



Taxonomic and nomenclatural notes on *Zygopetalinae* infraspecies (*Orchidaceae*)

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ABSTRACT: This article presents nomenclatural notes and keys on species and infraspecies of the subtribe *Zygopetalinae* (*Orchidaceae*), specifically the genera *Batemannia* Lindl., *Paradisanthus* Rchb.f., *Pescatoria* Rchb.f., *Promenaea* Lindl., *Zygopetalum* Hook. and *Zygosepalum* Rchb.f., for which are proposed 15 new combinations, 44 new synonyms, and 63 typifications.

Key words: biodiversity, neotropics, nomenclatural novelties, taxonomy.

RESUMO (Notas taxonômicas e nomenclaturais em infraespécies de *Zygopetalinae* (*Orchidaceae*):

Nesse artigo são apresentadas notas nomenclaturais e chaves para espécies e infraespécies da subtribo *Zygopetalinae* (*Orchidaceae*), especificamente para os gêneros *Batemannia* Lindl., *Paradisanthus* Rchb.f., *Pescatoria* Rchb.f., *Promenaea* Lindl., *Zygopetalum* Hook. e *Zygosepalum* Rchb.f., para os quais são propostas 15 novas combinações, 44 novas sinonimizacões e 63 tipificações.

Palavras-chave: biodiversidade, neotrópico, novidades nomenclaturais, taxonomia.

The subtribe *Zygopetalinae* (*Orchidaceae*) mainly occurs in the Neotropics and has 37 genera and ca. 400 species (Pupulin *et al.* 2009, Chase *et al.* 2015). Based on molecular data, it is comprised of four lineages and groups: the *Zygopetalum* clade/grade, the genus *Dichaea* Lindl., the genus *Cryptarrhena* R.Br., and the *Huntleya* clade/grade (Whitten *et al.* 2005). The *Zygopetalum* clade/grade had been subject of recent taxonomic revision by Meneguzzo (2018). It is basal to the subtribe and is composed of 13 genera which primarily occur in eastern Brazil and secondly in the Guianas Shield and the Andes (Meneguzzo 2018). Several species were recircumscribed by the inclusion of new synonyms and the combination of species to infraspecies for cases of constant but less relevant

taxonomic morphological features. Their nomenclature had also been revised and whenever necessary types were designated in order to fix the use of the names, as well as keys for identification have been provided. Since unpublished thesis are not considered effective publication (Turland *et al.* 2018: Art. 30.9), the author himself hereby publishes part of his findings concerning the matter of infraspecies (Meneguzzo 2018).

MATERIAL AND METHODS

This study uses standard methods of alpha taxonomy and was based on specimens examined since 2008 from 98 collections in 86 herbaria (acronyms according to Thiers 2020); those personally visited are in italic: A (includes AMES,

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GH), AAU, ALCB, ARIZ, B, BHCB, BM, BR, BRIT, C, CEN, CEPEC, CESJ, COAH, COL, CR, CRI, CTES, CUZ, CVRD, E, ESA, F, FUEL, G (includes G-DC), GENT, GOET, HAL, HB, HBG, HBR, HEPH, HERBAM, HJ, HPUJ, HRB, HTO, HUA, HUEFS, HUEM, HUFU, HUTU, IAN, IBGE, ICN, INPA, JAUM, K (includes K-L), L (includes U, WAG), LE, LPB, M, MBM, MBML, MEXU, MG, MPU, MO, MOL, NDG, NY, OXF, P, PACA, PH, R, RB (includes GFJP, GUA, ITA and RUSU), RENZ, S, SBT, SEL, SP, SPF, TO, UB, UEC, UFMT, UFP, UPCB, UPS (includes UPS-THUNB), US, USM, VEN, VIES, W (includes W-R) and WU. The herbarium material identified by the author for this study can be found at REFLORA (2020) and speciesLink (CRIA 2020).

Nomenclature follows the *International Code of Nomenclature for Algae, Fungi and Plants* (Turland *et al.* 2018). Types are designated when it was not possible to find internal or external evidence of a single element from the original material and in a specific collection that strictly corresponded to holotype (McNeill 2014, Turland *et al.* 2018: Rec. 9A.1). Species and infraspecies definitions follows the discussion in Meneguzzo *et al.* (2015). New synonyms are proposed for cases on which there were evidences of discontinuation or overlap of a state or set of character states amongst two or more previously accepted species.

RESULTS AND DISCUSSION

1. *Batemannia colleyi*

Batemannia colleyi Lindley subsp. *colleyi* in Lindley (1834: t. 1714). *Lycaste colleyi* (Lindl.) Planchon (1858: 70), *nom. illeg.* *Maxilaria colleyi* (Lindl.) Planchon (1858: 72), *nom. illeg.* Type (designated here):—GUYANA. Demerara: *s. loc.*, *ex*

hort., August 1834, *Colley* sub *J. Bateman s.n.* (lectotype K-L barcode K000395468!). Figure 1A.

Batemannia lepida Reichenbach in Moore & Reichenbach (1878: 558). Type (designated here):—BRAZIL. *S. loc.*, *ex hort.*, January 1877, *s. leg. s.n.* (lectotype W-R 38148 only bottom icon!). Amazonas. Negro River, *s.d.*, *E. Morris s.n.* (excluded as type W-R 30516!). *S. loc.*, *ex hort.*, 1882, *E.K. Bailey s.n.* (excluded as type W-R 38148 up icon!). *S. loc.*, *s.d.*, *s. leg. s.n.* (possible syntype W-R 38148 envelope and bottom flowers!), *syn. nov.*

Petronia regia Barbosa Rodrigues (1877: 107). *Batemannia petronia* Barbosa Rodrigues (1891: 131), *nom. superfl. et illeg.* Type (designated here):—BRAZIL. Amazonas: Manaus [“Manáos”], Negro River, March, *J. Barbosa Rodrigues s.n.* (lectotype is the original illustration! that was to be published by J. Barbosa Rodrigues in *Iconographie des Orchidées du Brésil* t. 299, deposited in the library of Jardim Botânico do Rio de Janeiro, bound in volume 5 of the book with same title published by Barbosa Rodrigues 1996: 350, t. 225!; type specimen João Barbosa Rodrigues’ personal herbarium destroyed).

Batemannia yauaperiensis Barbosa Rodrigues (1891: 131). Type (designated here):—BRAZIL. Amazonas: Jauaperi [“Yauapery”] River, June, *J. Barbosa Rodrigues s.n.* (lectotype is the original illustration! that was to be published by J. Barbosa Rodrigues in *Iconographie des Orchidées du Brésil* t. 854, deposited in the library of Jardim Botânico do Rio de Janeiro, bound in volume 6 of the book with same title published by Barbosa Rodrigues 1996: 380, t. 252 C!; type specimen João Barbosa Rodrigues’ personal herbarium destroyed).

Batemannia wolteriana Schlechter (1915a: 28). *Batemannia wolteriana* Schlechter (1915b: 52), *nom. superfl.* Type (designated here):—*S. loc.*, *ex*

hort., February, *P. Wolter s.n.* (neotype is the illustration later published by Schlechter 1915b: t. 5, fig. 7–14!; type B destroyed).

Batemannia colleyi* subsp. *peruviana (Mast.) Meneguzzo, ***comb. et stat. nov.*** *Batemannia peruviana* Masters (1895: 551), as “*Batemanian peruviana*”. *Batemannia peruviana* Rolfe (1895: 193), as “*Batemanian peruviana*”, *nom. superfl.* *Zygopetalum peruvianum* (Mast.) Nicholson (1901: 747). Type (designated here):—PERU. *S. loc.*, *ex hort.*, March 1895, *Messrs. F. Sander and Sons s.n.* (lectotype K barcode K000589110!). Figure 1B.

Batemannia leferenzii Senghas (1993: 171). Type:—BOLIVIA. La Paz: between Coroica and Caranavi, 50 km before Caranavi, *s.d.*, *P. Leferenz* sub *Heidelberg Botanical Garden O-20702* (holotype HEID, isotype Roberto Vásquez Chávez’s private herbarium), *syn. nov.*

KEY TO THE INFRASPECIES OF *BATEMANNIA COLLEYI*

1. Flowers with sepals and petals light green to brown and no maculae, labellum white
..... ***B. colleyi* subsp. *colleyi***
- 1'. Flowers with sepals and petals light green with no maculae or with confluent dark red maculae, labellum lateral lobes light rose with small dark red spots, midlobe white to light rose
..... ***B. colleyi* subsp. *peruvianum***

Batemannia colleyi Lindl. subsp. *colleyi* is an epiphyte species that mainly grows in rainforests throughout northern South America, in Colombia, Venezuela, Guyana, Suriname, French Guiana, northern and central-eastern Brazil, Ecuador, Peru, Bolivia, and on the South American continental shelf island of Trinidad. Its flower morphology is relatively homogeneous along its range with sepals

and petals light green to brown with no maculae and a white labellum. *Batemannia lepida* Rchb.f. has been accepted in the taxonomic literature since its publication, although it had not virtually been used in herbarium specimens. The study of its nomenclatural type and protologue indicates the differences of it with *B. colleyi* could be attributed to the labellum midlobe which is somewhat longer and narrower. Notwithstanding, *B. lepida* is herein formalized as a synonym since it neatly fits within the *B. colleyi* morphological range.

In the eastern distribution of *Batemannia colleyi*, in Peru and Bolivia, a biological entity firstly described as *B. peruviana* Mast. occurs that was later redescribed as *B. leferenzii* Senghas, based solely on differences in the flower colouration. It is characterized by light green sepals and petals with red maculae that are confluent or not, light rose labellum with small dark red spots, and midlobe white to light rose. Since this colour variation is readily diagnosable, constant within its populations, i.e., there are no populations with intermixed types of flower colouration between this eastern form and *B. colleyi*, it is herein proposed to be considered an infraspecific taxon at level of subspecies, hence *Batemannia colleyi* subsp. *peruviana* (Mast.) Meneguzzo.

The authorship of *Batemannia peruviana* is herein attributed to Maxwell Tylden Masters (1895) who was editor and writer of the unsigned matters of the journal *The Gardeners' Chronicle* at that time (Britten 1907). It is worthy noting that Nicholson (1901) had also attributed the publication of *B. peruviana* to *The Gardeners' Chronicle* publication, even though he omitted the author as he also did for other works. Notwithstanding *B. peruviana* had been misattributed to a publication about three months latter by Robert Allen Rolfe (1895), which

turns to be a superfluous name (Turland *et al.* 2018: Art. 52.1 and 52.2).

2. *Paradisanthus bahiensis*

Paradisanthus bahiensis Reichenbach subsp. ***bahiensis*** in Reichenbach (1852b: 931). *Warrea bahiensis* Hortulanorum in Reichenbach (1854: 30), *non valid. publ.* Type (designated by Meneguzzo *et al.* 2015: 26):—BRAZIL. Bahia: Valença, road from Valença to road BR-101, 25 February 1986, J.L. Hage, L. Anderson & M. Hagberg 1958 (neotype MBM 117077!, isoneotypes CEPEC 38252!, K barcode K000293788!, VIES 1929!). Original material:—BRAZIL. Bahia: *s. loc., ex hort., s.d., M.J. Jenisch Junior* sub *F. Kramer s.n.* (W-R not found). Figure 1C.

Paradisanthus bahiensis Reichenbach subsp. ***micranthus*** (Barb.Rodr.) Meneguzzo, ***comb. et stat. nov.*** *Zygopetalum micranthum* Barbosa Rodrigues (1877: 109). *Paradisanthus paranaënsis* Barbosa Rodrigues (1882: 215), *nom. superfl. et illeg.* *Paradisanthus micranthus* (Barb. Rodr.) Schlechter (1918: 36). Type (designated by Meneguzzo *et al.* 2015: 27):—BRAZIL. *S. loc., s.d., J. Barbosa Rodrigues s.n.* (the lectotype is the original illustration! that was to be published in *Iconographie des Orchidées du Brésil* t. 502, deposited in the library of the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, bound in volume 5, and later published in the book with same title by Barbosa Rodrigues 1996: 357, t. 232 and 358, t. 233, fig. A!; type J. Barbosa Rodrigues personal herbarium destroyed). Original materials:—BRAZIL. Paraná: Curitiba [“Curityba”], *s.d., J. Barbosa Rodrigues s.n.* (syntype João Barbosa Rodrigues’ personal herbarium destroyed). Paranaguá, *s.d., J. Barbosa Rodrigues s.n.* (syntype J. Barbosa Rodrigues’s personal herbarium

destroyed). Rio de Janeiro: [Casimiro de Abreu,] Barra de São João, *s.d., J. Barbosa Rodrigues s.n.* (syntype J. Barbosa Rodrigues’s personal herbarium destroyed).

Paradisanthus mosenii Reichenbach (1881a: 298). *Paradisanthus paulensis* Barbosa Rodrigues (1882: 215), *nom. superfl. et illeg.* *Paradisanthus mosenii* var. *paulensis* (Barb. Rodr.) Hoehne (1953: 153), *non valid. publ.* *Paradisanthus geraënsis* Barb.Rodr., *in sched.* Type (designated by Meneguzzo *et al.* 2015: 27):—BRAZIL. São Paulo: Santos, Burutoca River, 10 January 1875, C.W.H. Mosén 3486 (lectotype W-R 38119!, isolectotypes BR 658479!, P barcode P00447842!, P barcode P00447843!, S 7-7768!, S 6-6246 spirit), *syn. nov.*

Paradisanthus neglectus Schlechter (1918: 34). Type (designated by Meneguzzo *et al.* 2015: 27):—BRAZIL. Southern region: *s. loc., ex hort., ca.* 1901, C. Grossmann sub A. Malmquist *s.n.* (lectotype is the illustration published in the protologue by Schlechter 1918: 31, t. 3!; type specimen B destroyed), *syn. nov.*

Koellensteinia espiritosantensis Ruschi (1954: 551). *Paradisanthus espiritosantensis* (Ruschi) Ruschi (1964: 1). Type (designated by Meneguzzo *et al.* 2015: 27):—BRAZIL. Espírito Santo: Santa Teresa, Canaan Valley, 22 April 1951, A. Ruschi *s.n.* (lectotype is the original illustration! deposited the library of Instituto Nacional da Mata Atlântica and published in the protologue, Ruschi 1954: 550, t. s.n.!; holotype MBML 1431 destroyed), *syn. nov.*

Paradisanthus mosenii var. *virens* Ghillány, *in sched.* Material:—BRAZIL. Bahia: Una, Santa Rosa farm, 7 km east-northeast of São José, 27 February 1986, E.B. Santos & E.J. Judziewicz 4044 (CEPEC 39443!, K barcode K000293787!, MBM 117076!, RB 554744!, VIES 1931!).

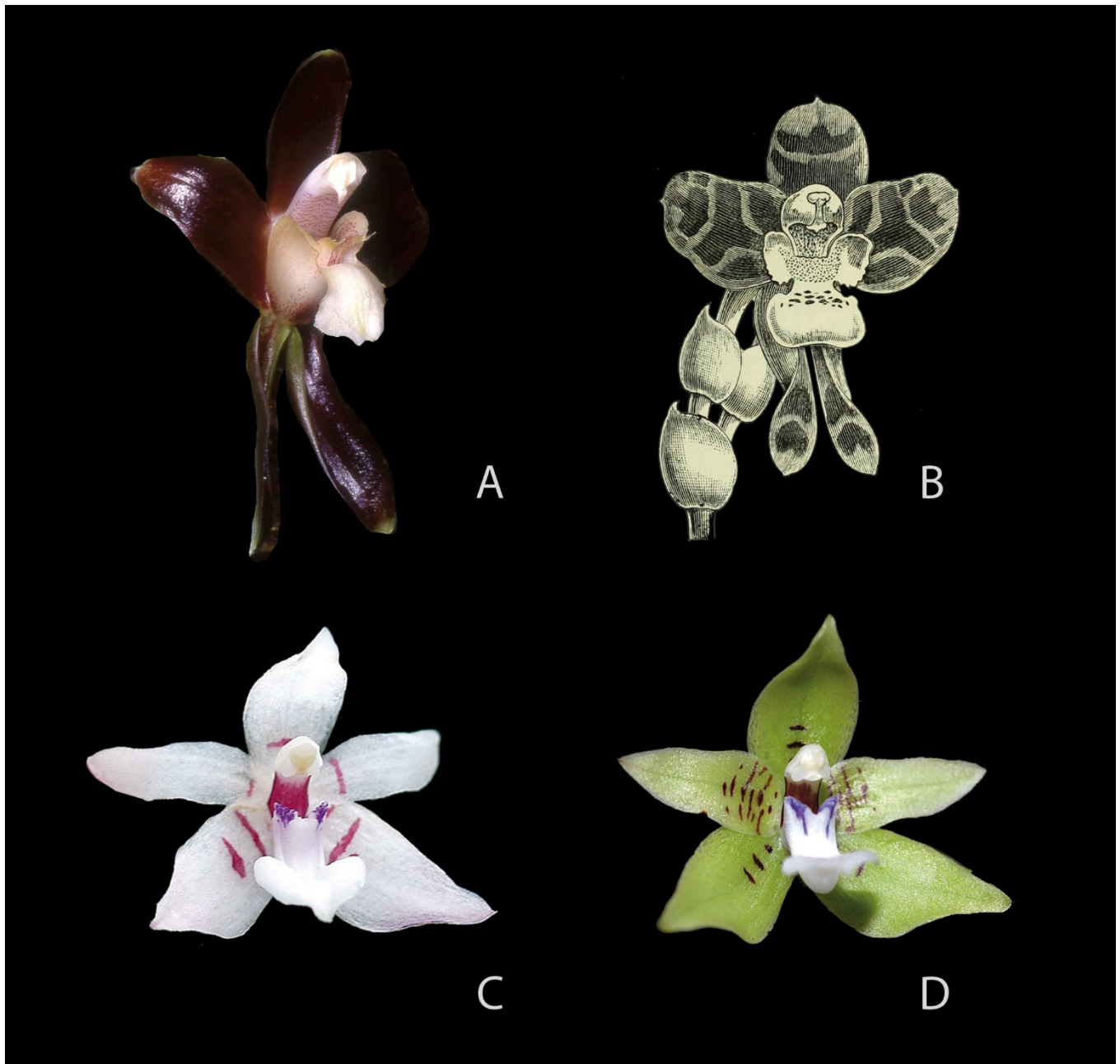


Figure 1. Pictures of living specimens of *Batemannia* and *Paradisanthus*. A. *Batemannia colleyi* subsp. *colleyi*. B. *Batemannia colleyi* subsp. *peruviana*. C. *Paradisanthus bahiensis* subsp. *bahiensis*. D. *Paradisanthus bahiensis* subsp. *micranthus*. A, D. by user 'Orch' facilitated by Wikimedia Commons. B. published in Masters (1895) and facilitated by Biodiversity Heritage Library. C. by A. Popovkin.

KEY TO THE INFRASPECIES OF *PARADISANTHUS BAHIENSIS*

- 1. Flowers with sepals and petals white to light pink ***P. bahiensis* subsp. *bahiensis***
- 1'. Flowers with sepals and petals whitish green
..... ***P. bahiensis* subsp. *micranthus***

In a previous study, Meneguzzo *et al.* (2015) revised all published names for the genus

Paradisanthus Rchb.f. and accepted with reservations a single biological entity under the oldest name, *P. bahiensis* Rchb.f., hence synonymizing *P. micranthus* (Barb.Rodr.) Schltr., *P. mosenii* Barb.Rodr., *P. neglectus* Schltr., and *P. espiritusantensis* (Ruschi) Ruschi. At that time it was clear the existence of two distinct flower morphologies which differed only by flower colour, but with a not much known about the limits of the

distribution of each one. Later, Meneguzzo (2018) delineated that the variation with white to light pink sepals and petals is geographically distributed in the Brazilian state of Bahia, in the countryside in Chapada Diamantina and in the coast from its northernmost distribution point towards the southern municipality of Una. Therefore, the only name possibly linked to it is *P. bahiensis*. The second variation with sepals and petals green is totally allopatric, native from the coastal Bahia southern of Una and a few localities in the Brazilian countryside towards the southern state of Santa Catarina. All the remaining names have their type specimens with green sepals and petals and can be linked to this morphological type. Hence, the latter is herein proposed to be a subspecies, *Paradisanthus bahiensis* subsp. *micranthus* (Barb.Rodr.) Meneguzzo, which is based on the oldest name of the group, *Paradisanthus micranthus*.

The name *Warrea bahiensis* Hort. is a not validly published name because it is merely cited as a synonym of *Paradisanthus bahiensis* (Turland *et al.* 2018: Art. 36.1(b) and 36 Ex. 7). *Paradisanthus paranaënsis* Barb.Rodr. and *P. paulensis* Barb.Rodr. are respectively superfluous and illegitimate homotypic names of *Zygopetalum micranthum* Barb.Rodr. and *P. mosenii* Rchb.f. (l.c.: Art. 52.1 and 52.2). *Paradisanthus mosenii* var. *paulensis* (Barb.Rodr.) Hoehne is an illegitimate homotypic name of *P. mosenii* because it is based on the homotypic superfluous and illegitimate name *P. paulensis* (l.c.: Art. 6.10, 35.1, 52.2, and 52 Ex. 2).

3. *Pescatoria violacea*

Pescatoria violacea (Lindl.) Dressler f. *violacea* in Whitten *et al.* (2005: 95). *Huntleya violacea* Lindley (1839b: misc. 19). *Bollea violacea* (Lindl.)

Reichenbach (1852a: 668). *Huntleya tyrianthina* Hortulanorum in Reichenbach (1856b: 187), *non valid. publ. Zygopetalum violaceum* (Lindl.) Reichenbach (1863a: 650). *Warczewiczella violacea* (Lindl.) Rollisson in Burbridge (1874: 160). Type (designated here):—GUYANA. Demerara, *ex hort., s.d., R.H. Schomburgk* sub *Messrs. Loddiges s.n.* (neotype is the illustration published by Lindley 1839d: t. 26!; original material K-L not found). Figure 2A.

Pescatoria violacea f. *alba* (Christenson) Meneguzzo, **comb. nov.** *Bollea violacea* f. *alba* Christenson (1992: 440). Type:—FRENCH GUIANA. *S. loc., ex hort., s.d., C. Pavillowski s.n.* (holotype AMES 64900!). Saint-Laurent-du-Maroni ["Maroni"], île Portal, October 1857, *P.A. Sagot 1141* (paratype P barcode P00612157!).

KEY TO THE INFRASPECIES OF *PESCATORIA VIOLACEA*

1. Flowers with sepals and petals purple, callus yellowish to purplish with or without dark purple keels ***P. violacea* f. *violacea***
- 1'. Flowers with sepals and petals white, callus yellowish ***P. violacea* f. *alba***

Pescatoria violacea (Lindl.) Dressler f. *violacea* is a species widespread in the Guiana Shield in northern South America. It is characterized by flowers with sepals and petals purple with callus of the same colour or yellowish, with or without dark purple keels. It is presumable that sporadically within populations with typical purple flowers specimens with white flowers and yellowish callus appear, therefore categorized at form rank and named *Bollea violacea* f. *alba* Christenson. Since the genus *Bollea* Rchb.f. was synonymized under

Pescatoria Rchb.f. (Dressler in Whitten *et al.* 2005), and this infraspecies therefore lacks a combination in the latter genus, it is herein transferred and named *Pescatoria violacea* f. *alba* (Christenson) Meneguzzo.

At Herbarium Lindley there is a sheet (K-L barcode K000718360!) identified by Lindley as *Huntleya violacea* composed of one non-annotated flowering specimen, and a reproduction of the illustration published of the same species (Lindley 1839d: t. 26). There is no internal or external evidence that would allow recognizing this specimen as a type, so it remains a specimen with unidentified origin, and the designated neotype is the illustration of the specimen used in the description, but not published in the protologue (Lindley 1839d: t. 26). *Huntleya tyrianthina* Hort. is not validly published name as it was merely cited a synonym of *Bollea violacea* (Lindl.) Rchb.f. (Turland *et al.* 2018: Art. 36.1(b) and 36 Ex. 7).

4. *Promenaea stapelioides*

Promenaea stapelioides (Link & Otto) Lindl. subsp. *stapelioides* f. *stapelioides* in Lindley (1843: misc. 13). *Cymbidium stapelioides* Link & Otto (1821: 111). *Maxillaria stapelioides* (Link & Otto) Lindley (1832: 146). *Peristeria stapelioides* (Link & Otto) Loudon in Baxter (1850: 604). *Zygopetalum stapelioides* (Link & Otto) Reichenbach (1863a: 658). Type (designated by Christenson 2013: 793):—BRAZIL. Rio de Janeiro: Rio de Janeiro, *ex hort.*, *s.d.*, H.K. Beyrich *s.n.* (lectotype is the illustration published in the protologue, Link & Otto 1821: t. 52!; type B destroyed). Figure 2B.

Promenaea stapelioides var. *heteroptera* Reichenbach in N.E. Brown & Reichenbach (1883: 70). *Zygopetalum stapelioides* var. *heteropterum*

(Rchb.f.) Nicholson (1901: 747). Type (designated here):—*S. loc.*, *ex hort.*, *s.d.*, *s. leg. s.n.* (lectotype W-R 30809!). Remaining syntype:—*S. loc.*, *ex hort.*, Messrs. H. Low & Co. *s.n.* (remaining syntype W-R not found), *syn. nov.*

Promenaea dusenii Schlechter (1921: 476). Type (designated here):—BRAZIL. Paraná: Morretes, deviation Ipiranga [“desvio Ypiranga”], 9 February 1912, P.K.H. Dusén 13872 (lectotype S R-5276!; type B destroyed), *syn. nov.*

Promenaea malmquistiana Schlechter (1921: 475). Type (designated here):—BRAZIL. Rio de Janeiro: Nova Iguaçu, pipeline Orbel II, 11 July 2005, M. Bocayuva 150 (neotype RB 464 spirit!). Original material:—*S. loc.*, *ex hort.*, *s.d.*, *s. leg. s.n.* (type B destroyed), *syn. nov.*

Promenaea stapelioides var. *macrantha* Hoehne (1952: 126). Type:—BRAZIL. Rio de Janeiro: half way on Petrópolis Range, December 1927, C. Spannagel 113 (holotype SP 25447!).

Promenaea stapelioides subsp. *stapelioides* f. *viridiflora* (F.Barros & Barberena) Meneguzzo, **comb. et stat. nov.** *Promenaea viridiflora* Barros & Barberena in Barberena & Barros (2015: 206). Type:—BRAZIL. São Paulo: Cananéia, Ilha do Cardoso State Park, *ex hort.*, 1988, flowered in cultivation 10 January 2014, F. Barros *s.n.* [*sic*] [*recte* F. Barros 3248] (holotype SP 465171!). Santo André, Alto da Serra de Paranapiacaba Biological Reserve, *ex hort.*, 23 July 1982, flowered in cultivation 10 January 2014, F. Barros *s.n.* [*sic*] [*recte* F. Barros 3249] (paratype SP 465170!).

Promenaea stapelioides nothosubsp. *nigricans* (Königer & J.G.Weinm.bis) Meneguzzo, **comb. et stat. nov.** *Promenaea* × *nigricans* Königer & Weinmann in Königer (1995: 113). Type:—BRAZIL.

Paraná or São Paulo: *s. loc., ex hort., s.d., J.G. Weinmann & E.B. Pfeifer sub W. Königer WK-55* (holotype M not found, isotypes HB not found, K not found, Willibald Königer's private herbarium not seen). Parent taxa (postulated here):—*Promenaea stapelioides* (Link. & Otto) Lindl. subsp. *stapelioides* f. *stapelioides* × *Promenaea stapelioides* subsp. *xanthinum* (Lindl.) Meneguzzo.

Promenaea ovatiloba nothovar. *robertii* Menezes (1995: 12). Type:—BRAZIL. Espírito Santo: *s. loc., ex hort.,* January 1995, *P.H.S. Robert s.n.* [*sic*] [*recte L. Robert s.n.*] (holotype MBM 170073 [*sic*] [*recte* MBM 170894!]; epitype designated here — the original picture published in the protologue, Menezes 1995: 13, t. s.n.!). Parent taxa (postulated here):—*Promenaea stapelioides* (Link. & Otto) Lindl. subsp. *stapelioides* f. *stapelioides* × *Promenaea stapelioides* subsp. *xanthinum* (Lindl.) Meneguzzo, *syn. nov.*

Promenaea stapelioides subsp. ***rollissonii*** (Lindl.) Meneguzzo, ***comb. et stat. nov.*** *Maxillaria rollissonii* Lindley (1837: sub t. 1986). *Promenaea rollissonii* (Lindl.) Lindley (1843: misc. 13). *Zygopetalum rollissonii* (Lindl.) Reichenbach (1863a: 659). Type (designated by Barberena *et al.* 2016: 326):—BRAZIL. *S. loc., ex hort., s.d., Messrs. Rollisson s.n.* (neotype is the published illustration by Lindley 1838: t. 40!; original material K-L not found). Figure 2C.

Maxillaria lentiginosa Lindley (1839c: misc. 61). *Promenaea lentiginosa* (Lindl.) Lindley (1843: misc. 13). *Zygopetalum lentiginosum* (Lindl.) Reichenbach (1863a: 659). Type (designated here):—BRAZIL. *S. loc., ex hort., s.d., Messrs. Loddiges s.n.* (lectotype K-L barcode K000857188!).

Promenaea rollissonii var. *obtusa* Regel in von Kuester *et al.* (1856: 23). Type (designated

here):—BRAZIL. Rio de Janeiro: Mangaratiba, margin of Grande River, 20 April 2003, *E. Saddi 66* (neotype RB 462 spirit!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found), *syn. nov.*

Promenaea albescens Schlechter (1919: 327). *Promenaea paranaënsis* var. *albescens* (Schltr.) Hoehne (1953: 81). Type (designated by Barberena *et al.* 2016: 326):—*S. loc., ex hort., s.d., s. leg. s.n.* (neotype is the illustration published by Mansfeld [*sic*] [*recte* Schlechter] 1930: t. 50, n. 197!). Original material:—*S. loc., ex hort., s.d., Grossmann s.n.* (type B destroyed).

Promenaea acuminata Schlechter (1919: 327). Type (designated here):—BRAZIL. Paraná: Morretes, Floresta Colony, 24 January 1969, *G. Hatschbach & C. Kocicki 20907* (neotype MBM 12694!). Original material:—BRAZIL. Southern region, *s. loc., ex hort.,* November 1918, *Grossmann s.n.* (type B destroyed), *syn. nov.*

Promenaea catharinensis Schlechter (1921: 479). Type (designated here):—BRAZIL. Paraná: São José dos Pinhais, Garuva [*sic*] [*recte* Santa Catarina: Garuva], 6 January 1950, *G. Hatschbach 1849* (neotype MBM 50058!). Original material:—BRAZIL. Santa Catarina: *s. loc., ex hort., s.d., von Fürstenberg s.n.* (type B destroyed), *syn. nov.*

Promenaea paulensis Schlechter (1922b: 63). Type (designated by Christenson 1996: 22):—BRAZIL. São Paulo: Iguape, Pedras Peak, Iguape River Valley, January 1918, *A.C. Brade 7758* (lectotype US 1208125!, isolectotypes AMES 30646!, HB 8540!, R 29940!, SP 8255!; type B destroyed).

Promenaea riograndensis Schlechter (1925: 87). Type (designated by Barberena *et al.* 2016: 326):—BRAZIL. Santa Catarina: Araranguá, Veado River, 14 April 2011, *L.C. Oliveira s.n.* (neotype CRI 8945!). Original material:—BRAZIL. Rio Grande do

Sul: Torres, February 1922, *L. Burger* sub *F. Aquino* 33 (type B destroyed).

Promenaea stapelioides subsp. ***xanthina*** (Lindl.) Meneguzzo, **comb. et stat. nov.** *Maxillaria xanthina* Lindley (1839a: sub t. 17). *Zygopetalum xanthinum* (Lindl.) Reichenbach (1863a: 659). Type (designated here):—BRAZIL. Rio de Janeiro: Organ Mountains, May 1837, *G. Gardner* 652 (lectotype K-L barcode K000857191!, isolectotypes BM barcode BM000533456!, BM barcode BM001122605!, G barcode G00359929!, P barcode P00447850!, SP 114332!, OXF s.n.). Remaining syntype:—BRAZIL. Rio de Janeiro: Angra dos Reis, Island Ilha Grande, June, *J.T. Descourtilz* s.n. (remaining syntype is the original illustration that was to be published by Jean Théodore Descourtilz in *Epidendres des Forestes Vierges du Brésil* 3 (16): t. 63!, deposited at the library of l'Institute de France). Figure 2D.

Maxillaria citrina Lyons (1845: 76). *Promenaea citrina* (J.Lyons) Don (1845: 720). *Zygopetalum citrinum* (J.Lyons) Nicholson (1887: 245). Type (designated here):—BRAZIL. São Paulo: São Luiz do Paraitinga, 13 October 1999, *G. Martinelli, T. Barbará, G.M. Souza & R. Azoury* 15930 (neotype RB 429828!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found).

Maxillaria guttata Reichenbach (1852b: 672), *nom. nud.* *Promenaea guttata* Reichenbach (1856a: 323). *Zygopetalum guttatum* (Rchb.f.) Reichenbach (1863a: 659). Type (designated here):—*S. loc., ex hort., s.d., s. leg. s.n.* (lectotype W-R 40602 specimen by side of red label!). Remaining original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (remaining syntype W-R 40602 two envelopes!). *S. loc., ex hort., s.d., s. leg. s.n.* (remaining original material W-R 40601 two icons!), *syn. nov.*

Promenaea microptera Reichenbach

(1881b: 134). *Zygopetalum microptera* Reichenbach (1881b: 134). *Zygopetalum microptera* (Rchb.f.) Bentham & Hooker filius ex Bois in Bois (1893: 133), *nom. illeg.* Type (designated here):—*S. loc., ex hort.*, July 1881, *d'Haede* sub *H. Veitch* s.n. (lectotype W-R 40606 pencil icon on left!). Remaining original material:—*S. loc., ex hort., s.d., B.S. Williams* s.n. (remaining syntype W-R not found), *syn. nov.*

Promenaea citrina Bull ex Regel in Regel (1887b: 694), *nom. illeg.* Type (designated here):—BRAZIL. Rio de Janeiro: Nova Friburgo, Sitio Baccus, October 1998, *D. Miller* s.n. (neotype RB 729 spirit!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (LE not found).

Zygopetalum ovatilobum Klinge (1898: 144). *Promenaea ovatiloba* (Klinge) Cogniaux (1906a: 468). Type (designated here):—BRAZIL. *S. loc., ex hort.*, 25 April 1897, *Lietze* s.n. (lectotype LE barcode LE00001454!), *syn. nov.*

Zygopetalum xanthinum var. *major* Masters (1901: 106). *Promenaea xanthina* var. *major* (Mast.) Cogniaux (1906a: 465). Type (designated here):—BRAZIL. São Paulo: Piquete, Área de Proteção Ambiental Serra da Mantiqueira, 28 December 2013, *L.N. Gonçalves & P. Duffles* 293 (neotype RB 597001!). Original material:—*S. loc., ex hort.*, 1901, *H.A. Tracy* sub *I. Bradt* s.n. (not found).

Promenaea fuerstenbergiana Schlechter (1921: 481). Type (designated here):—BRAZIL. Santa Catarina: Camburiú, Guarita Peak, 9 March 2000, *A.C. Cervi* 7008 (neotype MBM 256016!, isoneotype UPCB 42082!). Original material:—*S. loc., ex hort., s.d., von Fürstenberg* s.n. (type B destroyed), *syn. nov.*

Promenaea paranaënsis Schlechter (1921: 477). Type (designated here):—BRAZIL. Paraná: Morretes, Parque Estadual do Marumbi, 6 February

1999, Pico Facãozinho, *C. Giongo 101* (neotype UPCB 47310!). Original material:—idem, [“Fazenda Morumby”], *ex hort.*, October–November 1914, *P.K.H. Dusén 1581* (type B destroyed), *syn. nov.*

Promenaea sincorana Castro Neto & Campacci (1993: 10). Type:—BRAZIL. Bahia: Itacoatiara [*sic*] [*recte* Ibicoara], Sincorá Range, *ex hort.*, 15 November 1990, *V.P. Castro Neto s.n.* (holotype SP 333604!), *syn. nov.*

Promenaea silvana Barros & Catharino (1995: 94). Type:—BRAZIL. Southern Bahia: *S. loc.*, *ex hort.*, 20 November 1980, *E.P. Silva s.n.* (holotype

SP 247598!), *syn. nov.*

Promenaea chautinana Reichenbach, *in sched.* Material:—*S. loc.*, *ex hort.*, June 1888, *A. Chautin s.n.* (W-R 40607!).

Promenaea xanthina var. *minor* Hoehne, *in sched.* Material:—BRAZIL. Rio de Janeiro: Teresópolis, December 1929, *A.C. Brade 9465* (R 32293!).

Promenaea xanthina f. *concolor* Pabst, *in sched.* Material:—BRAZIL. Espírito Santo: Domingos Martins, Azul Peak, 3 December 1970, *R. Kautsky 310* (HB 57258!).

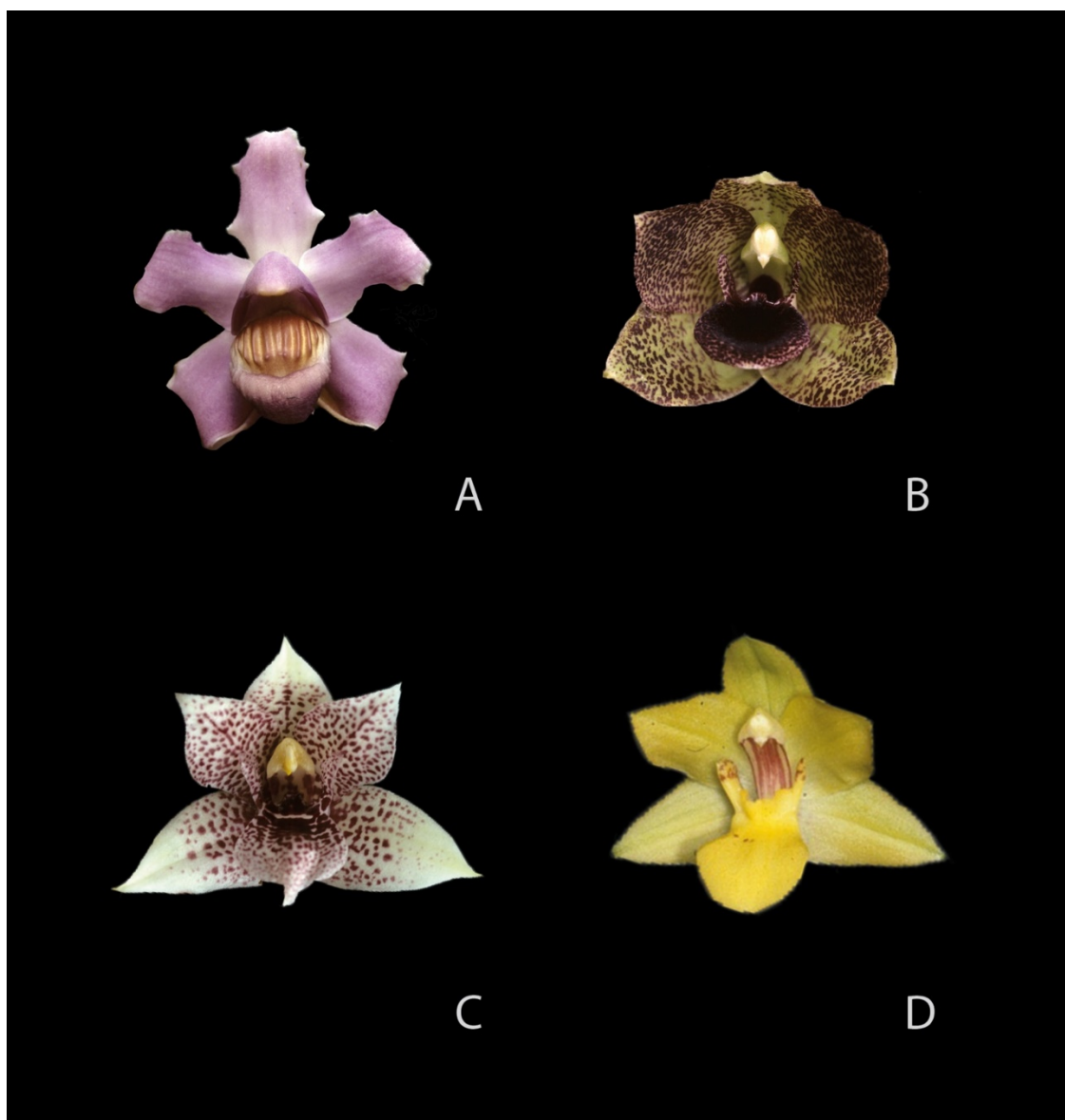


Figure 2. Pictures of living specimens of *Pescatoria* and *Promenaea*. A. *Pescatoria violacea* f. *violacea*. B. *Promenaea stapelioides* subsp. *stapelioides* f. *stapelioides*. C. *Promenaea stapelioides* subsp. *rollissonii*. D. *Promenaea stapelioides* subsp. *xanthina*. A–C. by K. Senghas and facilitated by Swiss Orchid Foundation at Herbarium Jany Renz. D. by R. Jenny and facilitated by Swiss Orchid Foundation at Herbarium Jany Renz.

KEY TO THE INFRASPECIES OF *PROMENAEA STAPELIOIDES*

1. Labellum callus with distal portion rounded **2**
 1'. Labellum callus with distal portion obtuse **4**
 2. Sepals, petals, and labellum light green with dark brown maculae, labellum more densely maculate
 ***P. stapelioides* subsp. *stapelioides* f. *stapelioides***
 2'. Sepals, petals and labellum dull coloured (no maculae) **3**
 3. Sepals and petals dull dark crimson to reddish purple, labellum dark purple with the proximal portion of a darker hue than the distal portion
 ***P. stapelioides* nothosubsp. *nigricans***
 3'. Sepals and petals dull light green, labellum light green with distal portion of midlobe white
 ***P. stapelioides* subsp. *stapelioides* f. *viridiflora***
 4. Sepals, petals, and labellum light green with light brown spots; labellum callus lateral margin irregularly denticulate and distal margin 2-lobed
 ***P. stapelioides* subsp. *rollissonii***
 4'. Sepals, petals, and labellum light to dark yellow and dull coloured, or with few and sparse crimson spots on proximal portion, or rarely with thin to thick coloured radial bars on proximal portion; labellum callus margin entire, distal margin 2 or 3-lobed ***P. stapelioides* subsp. *xanthina***

The genus *Promenaea* had been comprised of 16 species widespread in eastern and southern Brazil (Govaerts *et al.* 2020) which grow in shady areas under the forest canopy and seem to prefer moister niches. By the end of the 20th century less than half of the 27 names had been described. Most of them were described over a short period by Schlechter (1919, 1921, 1922b, 1925) based on wild

specimens cultivated in Europe. The authors that published on this genus (Rolfe 1905, Cogniaux 1906a, Hoehne 1953, Pabst & Dungs 1977) more or less accepted nearly all published species at the time, probably due to the lack of access to representative samples of herbarium collections, difficulties in understanding species delimitation, and also almost certainly by not having studied the type materials. It led to a substantial taxonomic inflation which does not reflect this genus in the natural world by the use of tenuous morphological characteristics which were commonly superimposed on the formerly accepted species circumscriptions.

The study of all type specimens accompanied by their original illustrations and protologues, as well as of a good amount of herbarium specimens and observations of living specimens, led to the recognition that in fact there are constant morphological differences that separate the genus into a small number of recognizable biological entities. Although, when those biological entities are accessed within the scope of the *Zygopetalinae*, it is clear that their characterization are very subtle in a way that do not merit the recognition as distinct species. The differences between them are comprised of the variations in flower colour and subtle variations in labellum callus. Since there are no populations intermixed, except by a case latter discussed, they are classified as subspecies under oldest described name for the genus, *Promenaea stapelioides* (Link & Otto) Lindl. A significant quantity of typifications are proposed to ascertain the placement of synonyms and to fulfil the requirement of a type material for each published name.

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Promenaea stapelioides (Link & Otto) Lindl. subsp. *stapelioides* is characterized by sepals and petals light green with dark brown maculae on which the labellum is more densely maculate, and the distal margin of the labellum callus distal portion is rounded and 2-lobed. The study of the type and protologues of *P. dusenii* and *P. stapelioides* var. *heteroptera* led to the conclusion they are conspecific with *P. stapelioides* subsp. *stapelioides* since their colour variation and labellum callus shape neatly fit within the morphological range of the subspecies.

Promenaea viridiflora F.Barros & Barberena was described as a distinct species which differed from *P. stapelioides* only by the dull green flower colour and by what is tentatively interpreted from the protologue as an erect labellum callus with a conic trunk like protuberance (Barberena & Barros 2015). The last morphologic feature is not diagnostic because it is not exclusive to the taxon, but neatly falls within the morphological range commonly found in *P. stapelioides* subsp. *stapelioides*. Moreover, subtle differences in labellum morphology do not differentiate *Zygopetalinae* species (Meneguzzo 2018). Flower colour is not a good distinctive feature at species level since it clearly has the same light green perianth of *P. stapelioides* but with a lack of spots. Contrary to what was mistakenly cited in the protologue, the holotype and paratype bear collection numbers of the senior author which are herein rectified. Both specimens were prepared from cultivated specimens collected over 30 years ago; the authors did not access their populations and the provided data is of a speculative nature. *Promenaea viridiflora* occurs within the geographic distribution and niche of *P. stapelioides*. All these evidences indicate that *P. viridiflora* is merely a

sporadic colour shift in some specimens within *P. stapelioides* subsp. *stapelioides*, which is most probably less frequent, as commonly happen in orchids. Thus it is accordingly reduced to the infraspecific rank of form: *Promenaea stapelioides* subsp. *stapelioides* f. *viridiflora* (F.Barros & Barberena) Meneguzzo.

Promenaea stapelioides subsp. *rollissonii* (Lindl.) Meneguzzo is herein proposed as a subspecies characterized by flowers with sepals, petals and lip light green with light brown maculae, labellum callus distal portion obtuse, lateral margin irregularly denticulate, and terminal portion 2-lobed. Barberena *et al.* (2016) proposed the synonymization of *P. lentiginosa* Lindl., *P. albescens* Schltr., *P. paulensis* Schltr., and *P. riograndensis* Schltr., which are here scrutinized and accepted as good. To that list the new synonyms *P. rollissonii* var. *obtusa* Regel, *P. acuminata* Schltr., and *P. catharinensis* Schltr., which were overlooked in by Barberena *et al.* (2016) have also been added. The designation of their neotypes in accordance to the description in the protologue and original type localities well characterize them to reinforce the proposed synonymy.

Promenaea stapelioides subsp. *xanthina* (Lindl.) Meneguzzo is the only yellow flowered subspecies of the genus. It is characterized by sepals, petals, and labellum light to dark yellow and dull coloured, or with few sparse crimson spots on the proximal portion, or rarely thin to thick coloured radial bars on the proximal portion. The labellum callus margin is entire, and the distal margin is 2 or 3-lobed. Specimens commonly identified as *P. ovatiloba* (Klinge) Cogn. and *P. guttata* Rchb.f. have somewhat narrower petals and sepals and commonly have thick coloured radial bars on its proximal portion (including personal field

observations in Ilha Grande and surrounding areas, Rio de Janeiro). *Promenaea silvana* was described for a group of specimens from southern Bahia with golden yellow flowers (orange in the protologue) and petals and sepals sometimes tending to be more acute. The complicated matter of accepting the last name as a good and separate species is that plants with the typical yellow colouration are found amongst them in natural populations (including personal field observations in Arataca Range and surrounding areas, Bahia), as well as some with narrower or more acute sepals and petals; thus these characters are non-correlated and not an exclusive but rather common feature which comprise the variability of this subspecies. For these reasons *P. ovatiloba*, *P. guttata*, and *P. silvana* are herein synonymized. The designation of a neotype for *P. citrina* (J.Lyons) P.N.Don, *P. citrina* Bull ex Regel, *P. xanthina* var. *major* (Mast.) Cogn., *P. fuerstenbergiana* Schltr., and *P. paranaënsis* Schltr. along with the study of their protologues led to the new synonymizations under *P. stapelioides* subsp. *xanthina*. In the same way the study of the types of *P. microptera* Rchb.f. and *P. sincorana* V.P.Castro & Campacci led to the conclusion they do not differ from this species and are also synonymized.

It has been found that the name "*Promenaea citrina* P.N.Don", as cited in the nomenclatural indexes, had been incorrectly treated as a new species attributed to Patrick Neill Don (1845). However, this name is hereby traced to its basionym, *Maxillaria citrina* J.Lyons by John Charles Lyons (1845). Don (1845) himself clearly indicated that *P. citrina* is a combination based on *M. citrina*. Although, he did not cite the reference and did this for other names throughout his publication, which was not required for validly published combinations publications at that time (Turland *et al.* 2018: Art.

41.3). Similarly "*Promenaea xanthina* var. *major* Cogn." had been mistakenly considered a new variety by Cogniaux (1906a) in the botanical indexes. The author explicitly indicated "*Zygopetalum xanthinum* var. *major* Hort." as basionym along with its full reference. The authorship of the basionym itself is hereby identified as Maxwell Tylden Masters (1901), who was editor and writer of the unsigned matters of the journal at that time (Britten 1907). Therefore *Promenaea citrina* (J.Lyons) P.N.Don is based on *Maxillaria citrina* J.Lyons, and *Promenaea xanthina* var. *major* (Mast.) Cogn. is based on *Zygopetalum xanthinum* var. *major* Mast.

Maxillaria guttata Reichenbach (1852b: 672) is a denomination or naked name due to the lack of a diagnosis or description (Turland *et al.* 2018: Art. 6.3, 38 Ex. 1, and Rec. 50B.1); therefore, it must not be cited as the basionym of *Promenaea guttata* Reichenbach (1856a: 323) as frequently found in botanical literature; the later name is the basionym itself. *Promenaea citrina* Bull ex Regel is an illegitimate later homonym of *P. citrina* (J.Lyons) P.N.Don (l.c.: Art. 52.1 and 52.2).

Königer & Weinmann *in* Königer (1995) published *Promenaea nigricans* as a new species from a specimen obtained from cultivation from the state of Paraná or São Paulo. It is unique in the genus due to its immaculate reddish purple flowers on which the lateral sepals are darker and labellum dark purple with the proximal portion of a darker hue than the distal portion. Menezes (1995) reported in the protologue of *P. ovatiloba* var. *robertii* that only a single specimen of it was found amongst many wild collected specimens of *P. stapelioides* subsp. *xanthina* (cited as *P. ovatiloba* (Klinge) Cogn.) from an unreported provenance in the state of Espírito Santo. It was intentionally

described as a mere flower colour variation characterized by dull dark crimson flowers with the labellum callus of a darker hue.

The study of the original materials led to the conclusion that *P. nigricans* and *P. ovatiloba* var. *robertii* are conspecific, and completely spotless as confirmed by the iconography in the protologue. Both *P. nigricans* and *P. ovatiloba* var. *robertii* are not strictly conspecific with *P. stapelioides* subsp. *xanthina* due to the distal margin of the labellum callus having rounded instead of obtuse lobes. They are not strictly conspecific with *P. stapelioides* subsp. *stapelioides* f. *stapelioides* either, because of the darker, and sparsely-spotted flowers instead of light green and densely spotted, although the obtuse distal margin of the labellum callus is a shared diagnostic character. Empirical observations on the hybrid crossings by horticulturists and widely presented in the horticulture literature and in orchid nurseries show that whenever the last species is crossed with a yellowish specimen that bear spotless flowers or with some spots (like *P. stapelioides* subsp. *xanthina* or a yellowish hybrid), the results are siblings with flowers of the same colour pallet of the spots. Due to that, the two postulated parental species (*P. stapelioides* subsp. *stapelioides* f. *stapelioides* and *P. stapelioides* subsp. *xanthina*) mostly co-occurs in its marginal distribution areas and the empirical observations on hybridization, it is herein proposed to combine *P. nigricans* the status of nothosubspecies (Turland *et al.* 2018: Art. 50.1 and H.10 Note 1), and thereafter synonymize *P. ovatiloba* var. *robertii* under it. For the last name, the original picture published in the protologue is selected as the epitype since the holotype lacks the labellum (l.c.: Art. 9.9).

Barberena *et al.* (2016) made some nomenclatural notes that must be revised under the

current Code (Turland *et al.* 2018). Lindley (1839c) did not designate the holotype in the protologue of *Maxillaria lentiginosa* Lindl., hence the lectotype is herein designated since the protologue lacked the indication of a unique specimen in a specific collection (McNeill 2014, Turland *et al.* 2018: Art. 9.1). The set of illustrations from which the neotype of *Promenaea albescens* Schltr. was designated was posthumously published by Schlechter (1930), not Mansfeld who edited the publication.

5. *Warreopsis colorata*

Warreopsis colorata (Linden & Rchb.f.) Garay subsp. ***colorata*** in Garay (1973a: 51). *Zygopetalum coloratum* Linden & Reichenbach in Reichenbach (1863a: 662). Type (designated here):—COLOMBIA [“New Granada”]. Eastern region: *s. loc.*, July, L.-J. Schlim 51 (lectotype W-R 40578 only left icon!). Figure 3A.

Zygopetalum pardinum Reichenbach (1863a: 662). *Warreopsis pardina* (Rchb.f.) Garay (1973a: 51). Type (designated by Meneguzzo *et al.* 2015: 30):—ECUADOR. Andes forests, western declivity: *s.d.*, W. Jameson [“Jamieson”] *s.n.* (lectotype K-L 364389!, isolectotype W-R 40577 fragment!); idem (remaining original material W-R 40577 right icon!), *syn. nov.*

Otostylis hirtzii C.H. Dodson in C.H. Dodson & P.M. Dodson (1984: t. 976). Type:—ECUADOR. Pichincha: old road between San Juan and Chiribonga, 7 March 1982, A. Hirtz & J. Leon 201 (holotype SEL 44290!, SEL spirit s.n.), *syn. nov.*

Warreopsis colorata subsp. ***parviflora*** (L.O. Williams) Meneguzzo, ***comb. et stat. nov.*** *Zygopetalum parviflorum* L.O. Williams in Woodson Junior & Schery (1941: 424). *Warreopsis parviflora*

(L.O.Williams) Garay (1973a: 51). Type:—PANAMA. Chiquirí: Bajo Chorro, 20–22 July 1940, *R.E. Woodson Junior & R.W. Schery 605* (holotype AMES 90660!, isotypes F 93942!, MO 102762!).

Warreopsis colorata subsp. *purpurea* (P.Ortiz) Meneguzzo, *comb. et stat. nov.* *Warreopsis purpurea* Ortiz Valdivieso (1994: 19). Type:—COLOMBIA. Putumayo: Sibundoy, April 1977, *P. Ortiz V. 927* (holotype HPUJ 10617!). Figure 3B.

KEY TO THE INFRASPECIES OF *WARREOPSIS COLORATA*

1. Labellum midlobe widely obovate, apex obtuse
 *W. colorata* subsp. *purpurea*
 1'. Labellum midlobe transverse-oblong, apex rounded **2**
 2. Sepals and petals yellow to green with brown maculae, labellum dull white
 *W. colorata* subsp. *colorata*
 2'. Sepals and petals dull brown, labellum magenta
 *W. colorata* subsp. *parviflora*

Warreopsis colorata (Lind. & Rchb.f.) Garay subsp. *colorata* inhabits the northern part of the Andes in the Ecuadorian, Colombian, and Venezuelan cloud forests. Its flowers are yellow to green with brown maculae and labellum dull white. Senghas & Gerlach (1993) considered *W. pardina* (Rchb.f.) Garay as a good species endemic to Ecuador and synonymized *Otostylis hirtzii* Dodson under it, whilst *W. colorata* was considered endemic to Venezuela and perhaps Colombia. The examination of the type specimens of *W. colorata*, *W. pardina*, and *O. hirtzii* led to the conclusion that they comprise a single biological entity that do not differ in the flower shape, size, and colours along all of its

geographical range, hence expended as aforementioned.

Warreopsis parviflora (L.O.Williams) Garay was initially described for Panama, but later also found in Costa Rica. It differs from *W. colorata* by the dull brown sepals and petals and magenta labellum. Since the differences are solely in the flower colours and both biological entities are disjunct and clearly distinguishable, it is proposed that *W. parviflora* be reduced to subspecific level: *Warreopsis colorata* subsp. *parviflora* (L.O.Williams) Meneguzzo.

In the southernmost areas of the northern Andes, *Warreopsis purpurea* occurs; it differs from the former species by the dull purple flowers or sepals and petals with darker maculae and labellum midlobe widely obovate with the apex obtuse, whilst the others subspecies have the midlobe transverse-oblong with a rounded apex, and different colours. *Warreopsis purpurea* inhabits western Colombia, northern Ecuador, and western Bolivia, but has not so far been collected in Peru. It is reduced to infraspecific level because it is allopatric, and although its morphological differences are readily identified, they are not strong enough to characterize it as a distinct species. Therefore it is recognized as *Warreopsis colorata* subsp. *purpurea* (P.Ortiz) Meneguzzo. In this way the four formerly accepted *Warreopsis* species are accepted as three subspecies of *W. colorata*.

6. *Zygopetalum crinitum*

Zygopetalum crinitum Loddiges subsp. *crinitum* in Loddiges (1831: t. 1687). *Zygopetalum mackaii* var. *crinitum* (Lodd.) Lindley (1833: 187). *Zygopetalum mackaii* var. *convexum* Mutel (1842: 9), *nom. superfl. et illeg.* *Eulophia crinita* (Lodd.)

Loudon in Steudel (1840: 605). *Zygopetalum microtus* Hoffmannsegg in Reichenbach (1863a: 661), *non valid. publ.* Type (designated here):—BRAZIL. Rio de Janeiro: *S. loc., ex hort., s.d., F. Warre* sub *C.L. Loddiges s.n.* (lectotype K-L barcode K000458550!). Figure 3C.

Zygopetalum stenochilum Loddiges (1833: t. 1923), *non valid. publ.* *Zygopetalum stenochilum* Loddiges ex Drapiez in Drapiez (1834: s.n.). *Eulophia stenochila* (Lodd. ex Drapiez) Steudel (1840: 605). Type (designated here):—BRAZIL. *S. loc., ex hort., 1828, F. Warre s.n.* (the lectotype is the original illustration! deposited at the library of Natural History Museum, London, and published by Loddiges 1833: t. 1923!).

Zygopetalum mackaii var. *nanum* Harrison (1835: 72), as "*mackayi*". Type (designated here):—*S. loc., ex hort., s.d., Cooper s.n.* (the lectotype is the illustration published in the protologue, Harrison 1835: between page 48 and 49 mistakenly named as *Zygopetalum crinitum*), *syn. nov.*

Zygopetalum pubescens Hoffmannsegg (1843: 63). Type (designated here):—BRAZIL. Rio de Janeiro: Macaé, Pico do Frade, 22 October 1985, *M. Leitman et al. 20* (neotype RB 241568!). Original material:—BRAZIL. Rio de Janeiro: *S. loc., ex hort., s.d., s. leg. s.n.* (type B destroyed), *syn. nov.*

Zygopetalum velutinum Hoffmannsegg (1843: 62). *Zygopetalum mackaii* var. *velutinum* (Hoffmanns.) Rollisson in Burbridge (1874: 160). Type (designated here):—BRAZIL. Rio de Janeiro: Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, 28 November 1990, *A.L.V. Toscano de Brito et al. 664* (neotype RB 294440!). Original material:—BRAZIL. Rio de Janeiro: *S. loc., ex hort., s.d., s. leg. s.n.* (type B destroyed), *syn. nov.*

Zygopetalum crinitum var. *coeruleum* B.S. Williams (1852: 98). *Zygopetalum mackaii* var.

coeruleum (B.S. Williams) Rollisson in Burbridge (1874: 160). Type (designated here):—BRAZIL. Rio de Janeiro: Nova Friburgo, Parque Estadual de Três Picos, 25 July 2011, *A. Bonnet & E. Caglioni 1200178* (neotype RB 530496!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found), *syn. nov.*

Zygopetalum crinitum var. *rubellum* Regel in von Kuester & Regel (1855: 23). Type (designated here):—BRAZIL. Rio de Janeiro: Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, trilha para Pico da Bicuda, 11 August 2016, *C. Baez, P. Rosa, D. Maurenza, L. Moraes & R. Overney 793* (neotype RB 660907!, isoneotype HUEFS 231950!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found), *syn. nov.*

Zygopetalum crepeauxii Carrière (1887: 420). Type (designated here):—BRAZIL. Rio de Janeiro: Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, 26 August 1987, *M. Leitman et al. 267* (neotype RB 295035!). Original material:—BRAZIL. *S. loc., ex hort., s.d., P. Binot* sub *Crepeaux s.n.* (not found), *syn. nov.*

Zygopetalum mackaii var. *macranthum* Rollisson in Burbridge (1874: 160), *nom. nud.* *Zygopetalum mackaii* var. *major* Rollisson in Burbridge (1874: 160), *nom. nud.* *Zygopetalum macranthum* Hortulanorum, in sched. Material:—*S. loc., ex hort., s.d., s. leg. s.n.* (BR s.n.!).

Zygopetalum mackaii var. *roseum* Rollisson in Burbridge (1874: 160), *nom. nud.* *Zygopetalum crinitum* var. *roseum* Rollisson ex Stein in Stein (1892: 599). Type (designated here):—BRAZIL. São Paulo: Serra da Bocaina, Mata da Garrafa, 14 May 1951, *A.C. Brade 20971* (neotype RB 74174!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found), *syn. nov.*

Zygopetalum ghillanyi Pabst (1976: 86). Type:—BRAZIL. São Paulo: Serra da Bocaina, *ex hort.,*

1 November 1974 [sic] [recte 3 November 1975], A. Ghillány sub R. Windish s.n. (holotype HB 63061!), *syn. nov.*

Zygopetalum reginae Pabst (1976: 87).

Type:—BRAZIL. São Paulo: Serra da Bocaina, *ex hort.*, 1 November 1974, R. Windish s.n. [sic] [recte A. Ghillány sub R. Windish s.n.] (holotype HB 63017!).

Original material:—BRAZIL. São Paulo: Santo Antônio do Pinhal, *ex hort.*, 5 April 1975, A. Ghillány s.n. (paratype HB 63171!), *syn. nov.*

Zygopetalum crinitum var. *triumphans*

L. Linden, *in sched.* Material:—*S. loc.*, *ex hort.*, *s.d.*, *s. leg. s.n.* (BR s.n.!).

Zygopetalum panduratum Reichenbach, *in*

sched. Material:—*S. loc.*, *ex hort.*, *s.d.*, *s. leg. s.n.* (W-R 28108!).

Zygopetalum crinitum* subsp. *pabstii (Toscano) Meneguzzo, ***comb. et stat. nov.*** *Zygopetalum pabstii* Toscano de Brito (1980: 115). Type:—BRAZIL. Espírito Santo: Alfredo Chaves, Todos os Santos, Pico do Sal, *ex hort.*, 31 March 1980, R.A. Kautsky 666 (holotype HB 71173!). Figure 3D.

KEY TO THE INFRASPECIES OF *ZYGOPETALUM CRINITUM*

1. Epiphyte; leaves blade short (20.9–38.0 cm long); inflorescences shorter than pseudobulb plus leaves; labellum narrow (midlobe 2.5–3.3 cm wide); sepals and petals convex ***Z. crinitum* subsp. *crinitum***
 1'. Terrestrial; leaves blade long (45.6–105.0 cm long); inflorescences longer than pseudobulb plus leaves; labellum wide (midlobe 4.3–7.1 cm wide); sepals and petals strongly convex
 ***Z. crinitum* subsp. *pabstii***

Zygopetalum crinitum Lodd. subsp. *crinitum* is a species distributed in the Atlantic Rain Forest

from southern state Bahia to Rio Grande do Sul, Brazil and northeastern Argentina. Its habit is epiphytic and the populations are not aggregated as commonly occurs in other species the genus, hence few specimens are seen during fieldwork. It is unique in the genus and easily distinguished by the labellum with hirsute veins and callus with the distal portion deeply fissured. The revision of the type specimens and protologues of *Z. crinitum* and *Z. maculatum* (Kunth) Garay, the latter as discussed below, led to the recognition of the herein proposed new synonyms. Most of the synonyms comprise minor variations in flower colour and labellum veining which does not merit distinct taxonomic status.

A variation named *Zygopetalum pabstii* Toscano is found in the central region of Espírito Santo, Brazil. Its habit is terrestrial and the plant itself is larger than *Z. crinitum* and consequently all the organs are consistently larger. The flowers mostly have the same characteristics of other species of *Zygopetalum*, except for a much larger side and sepals and petals strongly convex instead of convex. Since the only differences between *Z. crinitum* and *Z. pabstii* are the habit, the flower measurements are consistent, and populations do not intermix, it is herein proposed that it be reduced to subspecies level as *Zygopetalum crinitum* subsp. *pabstii* (Toscano) Meneguzzo.

The names *Zygopetalum mackaii* var. *convexum* Mutel and *Z. microtos* Hoffmanns. are not validly published because they were merely cited as synonyms of *Z. crinitum* (Turland *et al.* 2018: Art. 36.1(b) and 36 Ex. 7). *Zygopetalum mackaii* var. *roseum* Rollisson, *Z. mackaii* var. *macranthum* Rollisson, and *Z. mackaii* var. *major* are denoted as denominations or naked names by lack of a proper diagnosis or description (l.c.: Art. 6.3, 38 Ex. 1, and

Rec. 50B.1). *Zygopetalum stenochilum* Lodd. is not validly published due to the lack of a diagnosis or description and the fact that its illustration does not

present an analysis (l.c.: Art. 6.3, 38.7, 38.8, 38 Ex. 1, and Rec. 50B.1), but was latter validated by Drapiez (1834).

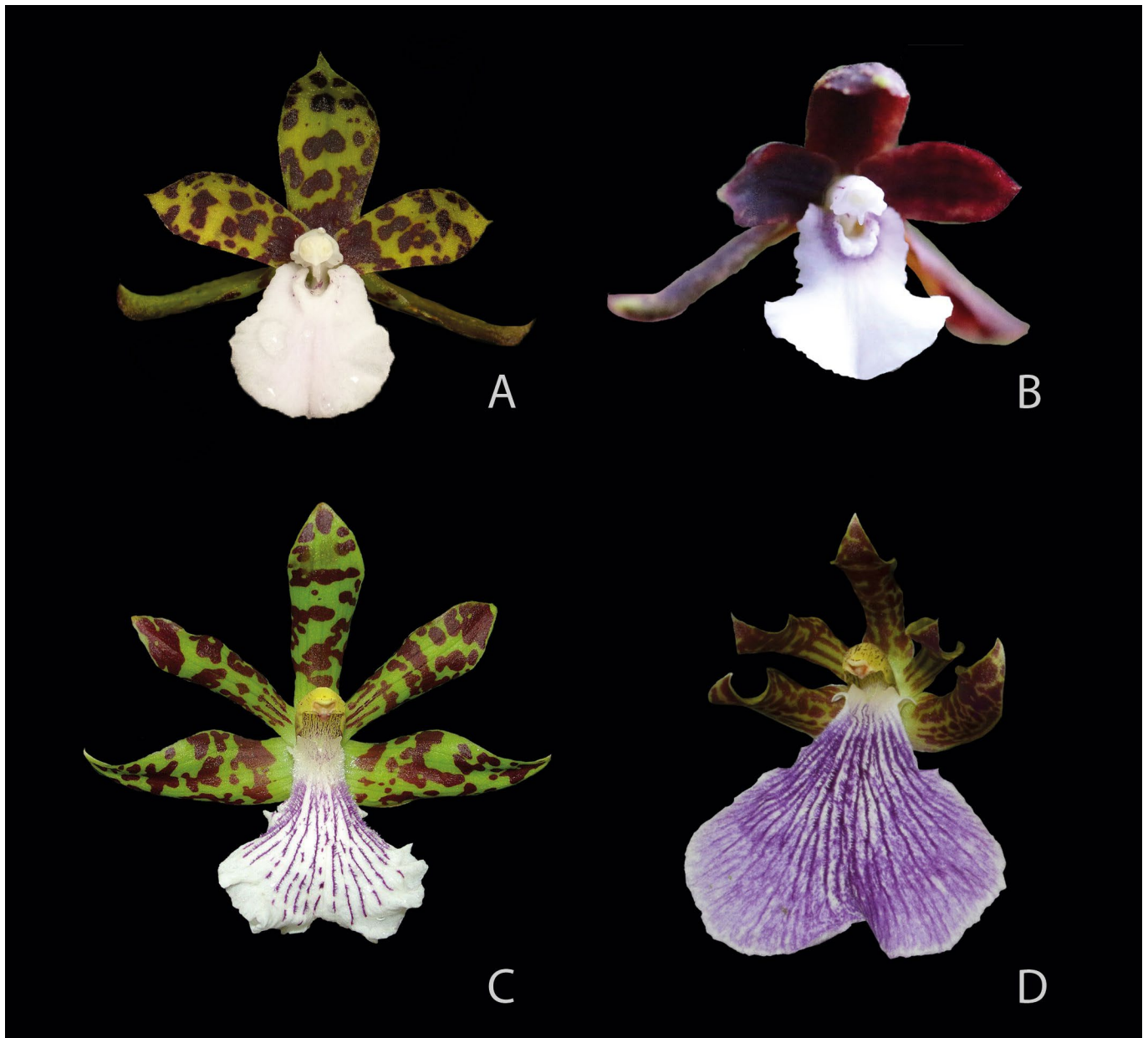


Figure 3. Pictures of living specimens of *Warreopsis* and *Zygopetalum*. A. *Warreopsis colorata* subsp. *colorata*. B. *Warreopsis colorata* subsp. *purpurea*. C. *Zygopetalum crinitum* subsp. *crinitum*. D. *Zygopetalum crinitum* subsp. *pabstii*. A. by A. Kay and facilitated by Flickr. B. by M. Stickrod and facilitated by iNaturalist. C. by user 'Orch' and facilitated by Wikimedia Commons. D. by T.E.C. Meneguzzo.

7. *Zygopetalum maculatum*

Zygopetalum maculatum (Kunth) Garay subsp. *maculatum* f. *maculatum* in Garay (1970: 189). *Dendrobium maculatum* Kunth in Humboldt *et al.* (1816: 359). *Broughtonia maculata* (Kunth)

Sprengel (1826: 735). *Maxillaria maculata* (Kunth) Lindley (1832: 149). Type (designated here):— PERU. Jaén: Between Jaén de Bracamoros, Sagique and Pucura, August, *F.W.H.A. Humboldt & A.J.A. Bonpland* 3621 (lectotype P QR code P00669292!). Figure 4A.

Zygopetalum mackaii Hooker (1827: t. 2748). *Eulophia mackaiana* Lindley (1831: t. 1433), *nom. superfl. et illeg.* *Eulophia mackaii* (Hook.) Steudel (1840: 605). Type (designated here):—BRAZIL. *S. loc., ex hort.*, February 1827, *J.T. Mackay s.n.* (lectotype K barcode K000589006!).

Zygopetalum mackaii var. *intermedium* Mutel (1842: 9), as “*mackayi*”. Type (designated here):—BRAZIL. Rio de Janeiro: Rio de Janeiro, Parque Nacional da Tijuca, ridge of Pedra da Gávea, 10 June 2007, *E.M. Saddi & L. Cardoso 275* (neotype RB 466296!). Original material:—BRAZIL. *S. loc., ex hort.*, August, *Taffin s.n.* (not found).

Zygopetalum brachypetalum Lindley (1844: misc. 9). Type (designated here):—BRAZIL. *S. loc., ex hort.*, July 1840, *Waterhouse s.n.* (lectotype K-L barcode K000857174!), *syn. nov.*

Zygopetalum intermedium Loddiges ex Lindley in Lindley (1844: misc. 9). *Zygopetalum mackaii* var. *intermedium* (Lodd. ex Lindl.) Nicholson (1887: 246), *nom. illeg.* Type (designated here):—BRAZIL. *S. loc., ex hort., s.d., C.L. Loddiges 1136* (lectotype K-L barcode K000857176!).

Zygopetalum mackaii var. *parviflorum* Regel in von Kuester & Regel (1855: 22), as “*Zygopetalon mackayi* var. *parviflorum*”. *Zygopetalum mackaii* var. *minor* Rollisson in Burbridge (1874: 160), *nom. superfl. et illeg.* Type (designated here):—BRAZIL. Espírito Santo. Castelo, arredores da sede do Parque Estadual do Forno Grande, 6 August 2003, *R.C. Forzza, J.A. Amaral, D. Monteiro & R.G.B. Silva 7654* (neótipo RB 585452!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found), *syn. nov.*

Zygopetalum mackaii var. *pictum* Regel in von Kuester & Regel (1855: 23), as “*Zygopetalon mackayi* var. *pictum*”. Type (designated here): BRAZIL. Rio de Janeiro: Petrópolis, Araras, Vale das Videiras, ridge of Morro do Cuca, 26 June 2011, *C.N.*

Fraga, M.M. Saavedra & M.O.O. Pellegrini 3326 (neotype RB 599865!). Original material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found), *syn. nov.*

Zygopetalum rivierii Carrière (1873: 191). Type (designated here):—BRAZIL. Minas Gerais. *S. loc., ex hort.*, 1870, *Rivièri s.n.* (the lectotype is the original illustration published in the protologue, Carrière 1873: s.n. between pages 190 and 191!), *syn. nov.*

Zygopetalum mackaii var. *superbum* Rollisson in Burbridge (1874: 160), *nom. nud.* Material:—*S. loc., ex hort., s.d., s. leg. s.n.* (not found).

Zygopetalum messangei Moore & Masters (1876: 603). Type (designated here):—BRAZIL. São Paulo: São Paulo, Campo Grande station, 21 August 1955, *O. Handro 504* (neotype RB 728512!, isoneotypes HB 85133!, SP 93159!, SPF 65077!). Original material:—*S. loc., ex hort.*, 30 April 1876, *Messrs. Jacob-Makoy & Co. s.n.* (not found), *syn. nov.*

Zygopetalum intermedium var. *peruvianum* Rolfe (1894: 71). Type (designated here):—PERU. *S. loc.*, 1835, *A. Matthews 1896* (lectotype K barcode K000880334!). Original material:—*S. loc., ex hort., s.d., L. Linden s.n.* (remaining syntype not found).

Zygopetalum protheroceanum Rolfe (1899: 287). Type (designated here):—BRAZIL. Rio de Janeiro: Itatiaia, Parque Nacional do Itatiaia, Macieiras, trek to Macieiras shelter, 3 December 1997, *J.M.A. Braga 4510* (neotype RB 414990!). Original material:—*S. loc., ex hort.*, 15 August 1899, *W. Cobb s.n.* (not found), *syn. nov.*

Zygopetalum mackaii var. *pallidum* Rollison in Burbridge (1874: 160), *nom. nud.* *Zygopetalum pallidum* Rolfe (1900: 320), *nom. nud.* *Zygopetalum brachypetalum* var. *pallidum* Cogniaux (1901: t. 5). *Zygopetalum pallidum* (Cogn.) Rolfe (1905: 27). Type (designated here):—*S. loc., ex hort., s.d., A. Buchan s.n.* (lectotype is the original illustration!

published in the protologue, Cogniaux 1901: t. 5!), *syn. nov.*

Zygopetalum bolivianum Schlechter (1922a: 50). Type (designated here):—BOLIVIA *S. loc.*, 1890, *M. Bang* 435 (lectotype US 814920!, isolectotypes AMES 75624!, BM barcode BM000074603!, F 77447!, G s.n., GH 90652!, K s.n., MO 2158877!, NY 1477510!, NY 1477511!, W 1890-1548!).

Zygopetalum sincoranum Castro Neto & Campacci (2000: 36). Type:—BRAZIL. Bahia. Barra da Estiva, Serra do Sincorá, *ex hort.*, 4 March 2000, *V.P. Castro s.n.* [sic] [recte *S. Koehler 11/00*] (holotype UEC 111157!), *syn. nov.*

Zygopetalum maculatum subsp. *maculatum* f. *charlesworthii* (R.H.Pearson) Meneguzzo, *comb. et stat. nov.* *Zygopetalum mackaii* [unranked infraspecies] *charlesworthii* Pearson (1912: 83), as "*Zygopetalum mackayi charlesworthii*". Type (designated here):—BRAZIL. *S. loc.*, *ex hort.*, 23 January 1912, *Messrs. Charlesworth & Co. s.n.* (the lectotype is the original illustration! published in the protologue, Pearson 1912: 83, t. 37!). Figure 4B–C.

Zygopetalum mackaii var. *albicans* Dronk, *in sched.*, as "*mackayi*". Material:—BRAZIL. Paraná: Balsa Nova. São Luiz do Purunã, 1 October 1998, *A.G. Dronk* [sic] [recte *A.G. Dronk*] 1 (MBM 235052!).

Zygopetalum maculatum subsp. *triste* (Barb.Rodr.) Meneguzzo, *comb. et stat. nov.* *Zygopetalum triste* Barbosa Rodrigues (1877: 108). Type (designated here):—BRAZIL. Minas Gerais: Caldas, Pedra Branca, March 1859, *J. Barbosa Rodrigues s.n.* (the lectotype is the original illustration! that was to be published in *Iconographie des Orchidées du Brésil* t. 11, deposited at the library of the Instituto de Pesquisas Jardim

Botânico do Rio de Janeiro, bound in volume 5, and later published in the book with same title by Barbosa Rodrigues 1996: 361, t. 236!; type *J. Barbosa Rodrigues* personal herbarium destroyed). Figure 4D.

Zygopetalum brachypetalum var. *stenopetalum* Regel (1887a: 374). Type (designated here):—BRAZIL. Minas Gerais. *S. loc.*, *ex hort.*, April, *Lietze s.n.* (the neotype is the illustration published by Regel 1888a: t. 1277!), *syn. nov.*

KEY TO THE INFRASPECIES OF *ZYGOPETALUM MACULATUM*

1. Leaves blade short (6.8–22.4 cm long); pseudobulbs short (2.4–3.6 cm long); inflorescences short (19.4–25.6 cm long); sepals and petals light green just on proximal portion and eventually on apex, distal portion dark brown, rarely light green background with large and almost completely confluent dark brown maculae; labellum purple with dark purple confluent veins, commonly fading towards the apex ***Z. maculatum* subsp. *triste***
- 1'. Leaves blade long (28.9–65.8 cm long); pseudobulbs long (3.9–12.5 cm long); inflorescences long (25.1–78.9 cm long); sepals and petals light green with maculae confluent or not, or light green to light brown with no maculae; labellum white with purple and non-confluent veins, rarely light rose **2**
2. Sepals and petals light green to light brown with no maculae; labellum white, rarely lateral lobes and midlobe with light rose veins ***Z. maculatum* subsp. *maculatum* f. *charlesworthii***
- 2'. Sepals and petals light green with light brown maculae either confluent or not; labellum lateral lobes and midlobe with purple veins **..... *Z. maculatum* subsp. *maculatum* f. *maculatum***

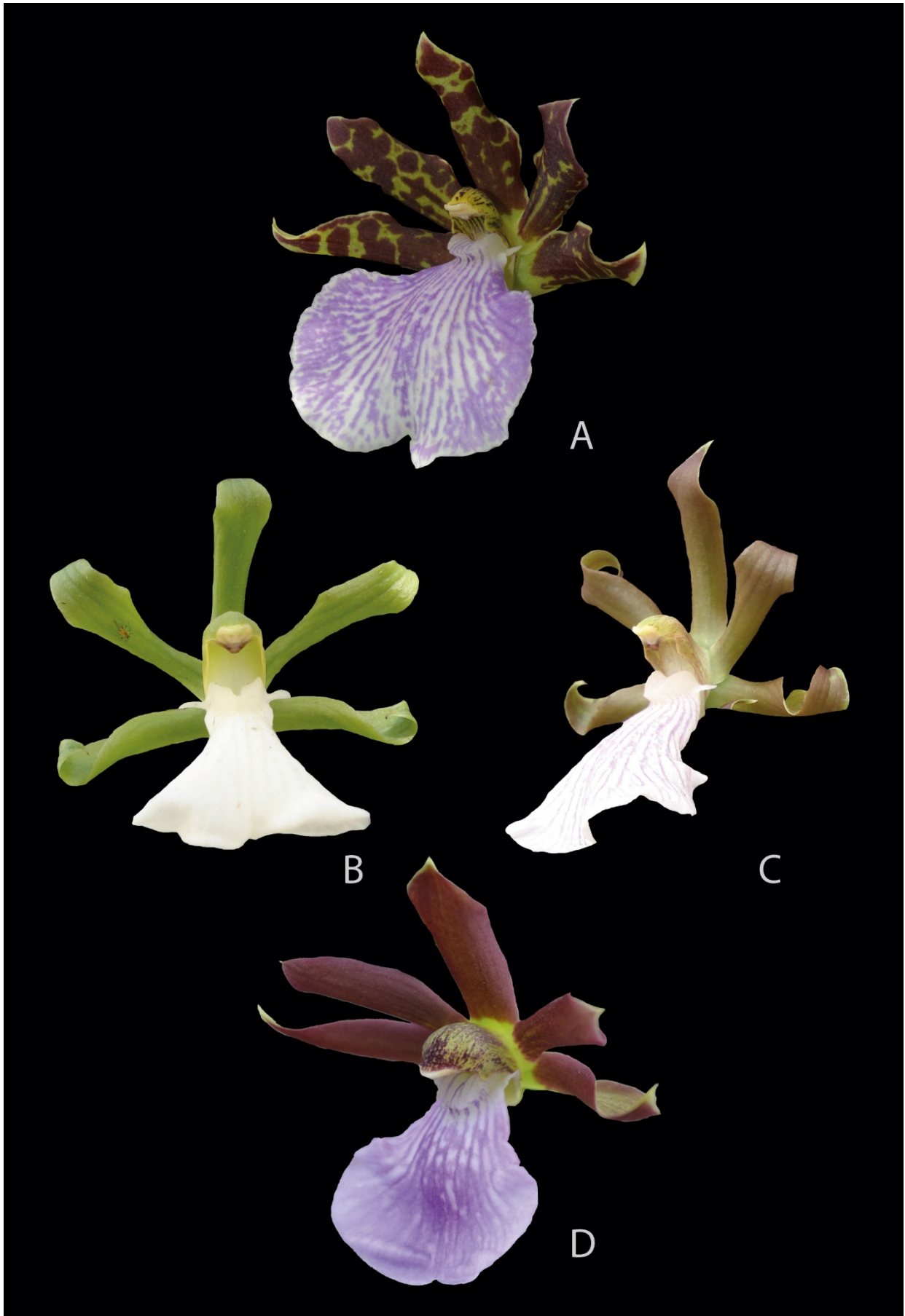


Figure 4. Pictures of living specimens of *Zygopetalum*. A. *Zygopetalum maculatum* subsp. *maculatum* f. *maculatum*. B–C. *Zygopetalum maculatum* subsp. *maculatum* f. *charlesworthii*. D. *Zygopetalum maculatum* subsp. *triste*. A, D. by T.E.C. Meneguzzo, B–C. by W. Pisoni.

Zygopetalum maculatum (Kunth) Garay subsp. *maculatum* f. *maculatum* is the species of its genus with the widest distribution and that has the most extensive list of synonyms. In Brazil it occurs from central Bahia to Rio Grande do Sul, and in the Bolivian and Peruvian Andean. It may also be possible to occur in Ecuador. The species is relatively common in high altitude regions usually bordering thickets and rupestrian fields. The study of the protologue of *Z. brachypetalum* Lindl., *Z. brachypetalum* var. *pallidum* Cogn., *Z. rivierii* Carrière, and *Z. sincoranum* V.P.Castro & Campacci led to their inclusion as new synonyms since their distribution and morphology agrees with that of the well established and accepted *Z. maculatum*. For the same reasons, the study of the protologues and neotype designation led to the inclusion of *Z. mackaii* var. *intermedium* Mutel, *Z. mackaii* var. *parviflorum* Regel, *Z. mackaii* var. *pictum* Regel, *Z. messangei* T.Moore & Mast., and *Z. protheroanum* Rolfe as new synonyms. It is worth noting that the last name is currently absent from all botanic name indexes.

In the states of Minas Gerais, São Paulo, and Paraná, in rupestrian fields, at high altitude areas like the top and ridges of ranges, a variation traditionally named *Zygopetalum triste* Barb.Rodr. occurs. It differs from *Z. maculatum* by being plants considerable shorter in stature with small pseudobulbs, which are frequently buried in the substrate, and by the petals and sepals being predominantly brown, rarely with a green background with large almost confluent maculae, and the purple labellum in which veining is very faint and fades towards the apex. The author himself and others (Thiago Vinicius Silva Campacci, pers. comm.) had reported that it is not uncommon to find *Z. maculatum* blooming simultaneously in

adjacent areas of lower altitude, but never sympatrically. Campacci *et al.* (2017) found that *Z. maculatum* and *Z. triste* freely cross and produce viable seeds under controlled experiments, which reinforces their affinity. These two biological entities present significant discontinuity in morphological features and do not co-occur in same habitat. Therefore, it is proposed that two distinct subspecies be recognized: *Zygopetalum maculatum* (Kunth) Garay subsp. *maculatum* and *Zygopetalum maculatum* subsp. *triste* (Barb.Rodr.) Meneguzzo.

As for *Zygopetalum maculatum* subsp. *maculatum*, there is a specimen in herbarium MBM, in which the flower colour differs from the typical by the sepals and petals being light brown with no maculae and the labellum with light pink veining. It was collected in the district of São Luiz do Purunã, municipality of Balsa Nova, Paraná. This variation has been known for some time among orchidists as *Zygopetalum mackaii* 'Dronk' (cultivar) in reference to its collector and grower Alessandro Garrett Dronk. It was reported (Valter Zomer Pisone, pers. comm.) that a similar cultivar named 'Valter Pisone' was also obtained from the self-crossing of the cultivar 'Dronk'. Among other siblings obtained, a new cultivar hence named 'Orleans' presents a different colour variation that widens the circumscription of the taxon by the sepals and petals being light green with no maculae and having a white labellum with no veining. During a bibliographic review of the *Zygopetalum*, it was retrieved that this variation had already been described and named as *Zygopetalum mackaii* [unranked infraspecies] *charlesworthii*, and that this was very similar indeed to those described for the cultivar 'Dronk'. As it occurs with *Batemannia peruviana* and *Zygopetalum xanthinum* var. *major*, the authorship of the debatable *Zygopetalum*

infraspecies is attributed to the editor of the journal *The Gardeners' Chronicle* at that time, in case Robert Hooper Pearson (1912) (Anonymous 1918). Because this variation is sporadic, and of low frequency amongst populations of *Z. maculatum* (Kunth) Garay subsp. *maculatum*, it is hereby recognized as a form by the name *Zygopetalum maculatum* subsp. *maculatum* f. *charlesworthii* (R.H.Pearson) Meneguzzo.

Eulophia mackaiana Lindl. and *Zygopetalum mackaii* var. *minor* Rollisson are respectively superfluous and illegitimate names of *Z. mackaii* Hook. and *Z. mackaii* var. *parviflorum* (Turland *et al.* 2018: Art. 52.1 and 52.2). *Zygopetalum mackaii* var. *intermedium* Nicholson (1899) is an illegitimate name of the earlier heterotypic name by Mutel (1842) (l.c.: Art. 53.1). *Zygopetalum mackaii* var. *superbum* Rollisson, *Z. mackaii* var. *pallidum* Rollisson, and *Z. pallidum* Rolfe are denoted as denominations or naked names due to the lack of a proper diagnosis or description (l.c.: Art. 6.3, 38 Ex. 1, and Rec. 50B.1). The spelling "*Zygopetalum mackayi*" has been massively favoured in the botanical literature in spite of the original spelling "*Zygopetalum mackaii*". However, the first spelling must stand not only because it is the original one (l.c.: Art. 60.1), but also because it resulted from the intentional Latinization of the surname Mackay to Mackaius, therefore the correct epithet is *mackaii* (Nicolson 1974).

8. *Zygopetalum maxillare*

Zygopetalum maxillare Loddiges f. *maxillare* in Loddiges (1832: t. 1772). *Eulophia maxillaris* (Lodd.) Loudon in Steudel (1840: 605). *Zygopetalum maxillare* var. *typicum* Regel in Regel & Maximowicz (1870: 34), *non valid. publ.* *Zygopetalum mandibulare* Hoffmannsegg (1844:

83), *nom. superfl. et illeg.* Type (designated here):—BRAZIL. Rio de Janeiro: *s. loc., ex hort.*, September 1831, *F. Warre s.n.* (the lectotype is the original illustration! deposited at the Natural History Museum, London, and published in the protologue, Loddiges 1832: t. 1772!). Figure 5A.

Zygopetalum gautieri Lemeire (1867: t. 535). *Zygopetalum maxillare* var. *gautieri* (Lem.) Regel in Regel & Maximowicz (1870: 34). Type (designated here):—BRAZIL. Santa Catarina: Florianópolis ["Île de Ste. Catherine"], September–October 1867, *A. Verschaffelt s.n.* (the lectotype is the original illustration published in the protologue, Lemeire 1867: t. 535!).

Zygopetalum obtusatum Reichenbach (1878: 300). Type (designated here):—*S. loc., ex hort.*, 11 June 1878, *T. Lawrence s.n.* (lectotype W-R 40643 inflorescence, upper left and bottom left icon!), *syn. nov.*

Zygopetalum graminifolium Rolfe in Rolfe & Baker (1892: 179). Type (designated here): BRAZIL.—Southern region, *s. loc., ex hort.*, April 1891, *Messrs. F. Sander & Co. s.n.* (lectotype K barcode K000589009!), *syn. nov.*

Zygopetalum hasslerianum Kränzlin (1906: 389). Type (designated here):—PARAGUAY. Guairá. Caraguazú ["Caaguazú"], February 1905, *É. Hassler 9020* (lectotype S 07-7834!, isolectotypes BR s.n.!, G 87511/1!, K barcode K000880339!, NY 9458!, W 1906-1439!).

Zygopetalum rigbyanum Ruschi (1975: 1). Type:—BRAZIL. Espírito Santo. Castelinho, 11 April 1974, *A. Ruschi s.n.* (holotype MBML spirit 2004!). Other material:—*S. loc.*, April, *s. leg. s.n.* (living specimen and orchid greenhouse F.C. Hoehne accession number 775 at MBML, not seen — misnamed as "paratype")

Zygopetalum silvanum Castro Neto & Campacci (1991: 27). Type:—BRAZIL. Bahia. Itororó, Serra de Ouricana, *ex hort.*, 17 April 1984, E.P. Silva s.n. (holotype SP 333601!), *syn. nov.*

Zygopetalum maxillare* f. *sanderianum (Regel) Meneguzzo, *comb. et stat. nov.* *Zygopetalum sanderianum* Regel (1888b: 657). *Zygopetalum maxillare* var. *sanderianum* (Regel) Cogniaux (1898a: 577). Type (designated here):—*S. loc.*, *ex hort.*, *s.d.*, H.F.C. Sander s.n. (the lectotype is the original illustration published in the protologue, Regel 1888b: t. 1287!). Figure 5B.

KEY TO THE INFRASPECIES OF *ZYGOPETALUM MAXILLARE*

1. Sepals and petals light green with light brown maculae, which are confluent in the proximal portion and non-confluent in the distal one; labellum lilac to purple occasionally attenuate towards the apex, callus darker

..... ***Z. maxillare* f. *maxillare***

1' Sepals and petals light green with no maculae, rarely with small light brown dots in the proximal portion; whole labellum light lilac to white or eventually light lilac in the proximal portion

..... ***Z. maxillare* f. *sanderianum***

Zygopetalum maxillare Lodd. subsp. *maxillare* is a widely spread species in the Atlantic Rain Forest from southern Bahia to Rio Grande do Sul, Brazil, and northeastern Argentina and eastern Paraguay. Typically its sepals and petals are light green with light brown maculae and its labellum is lilac to purple, occasionally with an attenuated hue towards the apex. The study of the type specimens accompanied by the protologue of *Z. obtusatum* Rchb.f., *Z. graminifolium* Rolfe, and *Z. silvanum* V.P. Castro & Campacci, led to their being newly proposed synonyms, since their putative

morphological dissimilarities fit in the circumscription of *Z. maxillare*.

By the end of the 19th century, Regel (1888b) described *Zygopetalum sanderianum* Regel from a specimen of unknown provenance which is characterized by green sepals and petals with small dots in the proximal portion and light lilac labellum. Later, Cogniaux (1898a) attributed it with a new status as a variety of *Z. maxillare*. It is proposed to keep *Z. sanderianum* as an infraspecies of *Z. maxillare*, therefore as *Zygopetalum maxillare* f. *sanderianum* (Regel) Meneguzzo. It is proposed as a form because the only difference is the variation in flower colour and only a few individuals with this flower colour sporadically appear among populations with the common coloured flowers. The circumscription is somewhat expanded to include specimens with sepals and petals green dotted or not and labellum light lilac to white.

The name *Zygopetalum maxillare* var. *typicum* Regel is not a validly published name because its final epithet might be equal to the second one (Turland *et al.* 2018: Art. 24.3 and 26.2). *Zygopetalum mandibulare* Hoffmann. is a superfluous and illegitimate name of *Z. maxillare* Lodd. (l.c.: Art. 52.1 and 52.2). The living nomenclatural type of *Zygopetalum rigbyanum* Ruschi is not a preserved specimen, therefore it can not be accepted as a type (l.c.: Art. 8.4).

9. *Zygosepalum labiosum*

Zygosepalum labiosum (Rich.) Garay subsp. ***labiosum*** in Garay (1967: 6). *Epidendrum labiosum* Richard (1792: 112). *Menadenium labiosum* (Rich.) Cogniaux (1898b: 582). *Zygopetalum labiosum* (Rich.) L.O. Williams (1942: 16). *Zygosepalum labiosum* (Rich.) Schweinfurth (1967: 184), *nom.*

superfl. Type (designated here):—FRENCH GUIANA. *S. loc.*, 1787–1789, *J.B. Leblond s.n.* (lectotype P barcode P00612111!). Figure 5C.

Zygopetalum rostratum Hooker (1828: t. 2819). *Menadenium rostratum* (Hook.) Rafinesque (1838: 45), *non valid. publ. Eulophia rostrata* (Hook.) Steudel (1840: 605). *Zygosepalum rostratum* (Hook.) Reichenbach (1859: 330). Type (designated here):—GUYANA. Demerara: *s. loc.*, *ex hort.*, October 1827, *C.S. Parker s.n.* (lectotype K barcode K000589024!).

Zygopetalum kegelii Reichenbach (1852a: 668). *Zygosepalum kegelii* (Rchb.f.) Reichenbach (1859: 330), *non valid. publ. Zygosepalum kegelii* (Rchb.f.) Reichenbach (1863b: 666). *Menadenium kegelii* (Rchb.f.) Cogniaux (1898b: 584). Type (designated here):—SURINAME. Geiersvlyt and Tourtonne, *ex hort.*, January 1849, *H.A.H. Kegel 1427* sub *van Houtte s.n.* (lectotype W-R 40623!); *idem*, May 1846, *H.A.H. Kegel 1427* sub *van Houtte s.n.* (remaining syntype W-R 17644!), *syn. nov.*

Zygosepalum labiosum nothosubsp. *ballii* (Rolfe) Meneguzzo, *comb. et stat. nov.* *Zygopetalum* × *ballii* Rolfe (1900: 149). *Zygopetalum* × *ballii* Rolfe (1906: 33), *nom. superfl.* *Menadenium* × *ballii* (Rolfe) Cogniaux (1906b: 576). *Zygosepalum* × *ballii* (Rolfe) Garay (1967: 8), *nom. valid. publ. Zygopetalum* × *ballianum* H.J.Veitch, *in sched.* Type (designated here):—BRAZIL. [*sic*] Pernambuco [*recte* northern South America, possibly Brazil], *ex hort.*, June 1898, *Messrs. J. Cowan & Co.* sub *G.S. Ball s.n.* (lectotype K barcode K000880371!, isoelectotype AMES 4693!). Parent taxa (postulated here):—*Batemannia colleyi* Lindl. subsp. *colleyi* × *Zygosepalum labiosum* subsp. *lindeniae* (Rolfe) Meneguzzo.

Zygosepalum labiosum subsp. *lindeniae* (Rolfe) Meneguzzo, *comb. et stat. nov.* *Zygopetalum*

lindeniae Rolfe (1891: 73). *Menadenium lindeniae* (Rolfe) Cogniaux (1898b: 584). *Zygosepalum lindeniae* (Rolfe) Garay & Dunsterville *in* Dunsterville & Garay (1965: 336). Type (designated here):—*S. loc.*, *ex hort.*, April 1891, *Bungeroth* sub *Messrs. Linden s.n.* (lectotype K barcode K000589026!). Figure 5D.

Zygosepalum revolutum Garay & Romero-González (1999: 487). Type:—COLOMBIA. Vaupés: Miraflores, Vaupés River, *s.d.*, *G. Escobar Restrepo 1039* (holotype AMES 287162!), *syn. nov.*

Zygosepalum labiosum nothosubsp. *marginatum* (Garay) Meneguzzo, *comb. et stat. nov.* *Zygosepalum* × *marginatum* Garay (1967: 8). *Zygopetalum* × *marginatum* (Garay) Garay (1973: 32), *nom. illeg.* *Mendoncella* × *marginata* (Garay) Garay (1973: 32). *Galeottia* × *marginata* (Garay) Dressler & Christenson *in* Christenson (1989: 222). Type:—COLOMBIA. *S. loc.*, *ex hort.*, *s.d.*, *C. Mark* sub *Joseph Redlinger Orchids* sub *W.C. Cornett s.n.* (holotype AMES 102311!). Parent taxa (postulated here):—*Galeottia grandiflora* A.Rich. & *Galeotti* × *Zygosepalum labiosum* subsp. *lindeniae* (Rolfe) Meneguzzo. Figure 5E.

KEY TO THE INFRASPECIES OF *ZYGOSEPALUM LABIOSUM*

1. Anther cap apex short-rostellate **2**
- 1'. Anther cap apex long-rostellate **3**
2. Labellum callus hippocrepiform and canaliculate with margin smooth, midlobe margin entire
..... **Z. labiosum** nothosubsp. **ballii**
- 2'. Labellum callus widely hippocrepiform and concave with margin digitate, midlobe margin irregularly serrate
..... **Z. labiosum** nothosubsp. **marginatum**
3. Sepals and petals light green to light brown,

labellum white, callus and proximal portion of the midlobe with a few crimson veins
 **Z. labiosum** subsp. **labiosum**
 3'. Sepals and petals light brown, dark brown to dark red (rarely light green), whole labellum white to light crimson and densely veined
 **Z. labiosum** subsp. **lindeniae**

Zygosepalum labiosum (Rich.) Garay subsp. *labiosum* is a widespread epiphyte species from rain forests along northeastern South America, occurring in Venezuela, the Guianas, and eastern Brazilian Amazon. It apparently grows in the proximity of water bodies and lower parts of tree trunks under dense forest canopy. Its flower morphology does not vary significantly, being the sole variation that the labellum has more or less prominent lobes or that the base is more or less cordate. Cogniaux (1898b) synonymized *Zygosepalum rostratum* under *Zygosepalum labiosum* (as *Menadenium* Raf. ex Cogn.), and he also proposed the inclusion of *Zygosepalum kegelii* in the synonymy.

In northwestern South America, in Venezuela, Colombia, Ecuador, Peru, and western Brazilian Amazon, a biological entity named *Zygosepalum lindeniae* (Rolfe) Garay & Dunst. occurs, which only differs from *Zygosepalum labiosum* by sepals and petals that are usually darker and the densely veined labellum. *Zygopetalum revolutum* is only known from the type specimen and has a more deeply cordate labellum than in *Zygosepalum lindeniae*, but this sole feature does not support its recognition as a good species and therefore it is synonymized. Since the two taxa are allopatric and only morphological difference is the flower colour, and mainly in the labellum, it is proposed it be reduced to subspecific rank: *Zygopetalum labiosum* subsp. *lindeniae* (Rolfe)

Meneguzzo.

Zygosepalum marginatum was described by Garay (1967) and shortly after combined by the author to *Zygopetalum*, then to *Mendoncella*, showing how unusual is its morphology. It was not a perfect fit to the generic concepts as stipulated by Garay himself in his overview of the *Zygopetalum* complex (Garay 1973). It is herein postulated that this entity is a nothospecies with parent taxa *Galeottia grandiflora* Richard & Galeotti (1845: 33) (Figure 5F) and *Zygopetalum labiosum* subsp. *lindeniae* due to the intermediate nature of its morphology in some aspects and equal to one or the other parent in others, and sympatry of both parents on its country of origin. It has a reptant and rhizomatose habit, pseudobulbs sheaths, subtend on base of pseudobulb, base margin hyaline, articulate, leafy, flower colour, lip callus widely hippocrepiform, and lateral lobes length between apices of the lateral lobes narrower than the midlobe width inherited from *Zygosepalum labiosum* subsp. *lindeniae*. Whilst the lip callus is widely hippocrepiform, wider than column width, composed of several longitudinal carinae, and the lip midlobe margin is denticulate, characters inherited from *Zygopetalum grandiflorum*. The short-rostellate column anther cap apex is clearly intermediate, as in the former parent it is rounded, and in latter parent it is long-rostellate. The rarity of nothotaxa in natural habitats is a feasible explanation why it has never been recollected. Since one of its postulated parents is of lower taxonomic rank than the other, the nothotaxon must equally be at the lowest rank (Turland *et al.* 2018: Art. H.5 Ex. 2 and H.11.2). Hence, it is herein stipulated to be under *Zygosepalum labiosum* and the new combination is proposed too: *Zygosepalum labiosum* nothosubsp. *marginatum* (Garay) Meneguzzo.

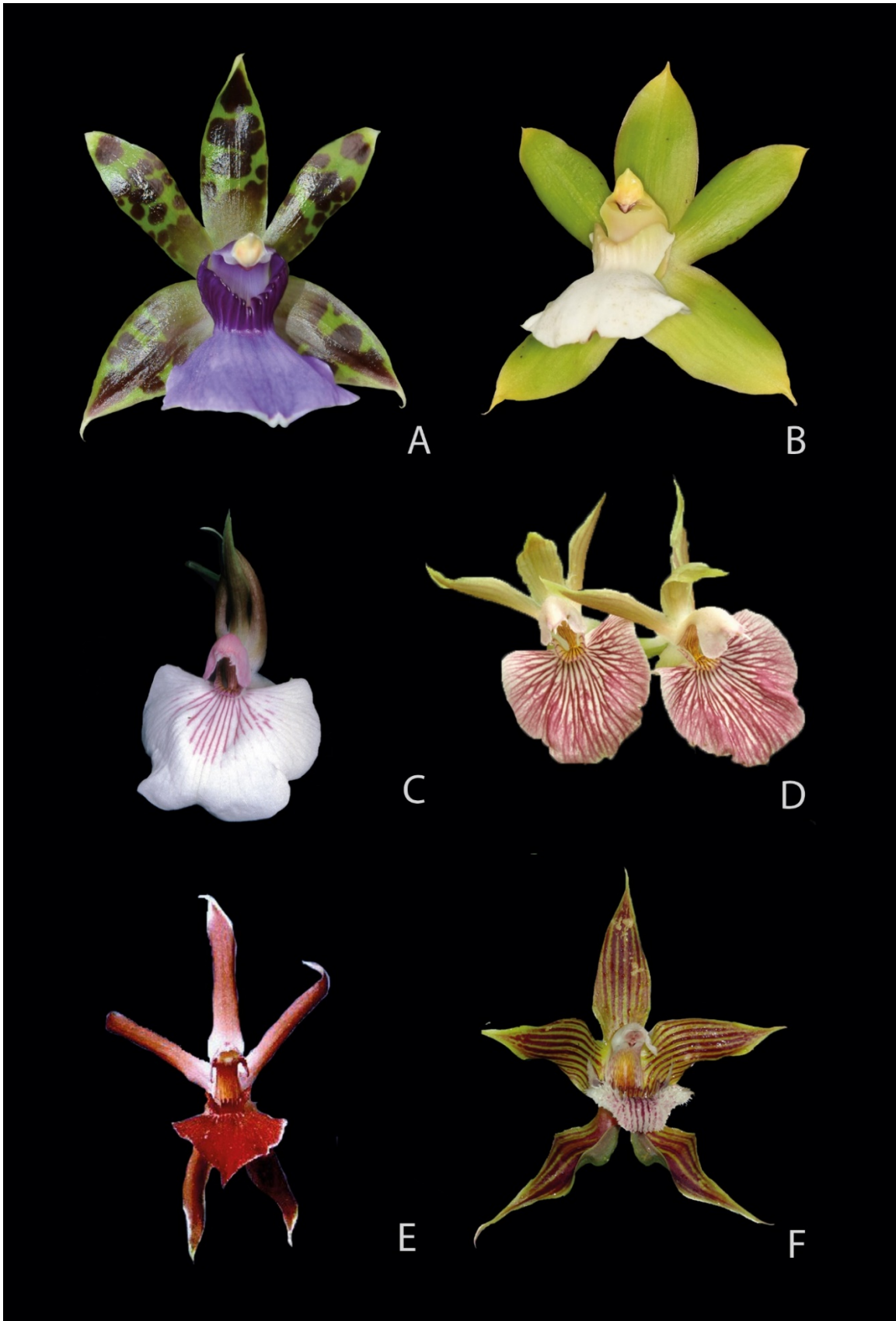


Figure 5. Pictures of living specimens of *Zygopetalum*, *Zygosepalum* and *Galeottia*. A. *Zygopetalum maxillare* f. *maxillare*. B. *Zygopetalum maxillare* f. *sanderianum*. C. *Zygosepalum labiosum* subsp. *labiosum*. D. *Zygosepalum labiosum* subsp. *lindeniae*. E. *Zygosepalum labiosum* nothosubsp. *marginatum*. F. *Galeottia grandiflora*. A. by T.E.C. Meneguzzo. B. by P. Fabro. C. by user 'Orch' facilitated by Wikimedia Commons. D. by K. Senghas and facilitated by Swiss Orchid Foundation at Herbarium Jany Renz. E. by L.A. Garay and facilitated by J. Pfahl. F. by Ecuagenera and facilitated by Swiss Orchid Foundation at Herbarium Jany Renz.

Rolfe (1900) described *Zygopetalum ballii* as a new species based on a cultivated specimen without precedence. He had access only to the preserved flowers and on the report of the vegetative part that was written by the owner of the plant, which is reflected on the state of the original materials. Later Rolfe (1906) redescribed the taxon and indicate to be from the state of Pernambuco, Brazil. Cogniaux (1898b) combined it to the genus *Menadenium* Raf. ex Cogn. and Garay (1967) to the genus *Zygosepalum*; none of them contributed to a better understanding of the biological entity and merely repeated the limited previously published data. Schlechter (1919: 86) cited its occurrence to Bolívar, Venezuela, without giving any extra information to track neither provenance, nor the specimen. The identity of this putative species had not been elucidated and recollected. It is herein postulated the nature of *Zygopetalum* × *ballii* as a nothospecies with parent taxa *Batemannia colleyi* subsp. *colleyi* and *Zygosepalum labiosum* subsp. *lindeniae* based on the unique combination of characters that does not neatly match any of both genera, but are quite intermediate and on which certain characteristics can clearly be picked from the parents. The similarities of *Zygopetalum ballii* with *Zygosepalum* is inevitable: pseudobulbs laterally compressed and 3–4 leaved, sepals and petals subsimilar in shape and slightly convex, lip ovate with inconspicuous lateral lobes, callus high, erect-patent, and canaliculate. When compared to *Batemannia*, sepals and petals subsimilar in size, convex and about 60° between them vs. sepals longer than petals, flat and about 30°, the lip lacks lateral lobes, the callus has no resemblance as already described vs. distally free and long aciculate to denticulate, but instead with sessile apex, column with inconspicuous stigmatic wings vs.

conspicuous, and the anther cap short rostellate vs. rounded. Both parent species and the hybrid shares column with peculiar morphology for the genera constituted by the clinandrium margin projected over the anther cap. On the grounds of the colours, both *Zygopetalum labiosum* subsp. *lindeniae* and *Batemannia colleyi* subsp. *colleyi* have petals and sepals brown with lighter hue towards the margins, the lip in the first is white to light crimson and densely veined and on the second white. *Zygopetalum* × *ballii* has sepals and petals with same colour, but in the original material the petals diffused and discreet blotched with dark rose instead of brown, the lip white with the proximal half portion crimson.

The locality of the type specimen of *Zygopetalum* × *ballii* is disputed as Pernambuco since none of the parent taxa occurs there, but instead a putative locality in northwestern north America area of the Amazon forest where both parents does occur. It concurs with the observation of a specimen confidentially identified as this taxon from São Gabriel da Cachoeira, Amazonas, Brazil, and kept under cultivation (Cássio van den Berg, pers. comm.). This specimen does not bears blotched marks on the perigonium as the original material does. Hence, following the same nomenclatural rule of nothospecies with parents different ranks, as in *Zygosepalum labiosum* nothosubsp. *marginatum* (Turland *et al.* 2018: Art. H.5 Ex. 2 and H.11.2), *Zygopetalum* × *ballii* is combined to the subspecies level under *Zygosepalum labiosum* and subsequently as it status changed to a nothospecies: *Zygosepalum labiosum* nothosubsp. *ballii* (Rolfe) Meneguzzo.

Some nomenclatural comments about *Zygosepalum* Rchb.f. and its synonym *Menadenium* Raf. ex Cogn. are necessary to clarify their tortuous

history. *Zygosepalum labiosum* (Rich.) Garay (1967: 6) and *Zygosepalum labiosum* (Rich.) Schweinfurth (1967: 184) were published in different journals. Surprisingly both bear the same year and month cover date, and therefore they are equal priority homonyms (Turland *et al.* 2018: Art. 53.5). Romero-González (2005) literally stated that Garay's name undoubtedly preceded Schweinfurth's, but failed by not presenting such evidence or rejecting the latter. Notwithstanding there is no internal evidence in both works of which was earlier published. *Zygosepalum labiosum* (Rich.) Garay (1967: 6) is herein adopted simultaneously rejecting *Zygosepalum labiosum* (Rich.) Schweinfurth (1967: 184), whose legitimate status is kept but turned to be superfluous (Turland *et al.* 2018: Art. 52.1, 53.5, and 53.5 Note 4).

The genus *Menadenium* Rafinesque (1838: 45) was not validly published because it was not accepted by the author at the time of its publication (Turland *et al.* 2018: Art. 36.1), i.e. by not citing the names in its own paragraph with unique numbering and by the absence of the genus in the index of the volume. The genus itself was later validly published by Cogniaux (1898b: 581) who also published the combination *M. kegelii* (Rchb.f.) Cogn., *M. labiosum* (Rich.) Cogn., and *M. lindeniae* (Rolfe) Cogn. A combination of *Zygopetalum rostratum* Hook. to *Menadenium* never was validly published because, as said, Rafinesque (l.c.) did not validly published the genus, and also he did not associate the genus name with the specific epithet (Turland *et al.* 2018: Art. 35.1 and 35.2). Subsequent authors accepted the synonymization of *Zygopetalum rostratum* under *Menadenium labiosum* or *Zygosepalum labiosum*, hence the combination to any of those last genera would be unuseful.

Zygosepalum kegelii (Rchb.f.) Reichenbach

(1859: 330) is not a validly published name as it is merely cited as a synonym of *Zygosepalum rostratum* (Hook.) Reichenbach (1859: 330) (Turland *et al.* 2018: Art. 36.1(b) and 36 Ex. 7), but later validly published by Reichenbach (1863b: 666). *Zygopetalum lindeniae* Rolfe (1891: 73) and *Zygopetalum lindonii* Rolfe (1892: 5) are legitimate names, not homonyms as commonly stated in botanical literature (Turland *et al.* 2018: Art. 53.2, 53 Ex. 12, and 60 Ex. 23), being the latter currently accepted as synonym of *Warczewiczella amazonica* Rchb.f. & Warsz.

Contrary to what Rolfe (1906) believed, the original publication of *Zygopetalum × ballii* (Rolfe 1900) is indeed validly published because it fulfils all the requirements, even though it lacks a Latin diagnosis which is mandatory from 1 January 1935 to 31 December 2011 (Turland *et al.* 2018: Art. 32.1 and 39.1). Hence, the second of Rolfe's publication on the name is superfluous (Rolfe 1906; Turland *et al.* 2018: Art. 52.1 and 52.2). It has direct consequence on the fact that the combination *Zygosepalum × ballii* (Rolfe) Garay (1967: 8) turns to be a not validly published name because it is not based on the original publication (Rolfe 1900: 149), but instead on the later publication that has a direct reference to the first one (Rolfe 1906: 33; Turland *et al.* 2018: 35.1 and 41.8).

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