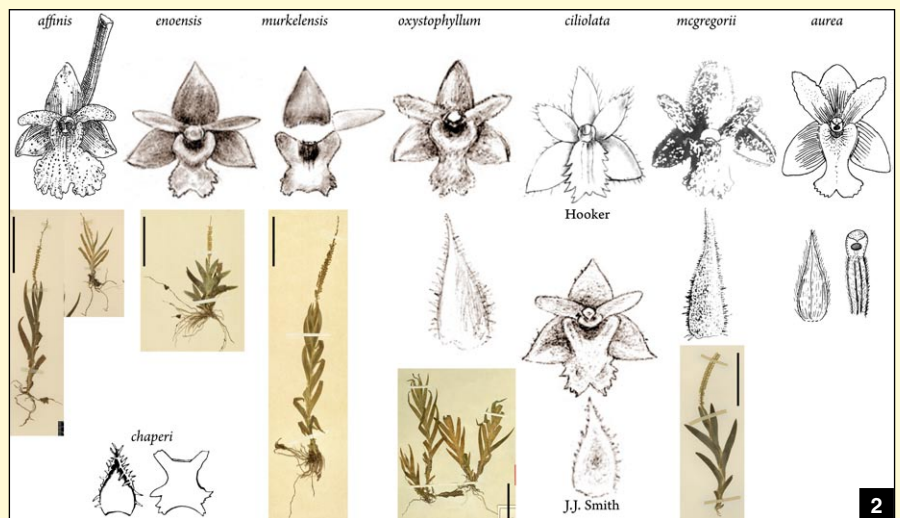
Oberonia flexuosa is a well-established synonym of *O. equitans* (e.g. Cribb and Whistler 1996, 2011) and is not further discussed here.

Oberonia mcgregorii shares the habit, the hairy backs of the flowers, the shape of the petals and every aspect of the lip shape with *O. equitans*, which makes the two synonymous. *Oberonia mcgregorii* has been cited for the Philippines.

The illustration of *Oberonia equitans* var. *chaperi* clearly represents *O. equitans* s.s. (G. Forst.) Mutel. Finet (1908) thoroughly mixed the two *equitans* in his treatment (see above) and his diagnostic characters (hairs on pedicelled ovary, all tepals, bract) address the distinction of *Oberonia disticha* from East Africa and *O. equitans* from the Pacific region. Due to this elementary confusion, he did not describe a variety of *O. equitans* s.s., hence, his variety is unjustified.

Oberonia lampongensis has previously been recognized as a synonym of *O. ciliolata* (e.g., Comber 1990). With *Oberonia ciliolata* as a synonym of *O. equitans*, *O. lampongensis* becomes a new synonym of *O. equitans*.

Oberonia affinis is described in the protologue as having hairs on rachis, pedicelled ovary and back of sepals, all indicative of conspecificity with *O. equitans*; those characters unfortunately were not shown in the drawings. The shapes of the floral elements as well as the habit of the type is equally compatible with *O. equitans*. Accordingly, the two species are considered as synonyms.



It is important not to confuse the type gathering of *Oberonia affinis* Clemens 275 syntype of *O. affinis* with Clemens 275A syntype of *Oberonia triangularis*.

Oberonia palawensis is an overlooked taxon that has rarely been used after the introduction by Schlechter (1921). A neotype is here designated for *O. palawensis*. The syntype in B has been destroyed (Fosberg and Oliver 1991); no other syntypes are known to exist. The species has never been illustrated and it is difficult to ascertain the identity of a taxon from verbal descriptions alone. This is particularly true for species-rich groups of microfloral species such as *Oberonia* spp. We here clarify the identity of the name by designating a gathering from as near as possible from the locus typicus. The neotype matches the protologue (Schlechter 1921) in every detail.

Oberonia palawensis is a clear synonym of *O. equitans*. The protologue indicates the erect habit with triangular leaves, the papillose rachis of the inflorescence, papillose pedicelled ovary, papillose flowers, and papillose lanceolate-acuminate bract, and also specifies the narrow oblong petals.

The cited commonalities offer abundant evidence for conspecificity. The shape of the petals shows some intraspecific variability from more narrow oblong so somewhat broader triangular. Once a large number of specimens have been examined, it becomes clear that those are merely the extremes of a continuous character state distribution, and accordingly, are of no taxonomic importance. It is merely intraspecific variability.

The drawing of *Oberonia enoensis* is indistinguishable from those of *O. oxystophyllum*, *O. murkelensis*, and *O. ciliolata*, all drawn by J.J. Smith. The

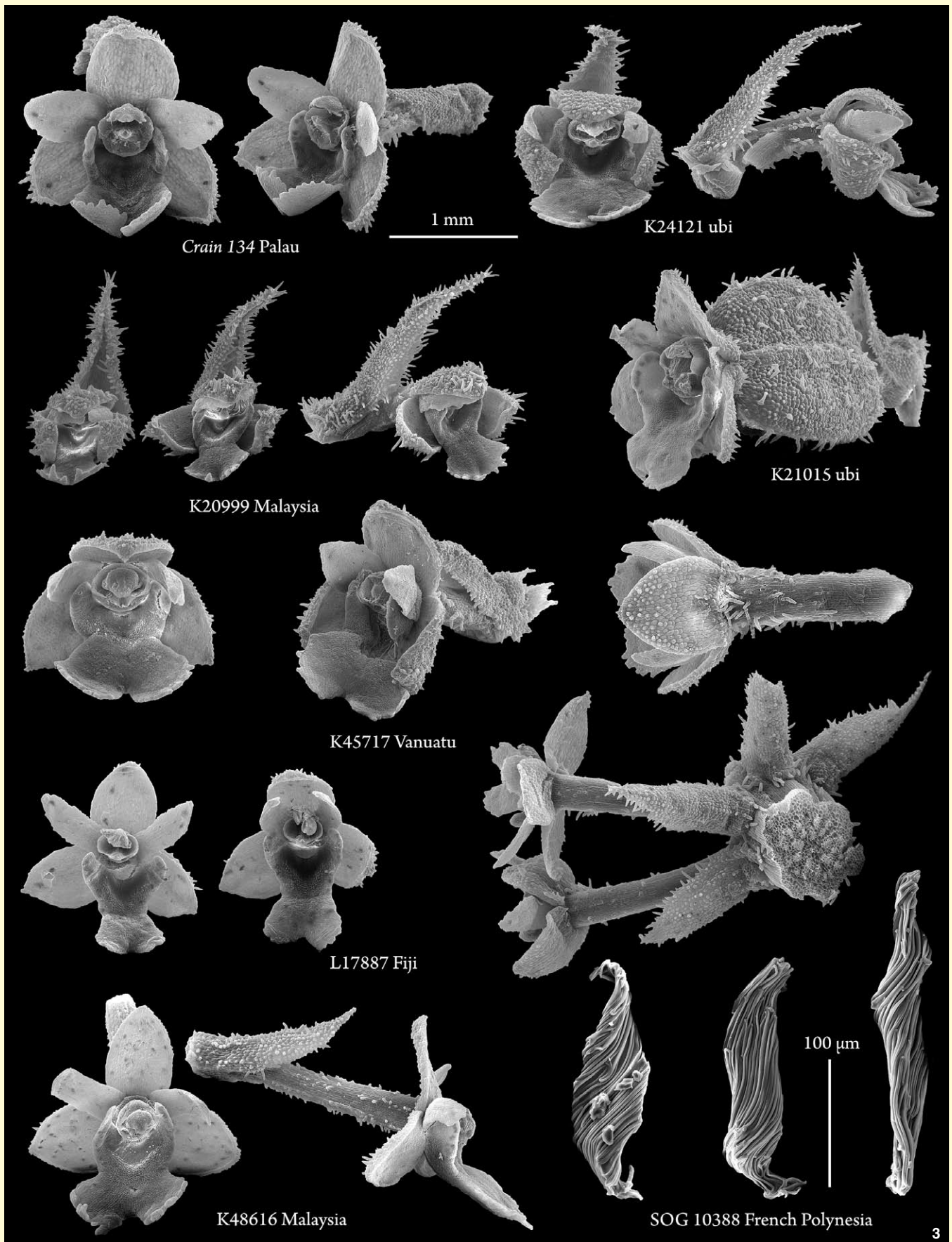
[2] Synonyms of *Oberonia equitans*.

Oberonia affinis: Drawing from protologue and habit of *O. affinis* syntypes AMES barcode 00101935. *Oberonia enoensis*: Flower illustration by J.J. Smith and habit of syntype. *Oberonia murkelensis*: Illustration of flower of *O. murkelensis* by J.J. Smith. Dissected floral parts digitally rearranged to match live position, and habit of *O. murkelensis* syntype. *Oberonia oxystophyllum*: Flower illustration by J.J. Smith and habit of syntype. *Oberonia ciliolata*: Stylized figure from Hooker (1895), drawing from type by J.J. Smith. *Oberonia mcgregorii*: Drawing from Ames (1908), and habit of AMES syntype. *Oberonia aurea*: Drawing of flower, bract and column from Schlechter (1923). *Oberonia equitans* var. *chaperi*: Drawing of lip and bract from Finet (1908). Scale bar for habits = 5 cm.

habits of the type specimens of those respective taxa is equally congruent. Smith (1928a) noted the similarity of his *O. enoensis* with *O. lampongensis* [= *O. ciliolata*]. Congruent characters cited in the protologue are the hairy pedicelled ovary, bracts, and sepals, as well as the light yellow color of the flowers. *Oberonia enoensis* is a synonym of *O. equitans*.

Smith (1928b) placed *O. murkelensis* in section *Otoglossum* (= *Menophyllum*), but the spreading epichile of the lip and the hairs on the pedicelled ovary place the species in *Adenorachis*.

As noted above, *Oberonia murkelensis* is indistinguishable based on floral shape and habit of the type. The protologue compared the new species to *Oberonia subanajamensis* (= *Oberonia punctata*; see Geiger 2019a) and noted the hairy bracts as well as the yellow color of the flower,



[3] *Oberonia equitans* flowers from throughout its distributional range, demonstrating intraspecific variability. Scale bars: flowers = 1 mm. Scale bar seeds = 100 µm. For details see text.

all compatible with *O. equitans*. The species was described from a herbarium specimen only. The drawing of the flower indicates that the specimen was not in the best condition, which explains why some of the finer details of flower morphology were not given. For instance, the sepals were not described as hairy, but not as glabrous either, hence, the absence of additional confirming characters cannot be taken as disconfirming.

INTRASPECIFIC VARIABILITY With the combined morphological–molecular approach we can demonstrate extensive intraspecific variability. Flowers and sequence data from *Crain 134* from Palau and the sequences from French Polynesia serve as anchor points; both are found in a large polytomy with short terminal branches. The flowers of *Crain 134* (Fig. 3) are typical *O. ciliolata* morphs with a rather narrowly constricted mesochile, more flared epichile lobes, and extreme pubescence all over the flower. From French Polynesia, only *O. equitans* is known, with a less constricted mesochile, a less flared epichile with fewer points, and somewhat less pubescence overall (Fig. 2: K45717 Vanuatu, K 21015), and K21015 showing additionally the turgid flower on an already developing seed capsule commonly seen in *O. equitans*. The few samples with multiple flowers (K12099 Malaysia and L17887 Fiji), demonstrate within sample variability in number and degree of point formation on the epichile, and degree of constriction of the mesochile. Absolute size also appears to be somewhat variable as shown by the smaller flowers of K20999 from Malaysia. While those flowers were not entirely open, they appear to be approximately one-third smaller compared to the average size of the remainder. L17887 from Fiji is somewhat intermediate between the above-cited sample from Malaysia and the others.

Extensive intraspecific variability is increasingly recognized in *Oberonia*. Bunpha et al. (2019) correctly synonymized two well-established names, *Oberonia falcata* King & Pantl. under *Oberonia anthropophora* Lindl. Those were distinguished based on size-dependent habit, flower size, and length of epichile lobes. The floristic characters vary extensively, and additional synonyms will be added to *O. anthropophora*. Horticultural data from plants grown over multiple years further support extensive intraspecific variability (Geiger 2018, unpubl. data). While minute differences are generally considered significant in the



systematics of orchids including *Oberonia* (e.g., Averyanov et al. 2019), it becomes increasingly clear that Comber’s (1990, p. 149) remarks on the “annoying variability” of *Oberonia* were correct.

That variability extends to the vegetative portion of the plant. Cameron (2005) demonstrated that major lineages within Malaxideae can be separated using vegetative characters. However, that discriminating power does not extend to the species level in *Oberonia*. Our illustrations can only show a limited sample of the range of morphologies. The extensive material examined (see above for listing) has shown every conceivable intermediate between those few samples shown and even further variation. The variability includes size of stem at flowering (5–20 cm), proportion of leaf length to leaf width (wider in smaller specimen, more narrow in larger specimens), leaf curvature (almost straight to distinctly falcate), and angle of spread of leaves (~10°–35°). No groupings can be formed, and there are no trends of covariation between vegetative and floral morphology. The simplest answer of a single species supported by a polytomy in our molecular analysis is the best explanation for all observations. We acknowledge that significant intraspecific variability in Orchidaceae goes against commonly held views, yet the available, multipronged, data-rich evidence clearly supports our conclusion.

COMPARISON There are several species with bifid epichile lobes bearing points. We include select comparisons to species with available material.

[4] *Oberonia punctata* habit (Andy’s Orchid plant), portion of inflorescence (DLG 680/HOAG 196) and SEM images of flowers (E00233059).

Oberonia punctata J.J.Sm. (Fig. 4) is overall smaller with more leaves of more or less equal lengths along the stem; the bract lacks hairs on the dorsal surface and along the margin, the pedicelled ovary and the back sides of the tepals lack hairs, and the epichile lobes separate at an acute angle from the mesochile.

Oberonia aporophylla Rchb.f. (= *Oberonia longirepens* J.J.Wood; Fig. 5) has much shorter leaves on the elongated stems, forms creeping stolons, and has white flowers.

Oberonia dubia J.J.Sm. (Fig. 6) has an acaulescent, fan-shaped habit with much more elongated leaves, auricles with some projections, and more elaborately fringed epichile lobes.

Oberonia disticha (Lam.) Schltr. (Fig. 7) is restricted to the East African province, is generally smaller, has more fleshy leaves, lacks hairs on rachis and back of tepals, and has an only slightly erose bract without distinct hairs.

Lewis and Cribb (1989) suggested that *Oberonia kaniensis* Schltr. [junior synonym of *Oberonia imbricata* (Blume) Lindl.] may be a synonym of *O. equitans*. The former is in the section *Labidous*, characterized by revolute sepals and a dual sac, while the latter is in section *Adenorachis* with spread sepals and a single sac. Accordingly, that suggested synonymy is in error.

ECOLOGY The ecological data are consistent with a broad synonymy of the

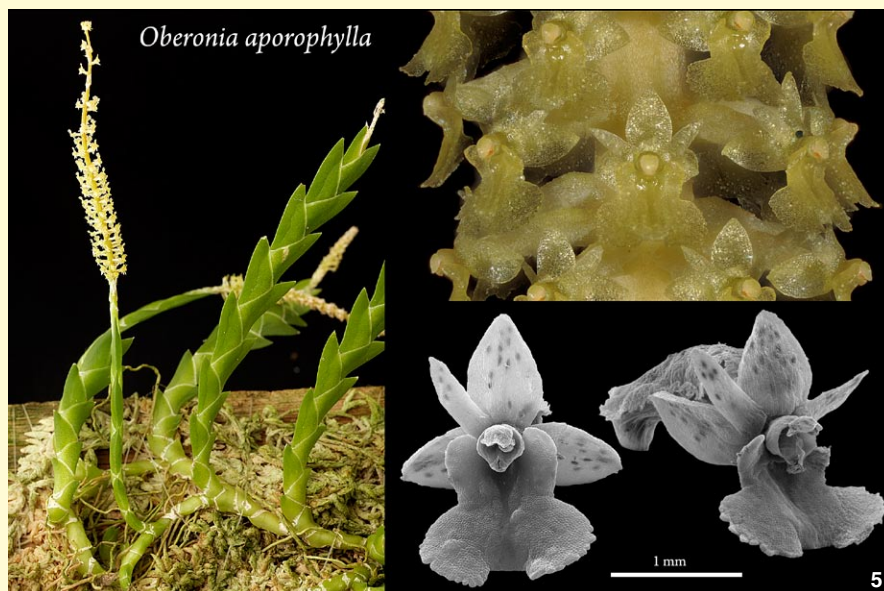
taxa in question. The available elevation data are shown in two groups, one for the Western Pacific Islands records, the traditional *O. equitans*, and one for the Malayan region, traditionally referred to as *O. ciliolata*. For the remaining taxa, there are too little data available to make meaningful frequency-based assessments. Those minor species are all known from the range of elevations covered by *O. equitans* s.l. For instance, *O. palawanesis* was described from 50 m elevation (Schlechter 1921).

The frequency distributions are remarkably similar. The observations near sea level are somewhat less frequent than at lower to intermediate elevations (~1,000 m), after which they drop rather steeply. There are fewer reports and records of the species at higher elevations in the Western Pacific. This can be explained in part by the overall lower elevations of the Western Pacific islands, particularly French Polynesia.

The phenology data show the species flowering throughout the year in both broad areas of its distribution. Phenology data in other species can show marked seasonality (Geiger 2016, unpubl. data). *Oberonia equitans* occurs on both sides of the equator, which may obscure seasonality patterns. However, seasonality is less pronounced around the equator, which lends credence to a true continuous phenology pattern. With respect to the Palau specimens (*Crain 134*, neotype *Crain 198*), they were found flowering in May and October, respectively; Schlechter's type was in bud in March and most likely would have flowered in April, the relative peak flowering time of *O. equitans* in the Malayan region.

Oberonia equitans has a distribution range that includes Thailand, Singapore, Malaysia, Indonesia, New Guinea, Palau, New Caledonia, Vanuatu, Niue, Wallis and Futuna, Tonga, Cook Islands, Fiji, French Polynesia, and the Austral Islands. Dispersal abilities seem to be pronounced as evidenced by samples from Palau, French Polynesia and Samoa all being found in a major polytomy in our molecular phylogeny. *Oberonia* has the smallest seeds in the Orchidaceae (~100 µm; Barthlott et al. 2014; Geiger 2014, unpubl. data), facilitating wind dispersal and making microendemism less likely. The seeds of *O. equitans* are slightly larger at 150–200 µm, but still small enough to permit wind dispersal over extensive distances (Fig. 3).

DISCUSSION The recent work on the alpha taxonomy of the overlooked genus



Oberonia (Bunpha et al. 2019; Geiger, 2016, 2019a, in press, unpubl. data) shows that critical global revisions are needed to clean up the accumulation of duplicate names in minor orchid groups. If the scale of overnaming in the genus *Oberonia* alone is taken as an indicator for orchids in general, then global orchid diversity could be overestimated by around one-third. The issue more likely affects diminutive or cryptic species, however, due to difficulties in field identification.

It is important to note that the issues stem not only from poorly known older names, but also from contemporary authors that continue to introduce a plethora of excess names. As a recent example, *Oberonia khuongii* Aver. & V.C.Nguyen in Averyanov et al. (2019) is identical to *Oberonia griffithiana* Lindl. (Geiger, in press), a fact communicated to one of the coauthors well prior to publication. They compared their *O.*

[5] *Oberonia aporophylla* habit (DLG 394/HOAG 49), portion of inflorescence (DLG 599/HOAG 50) and SEM images of flowers (DLG 394/HOAG 49, DLG 599/HOAG 50).

[6] *Oberonia dubia* habit (DLG 692/HOAG 272), portion of inflorescence (DLG 692/HOAG 272) and SEM images of flowers (DLG 692/HOAG 227).

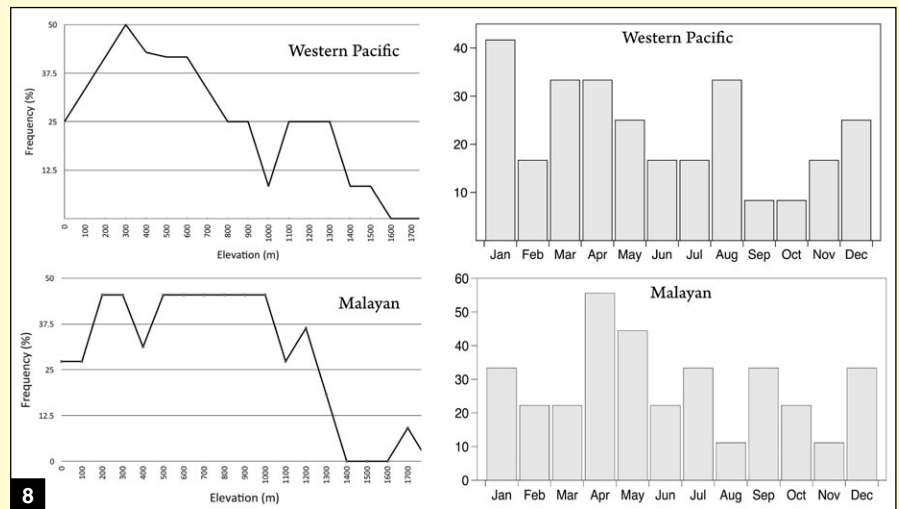
khuongii only to *O. cavaleriei*, a very different species with terete leaves, while *O. griffithiana* was only mentioned by name as another similar species without any further discussion of characters. A critical problem is that new species are not compared to the most similar species, but to seemingly random species occurring in the same geographic area, which is most likely due to the authors not being sufficiently familiar with the group in question. Formal synonymies for recent names will be detailed elsewhere

(Geiger, in press).

Another contributing factor, particularly in microfloral groups, is the outdated reliance on drawings and single-shot photographs to document morphology. While in systematic zoology (e.g., entomology, malacology), z-stack photography and electron microscopy have been considered standards for <5-mm specimens for at least two to three decades, those 21st century techniques are only rarely employed in systematic botany. Misleading drawings are a serious problem as shown with the case of *Oberonia carprina* Gilli, a synonym of *O. punctata* J.J.Sm. (Geiger 2019a).

Orchid systematics is still too 18th-century typological, where species are considered immutable and minute differences of individual specimens are considered diagnostic at the species level. Population thinking and explicit consideration of intraspecific variability is hardly taken into account when assessing biodiversity. Bunpha et al. (2019) doubted Geiger's (2019a) synonymization of *Oberonia fungumolens* Burkill under *O. padangensis* Schltr. due to slight differences in leaf shape and lip-to-sepal length ratio of 1.4× vs. 1.6×, which Geiger (2019a) was faulted for not explicitly addressing. Differences in vegetative shape were explicitly discussed under *O. rufilabris* by Geiger (2019a) as a proxy for range of variability in the genus overall. Variability in vegetative parts of *O. equitans* is clearly documented here and further supported by examination of the cited herbarium specimens. Proportional differences of floral parts can easily reach one-quarter to one-third among flowers on the same inflorescence (e.g., *Oberonia acaulis* Griff., *Oberonia ferruginea* C.S.P. Parish ex Hook. f., *O. cavaleriei*; Geiger, unpubl.), hence, proportional differences of <15 percent are clearly meaningless for taxonomy in *Oberonia*. Accordingly, the crystal-clear synonymy between *O. padangensis* and *O. fungumolens* is maintained. The complementary study of cultivated specimens and wild-collected material was noted by Geiger (2018), particularly considering intraspecific variability and genotype × environment effects. Intraspecific variability in *Oberonia* was discussed by Geiger (2019b). The “annoying variability” of *Oberonia* spp. had previously been noted by Comber (1990, p. 149).

Last but not least, in today's scientific climate of measurements of academic achievements, synonymizations are possibly the least recognized activity



- [7] *Oberonia disticha* habit (DLG 635/HOAG 14: yellow variant), portion of inflorescence (DLG 424/HOAG 12: orange variant) and SEM images of flowers (DLG 424/HOAG 12).
- [8] Elevation and phenology data for *Oberonia equitans*. The y-axis shows frequency of cited occurrence. Elevation data for *O. equitans* from Western Pacific Islands from Cribb and Whistler (1996), Hallé (1977), Lewis and Cribb (1989), Wood and Cribb (1994), Schlechter (1906: as *O. flexuosa*), Fleischmann and Rechner (1910), Brown (1931), Christophersen (1935), Kores (1989), Streitmann (1983), Sykes (2016), and various herbarium records. For Malayan region (as *O. ciliolata*) from O'Byrne (1994: as *O. aurea*, 2001), Beaman et al. (2001), Comber (1990), Wood and Cribb (1994), Carr (1930, 1935: as *O. lampongensis*), Schuiteman and de Vogel (2006: as *O. aurea*), Schlechter (1911: as *O. aurea*, 1921: as *O. palawensis*) and various herbarium records. Phenology data for *O. equitans* from Western Pacific Islands from Hallé (1977), Anonymous (1995), Guillaumin (1957), Kränzlin (1898), Schlechter (1906, 1910), Ames (1933), Brown (1931), Christophersen (1935), Yuncker (1959) and various herbarium records. For Malaysian region from Carr (1930, 1935: as *O. lampongensis*), Schuiteman and de Vogel (2006: as *O. aurea*), O'Byrne (1994: as *O. aurea*), Schlechter (1911: as *O. aurea*, 1921: as *O. palawensis*), Schlechter in Schumann and Lauterbach (1905: as *O. aurea*), and various herbarium records.

in systematics. While the introduction of a new name, including a synonym, and even the transfer of a species to a different genus, adds recognition, the cleanup of excessive taxonomic splitting garners far less recognition. No malus is attached to introducing synonyms either. Cleanup of superfluous names can have further implications beyond the raw tally of names. Recognizing *Oberonia attenuata* Dockrill, considered endemic to Queensland, Australia, and either extinct or at least critically endangered, as a southern range of the widespread *Oberonia insectifera* Hook.f. changes the outlook of the species' survival and conservation needs (Geiger 2019a).

A significant number of clear synonymies remain to be formally addressed in *Oberonia*. Furthermore, there are several names that are extremely difficult to assess due to limited verbal descriptions, lack of any illustrations, and unknown (lost or destroyed?) types. Examples include *Oberonia tahitensis* Lind., *Oberonia wernerii* Schltr., and *Oberonia zimmermanniana* J.J.Sm. Those nomina dubia are still listed as correct names in databases and inventories. Accordingly, the cleanup and revision of the genus will continue for several more years to help alleviate many of the issues discussed above.

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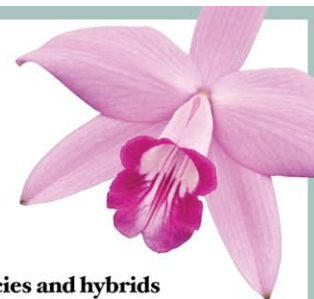
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