

# A molecular phylogeny reveals paraphyly of the large genus *Eulophia* (Orchidaceae): A case for the reinstatement of *Orthochilus*

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**Abstract** Phylogenetic relationships were inferred for the African-centred orchid subtribe Eulophiinae, which includes the large genus *Eulophia* and three closely related genera, *Oeceoclades*, *Pteroglossaspis* and *Acrolophia*. We sequenced one nuclear (ITS) and four chloroplast (*rbcl*, *trnK-matK*, *rpl32-trnL*, *trnQ-5' rps16*) markers for 86 samples, representing 58 species (62 taxa) and one outgroup. The combined sequence matrix had 6525 characters and was analysed using parsimony and Bayesian criteria. Our results show that *Acrolophia* and *Oeceoclades* are monophyletic but are nested in *Eulophia* as currently circumscribed, thus rendering it paraphyletic. We argue for retaining *Acrolophia* and *Oeceoclades*, and splitting *Eulophia* into two genera on the basis of evidence that each of these four clades is genetically and morphologically distinct. We propose to reinstate the genus name *Orthochilus* for one of the *Eulophia* clades and transfer 35 taxa, including those assigned to *Pteroglossaspis*, to *Orthochilus*. Thirty-two of these are new combinations.

**Keywords** *Acrolophia*; Africa; Cape Floristic Region; *Eulophia*; monophyly testing; *Oeceoclades*; *Pteroglossaspis*

**Supplementary Material** Electronic Supplement (Fig. S1) and alignment are available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>

## ■ INTRODUCTION

*Eulophia* R.Br. ex Lindl. is the largest genus in the orchid subtribe Eulophiinae (subfamily Epidendroideae; tribe Cymbidieae; Pridgeon & al., 2009). Eulophiinae orchids are mostly found in the palaeotropics, although six species extend into the neotropics, and their centre of diversity is undoubtedly Africa (Pridgeon & al., 2009). Two hundred species of *Eulophia* are currently accepted of which 156 are distributed over sub-Saharan Africa and the Western Indian Ocean Islands (WCSP, 2013). This terrestrial genus shows an extraordinary morphological diversity and occupies a surprisingly wide variety of habitats, from semi-arid regions and coastal dunes to swamps, and from grasslands to tropical forests, but is most diverse in the *Brachystegia* (*miombo*) woodlands of south-central Africa (Williamson, 1977; La Croix & Cribb, 1998). This habitat diversity is reflected in their phenotypic diversity, e.g., their perennating organs (fleshy rhizomes, tubers or pseudobulbs; Pridgeon & al., 2009), their ploidy levels (Poggio & al., 1986), their nutritional strategies from autotrophic to fully myco-heterotrophic species (Ogura-Tsujita & Yukawa, 2008), their diverse breeding systems from autonomous self-fertilization to obligate cross-pollination (Peter & Johnson, 2006, 2009a, b, c), and perhaps principally through specialised pollination systems by a diverse suite of bee and beetle pollinators (Peter & Johnson, 2013).

*Eulophia* was established by Lindley (1823) based on *E. guineensis* Lindl. The name *Eulophus* was first suggested by Brown (1821) in a paper in which he described an allied genus, i.e., *Lissochilus* R.Br., but was later changed to *Eulophia* upon the suggestion of Brown, when Lindley formally described it. Although there has been some controversy over the issue (see Cribb, 1989: 422), all modern authors now consider *Eulophia* and *Lissochilus* to be congeneric. *Eulophia* was later conserved over the less widely used *Lissochilus* and several other earlier names (see Summerhayes & Hall, 1962). Over time, several other genera were established which are now also considered synonyms of *Eulophia*. Lindley (1833: 189–191), who accepted both *Lissochilus* and *Eulophia*, even though he admitted that he could barely distinguish them from one another, added *Cyrtopera* Lindl. for similar species with a spurless subventricose lip. Richard (1850) described *Orthochilus* Hochst. ex A.Rich. based on *O. abyssinicus* (Rchb.f.) Hochst. ex A.Rich. ( $\equiv$  *E. abyssinica* Rchb.f.). Reichenbach (1878) established *Pteroglossaspis* Rchb.f. for *P. eustachya* Rchb.f. ( $\equiv$  *E. eustachya* (Rchb.f.) Geerinck), a species in which the gynostemium lacks a foot and the lip has no spur, but which otherwise has a *Eulophia*-like habit. Most authors of recent floristic treatments have maintained *Pteroglossaspis* as distinct, except for Geerinck (1987, 1992) who considered it congeneric with *Eulophia*. Indeed, lack of a spur or column foot is not restricted to *Pteroglossaspis* but also occurs in *Eulophia*. Although their preliminary

molecular evidence is inconclusive, Pridgeon & al. (2009: fig. A5) followed Geerinck (1992) and placed *Pteroglossaspis* within *Eulophia*. Most authors, apart from Geerinck (1987, 1992), have also accepted *Oeceoclades* Lindl. (Lindley, 1832) as a distinct genus (consisting of 39 species). Nevertheless, the generic boundaries between *Oeceoclades* and *Eulophia* have remained unresolved and whether certain species, such as for instance *E. pulchra* (Thouars) Lindl., are better placed in *Eulophia* or *Oeceoclades* is a matter of opinion (Clements & Cribb, 1989; Thomas, 1996; La Croix & Cribb, 1998; Cribb & Hermans, 2009; WCSP, 2013).

A monographic treatment of *Eulophia* is urgently needed, particularly in view of the fact that many species are widespread and show considerable regional variation, which has led to a proliferation of names (Hall, 1965; Thomas, 1998). Regional treatments for Africa, which could form the basis for a monograph, have been prepared for southern Africa (Hall, 1965), south-central Africa (La Croix & Cribb, 1998), Madagascar (Du Puy & al., 1999; Hermans & al., 2007), Central Africa (Geerinck, 1992), Gabon (Szlachetko & al., 2004), East Africa (Cribb, 1989), Ethiopia (Cribb & Thomas, 1997), West Africa (Summerhayes, 1968), Cameroon (Szlachetko & Olszewski, 1998) and Guinea (Szlachetko & Kowalkowska, 2007). Despite all this floristic attention, no workable infrageneric treatment of *Eulophia* exists. Some very early attempts (see Thomas, 1998 and Pridgeon & al., 2009 for details) are no longer useful. Cribb in Pridgeon & al. (2009: 102–103) suggested seven potential sections but refrained from formalising them in the absence of a proper morphological and/or molecular analysis that clarifies whether or not *Eulophia* and closely related genera, as currently circumscribed, are monophyletic.

Besides *Eulophia* and *Oeceoclades*, the other genera currently considered to belong to the Eulophiinae are *Geodorum* Jacks. (12 spp.), *Acrolophia* Pfitzer (7), *Eulophiella* Rolfe (5), *Cymbidiella* Rolfe (3), *Grammangis* Rchb.f. (2), *Paralophia* P.J.Cribb & Hermans (2), and *Cyanaeorchis* Barb.Rodr. (2) (Pridgeon & al., 2009; WCSP, 2013). Based on a preliminary phylogenetic analysis using a combination of morphological and molecular characters, Pridgeon & al. (2009) provided some insight into relationships between some of these genera. Their phylogeny indicates that *Eulophiella*, *Cymbidiella*, *Grammangis* and *Paralophia* form sister clades to the *Eulophia*-*Oeceoclades*-*Pteroglossaspis* clade (Pridgeon & al., 2009: fig. A5). However, it is clear that much more work is needed, principally to clarify the generic boundaries of *Eulophia*. For instance, its relationship to *Acrolophia*, which is largely endemic to the Cape Floristic Region and morphologically very similar to *Eulophia* (Linder & Kurzweil, 1999; Pridgeon & al., 2009), is unknown since it has never been included in any molecular phylogenetic analysis. Although *Acrolophia* has been treated in several floristic accounts (Rolfe, 1912; Stewart & al., 1982; Linder & Kurzweil, 1999), it has never been critically revised and a type species has not been selected.

In this study, we address the phylogenetic relationships between species of *Eulophia*, *Pteroglossaspis* and *Oeceoclades*—three genera that form a monophyletic clade within Eulophiinae according to Pridgeon & al. (2009: fig. A5)—and

also include the genus *Acrolophia* because of its morphological similarity with *Eulophia*. Our objective was to reconstruct a robust multi-gene molecular phylogeny from an extensive sampling of mainly South African and Western Indian Ocean representatives. We specifically aimed to test monophyly of *Eulophia*. We hypothesized that this genus as currently circumscribed (Pridgeon & al., 2009; WCSP, 2013) may not represent a monophyletic group.

## ■ MATERIALS AND METHODS

**Plant sampling.** — Eighty-six samples, representing 58 species (62 taxa) of Eulophiinae and one outgroup were included in this analysis (see Appendix 1). The samples included 46 *Eulophia* species (with one formerly included in *Pteroglossaspis*), 7 *Acrolophia* species and 5 *Oeceoclades* species. This covered 35 of 41 (85%) *Eulophia* species, and 7 of 7 (100%) *Acrolophia* species, occurring in South Africa (Linder & Kurzweil, 1999). Our sampling included the type species for *Eulophia* (*E. guineensis*) and *Oeceoclades* (*O. maculata* (Lindl.) Lindl.). The genus *Acrolophia* has not been typified (Pridgeon & al., 2009) but was comprehensively sampled. *Ansellia africana* Lindl. (subtribe Cymbidiinae) was used to root the trees based on Pridgeon & al. (2009: fig. A5). Voucher specimens were collected at flowering time, dried and mostly deposited at the Bews (NU) or Selmar Schonland (GRA) herbarium (see Appendix 1). In the case of rarely encountered species we only retained one or two flowers preserved in spirit and/or photographs as vouchers (see Appendix 1). Names used in the text, figures, and appendix, follow the World Checklist of Selected Plant Families (WCSP, 2013).

**DNA isolation amplification and sequencing.** — Fresh plant material was dried in silica gel and DNA was extracted with DNeasy Plant Mini Kit (QIAGEN, Hilden, Germany). The internal transcribed spacers of the 18S-5.8S-26S nuclear ribosomal DNA (= nrITS) were amplified using the primer pair 17SE/26SE (Sun & al., 1994) also called AB101/AB102 by Douzery & al. (1999). Four chloroplast markers were amplified, i.e., the ribulose-1,5-bisphosphate carboxylase oxygenase gene (= *rbcL*), the tRNA-Lys gene and intron and maturase K gene (= *trnK-matK*), the ribosomal protein L32-*trnL* intergenic spacer (= *rpl32-trnL*) and *trnQ*-ribosomal protein S16 (= *trnQ-5' rps16*) non-coding regions (Electr. Suppl.: Fig. S1). These were amplified using the primer pairs 1F/1360R (Kores & al., 2000), -19F/R1 (Kocyan & al., 2004), *rpl32-F/trnL*<sup>(UAG)</sup> and *rps16x1/trnQ*<sup>(UUG)</sup> (Shaw & al., 2007), respectively (Electr. Suppl.: Fig. S1). However, R1, designed for the orchid subfamily Apostasioideae (Kocyan & al., 2004), was modified to R1mod (CAGTTTTCATTGCACACGAC) to match the chloroplast genome of the orchid subfamily Epidendroideae based on the complete chloroplast genomes of *Phalaenopsis aphrodite* Rchb.f. (Chang & al., 2006) and *Oncidium* Gower Ramsey (Wu & al., 2010). PCR reactions contained 1× Colorless GoTaq Flexi Buffer, 2.5 mM MgCl<sub>2</sub> solution, 2 μg bovine serum albumin, 0.2 mM of each of the dNTPs, 0.5 μM forward primer, 0.5 μM reverse primer, 1.25 u GoTaq Flexi

DNA Polymerase (Promega, Madison, Wisconsin, U.S.A.), 0.3–0.5 µg template DNA, and nuclease-free water to 50 µL volume. PCR amplification was performed in a Veriti Thermal Cycler (Applied Biosystems, Life Technologies, Carlsbad, California, U.S.A.) as follows: 2 min initial denaturation at 95°C; 35 cycles of 1 min denaturation at 95 °C—1 min annealing at 59°C for ITS, 50°C for *rbcL*, 52°C for *matK*, 55°C for *rpl32-trnL*, and 60°C for *trnQ-5' rps16*—3 min elongation at 72°C; followed by a 5 min final elongation at 72°C. PCR products were visualised by electrophoresis on 1.5% agarose gels. We did not detect paralogous copies of nrITS during this study. In about 20% of the samples we could not amplify the long fragment *trnK-matK* of approximately 1700 bp with the use of the external primers -19F and R1mod only. In such cases we made use of the internal primers, 1326R (Cuénoud & al., 2002) and 580F (Kocyan & al., 2004) to amplify the *trnK-matK* in two parts.

PCR products were purified using a Macherey-Nagel Nucleic Acid and Protein Purification Kit NucleoFast 96 PCR Plate on a Tecan EVO150. Sense and antisense sequencing was carried out with BigDye Terminator v.3.1 Cycle Sequencing Kit (LTC/Applied Biosystems) using the same primer sets as for PCRs, except for *trnK-matK* which required an extra internal sequencing primer namely 1326R (Cuénoud & al., 2002). Sequencing products were treated with SDS before they were transferred onto Sephadex columns (LTC/Applied Biosystems) using a Tecan EVO150 and then centrifuged. Cleaned products were dried using a heated vacuum drier and re-suspended in Hi-Di (LTC/Applied Biosystems). Electrophoresis was performed on either an ABI3130xl or an ABI3730xl machine using a 50 cm capillary array and POP7 (all supplied by LTC/Applied Biosystems).

**Phylogenetic analysis.** — Sequence chromatograms were imported into Geneious Pro v.6 (Drummond & al., 2005), automatically trimmed at both ends using a 5% chance of error per base, after which the sense and antisense chromatograms were assembled to generate a consensus sequence. All incongruities and ambiguities were manually checked and edited, and 382 sequences were then submitted to GenBank (Appendix 1). Consensus sequences of each locus were aligned using MUSCLE and MAFFT v.7.017 (Katoh & al., 2002) as integrated into Geneious Pro. Alignments were visually checked and edited wherever necessary. We then concatenated the five loci into a single alignment matrix prior to phylogenetic analysis. This matrix included 86 samples and 6525 characters and was partitioned with MacClade v.4.08 (Maddison & Maddison, 2000) as follows: a character partition was created between nuclear- (822 bp) and chloroplast-derived (5703 bp) characters in order to assess phylogenetic congruence between nuclear and chloroplast DNA; a generic partition was created to test monophyly of each of the three genera under study.

Under the parsimony criterion, we applied an heuristic search using the tree-bisection-reconnection (TBR) branch-swapping algorithm with 1000 replicates starting from random taxon addition, followed by a bootstrap analysis with 1000 repetitions, in PAUP\* v.4.0b10 (Swofford, 2002); gaps were treated as missing data. Under the Bayesian criterion, we used two independent parallel runs, each one with one cold chain and

three heated chains, over 5 million Markov Chain Monte Carlo (MCMC) generations in MrBayes v.3.2 (Ronquist & al., 2012). Trees were sampled every 500 generations across General Time Reversible (GTR) model space. This approach was preferred over selecting a best-fit substitution model (i.e., a model testing approach) because it integrates out the uncertainty of choosing the correct model by sampling across the entire GTR model space (Ronquist & al., 2011). We assessed convergence by making sure that probabilities of the sampled models were the same across the two independent parallel runs. Subsequently, we repeated a Bayesian analysis by setting the best-fit model as selected by AIC in MrModeltest v.2.3 (Nylander, 2004), i.e., the GTR+I+G model for each partition.

**Monophyly testing.** — Our main objective was to test the monophyly of *Eulophia*. Specifically we wanted to contrast the hypotheses H0—*Eulophia* is monophyletic—against H1—*Eulophia* is not monophyletic. In order to do this we specified two different constraints: a hard constraint forcing continuous monophyly along the tree sampling (i.e., model H0); and a negative constraint allowing sampling across all trees that did not respect the monophyly (i.e., model H1). We then ran a Bayesian analysis enforcing either the hard or the negative constraint, and using a stepping-stone sampling method (Ronquist & al., 2011: 52–57). Unlike MCMC runs, stepping-stone runs move from the posterior to the prior through a number of steps in which the sampled distribution is a mixture of varying proportions of the two, hence it provides a more accurate estimation of the model likelihood. A comparison of the marginal likelihood estimate then allows H0 or H1 to be selected as the best model for explaining the data. We repeated this procedure to test the monophyly of *Oeceoclades* and *Acrolophia*.

## ■ RESULTS

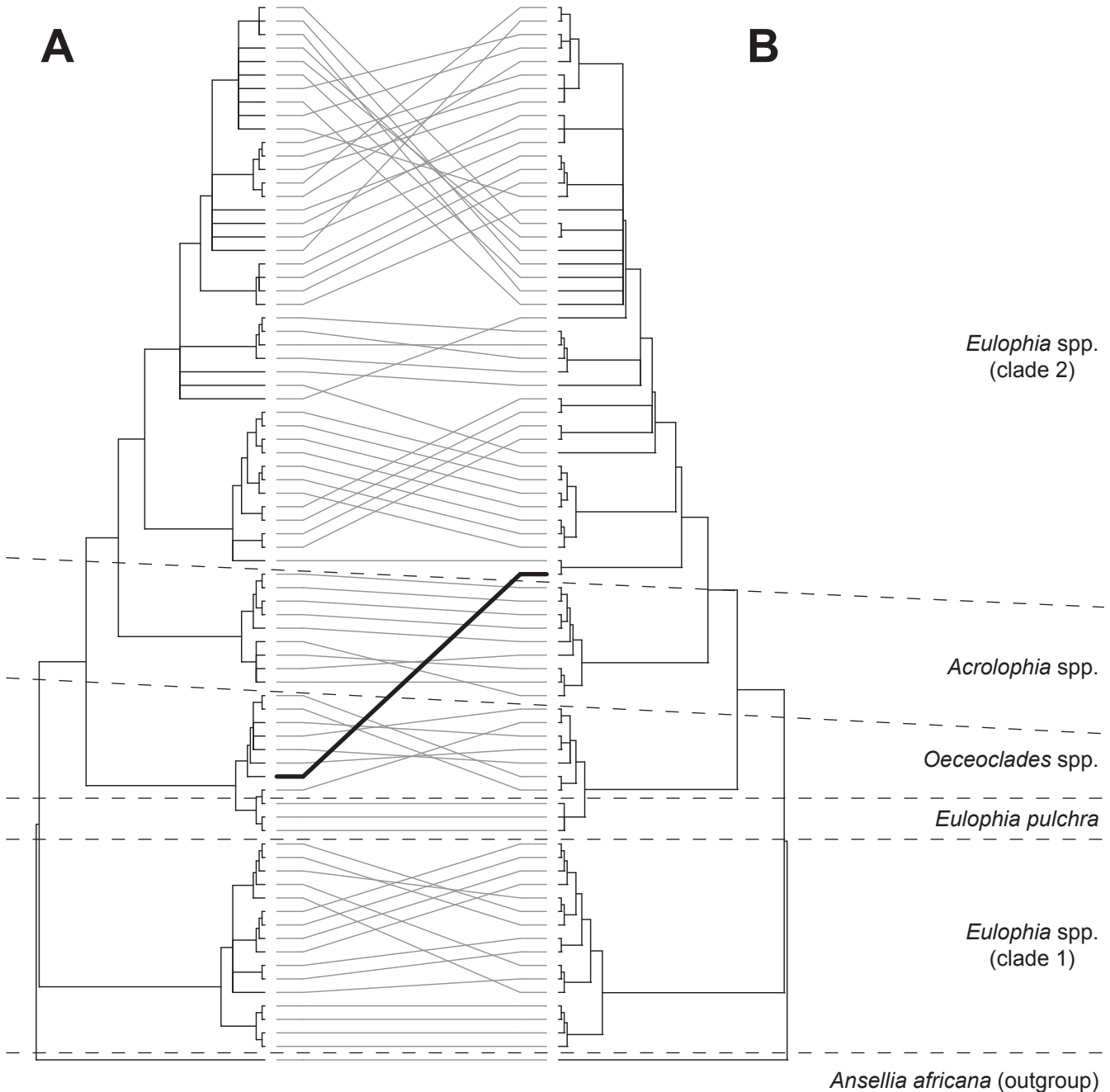
**Sequence variation.** — There was extensive length variation in the *trnK-matK*, *trnQ-5' rps16* and *rpl32-trnL* regions but much less in nrITS and none in *rbcL*. The *trnK-matK* sequences varied between 608 and 1680 bp. This large variation was mostly due to a single sequence (*E. litoralis* Schltr.) which was only 608 bp, whereas all others varied between 1392 and 1680 bp. Substantial length variation was also noticed in *trnQ-5' rps16* (331–1225 bp) and *rpl32-trnL* (519–788 bp). On the other hand, nrITS varied between 751 and 796 bp, and all *rbcL* sequences were 1231 bp long. Based on the alignments, the average percentage of pairwise variability was higher for *trnQ-5' rps16* (25.9%) than for *rpl32-trnL* (19.9%), nrITS (11%), *trnK-matK* (5.1%), or *rbcL* (0.8%). Therefore, the chloroplast non-coding regions *trnQ-5' rps16* and *rpl32-trnL* were by far the most variable loci in this study. Together with nrITS, these markers proved efficient in resolving phylogenetic relationships between closely related species, whereas the more conserved markers *trnK-matK* and *rbcL* were important to resolve deeper nodes.

**Phylogenetic congruence between nuclear and chloroplast loci.** — Convergence between the two parallel MCMC runs was reached before 5 million generations for all locus

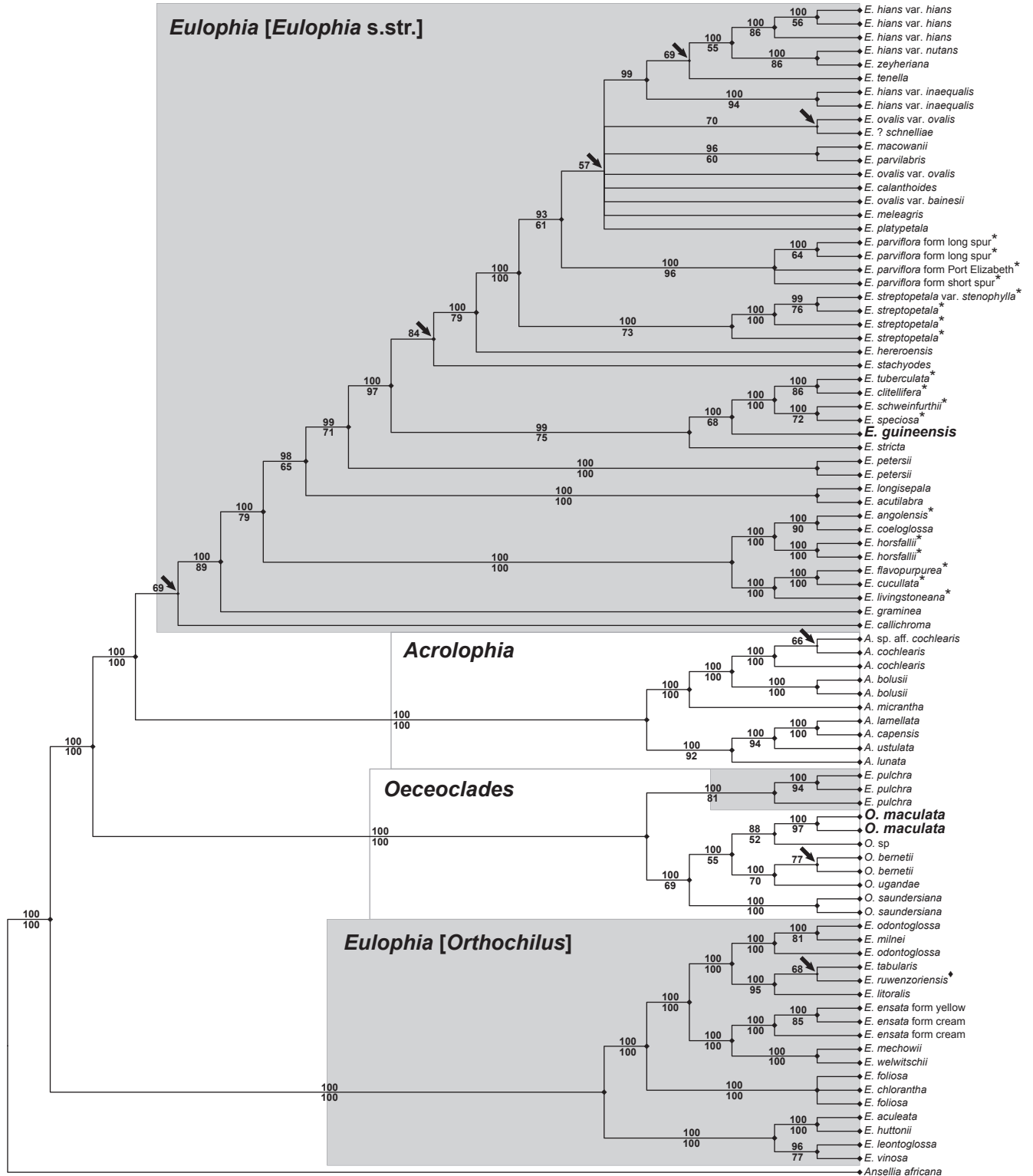
partitions (i.e., nrITS, four chloroplast loci, or five concatenated loci). The overall topology generated from the nuclear dataset was congruent with that generated from the chloroplast dataset except for the placement of one species, namely *E. callichroma* Rchb.f., which switched from one clade to another (Fig. 1). To make sure that the inclusion of this species did not affect the general topology, we reran the analysis after excluding it from the alignment matrix. This resulted in nuclear and chloroplast trees identical to those seen in Fig. 1. In view of the fact that the nuclear and chloroplast markers were congruent,

we concatenated all loci to increase the number of informative characters. The result of the Bayesian analysis based on the concatenated dataset is presented in Fig. 2. The general topology did not change when the tree sampling was set to follow the best-fit model (GTR+I+G) instead of sampling across the entire GTR model space (data not shown).

Under the parsimony criterion, 937 out of 1471 variable characters in the alignment matrix were parsimony-informative. The parsimony analysis yielded 5203 equally most parsimonious trees (MPTs) with a length of 2626 steps, a consistency



**Fig. 1.** Plot of congruence between two Bayesian consensus trees inferred from **A**, nuclear ITS and **B**, four chloroplast loci. Most perceived incongruence is as a result of polytomies. Only *E. callichroma* resolves in a different major clade in the two trees (bold line). Graph generated using *cophyloplot* in the R package *ape* 3.0-7 (Popescu & al., 2012).



**Fig. 2.** Bayesian consensus tree inferred from 6525 bp including one nuclear locus (nrITS) and four chloroplast loci (*rbcL*, *trnK-matK*, *rpl32-trnL*, *trnQ-5' rps16*). This tree was obtained after running two independent MCMC runs over 5 million generations and sampling across the GTR model space. Posterior probabilities are shown above branches. Bootstrap values from a parsimony analysis are shown below branches. Arrows indicate nodes that collapse in the parsimony strict consensus tree. Asterisks and diamond indicate species that have in the past been assigned to *Lissochilus* and *Pteroglossaspis* respectively.

**Table 1.** Marginal likelihood estimates (in natural log units) derived from six topological hypotheses. Each value is the mean of two marginal likelihood estimates calculated for two independent runs, each one using a stepping-stone sampling method. Bold indicates the better model between H0 and H1.

Genera	H0: monophyletic	H1: non-monophyletic
<i>Eulophia</i>	–26981.0	<b>–26920.0</b>
<i>Oeceoclades</i>	<b>–26873.5</b>	–26905.0
<i>Acrolophia</i>	<b>–26870.5</b>	–26882.0

index (CI) of 0.676, a homoplasy index (HI) of 0.324, a retention index (RI) of 0.864, and a rescaled retention index (RC) of 0.505. The strict consensus tree derived from MPTs (not shown) was congruent with the Bayesian majority-rule consensus tree seen in Fig. 2.

#### Marginal likelihood estimates from tested topologies.

— Model H0<sub>Eu</sub>, which enforced the monophyly of *Eulophia*, resulted in a considerably lower likelihood estimate than the alternative model H1<sub>Eu</sub>. Whereas a difference in marginal likelihood above 5 natural log units is generally considered very strong evidence in favour of the better model (Kass & Raftery, 1995), the difference between H1<sub>Eu</sub> and H0<sub>Eu</sub> was 61 natural log units (Table 1), and thus the monophyly of *Eulophia* could be confidently rejected. The paraphyly of *Eulophia* is indeed clear and well supported in the consensus cladogram (Fig. 2) and indicates that *Eulophia* s.l. consists of two clades which we will refer to as the “*Eulophia* s.str.” and “*Orthochilus*” clade. Conversely, the models H0<sub>Oe</sub> and H0<sub>Ac</sub> forcing monophyly on *Oeceoclades* and *Acrolophia* respectively, led to greater likelihood estimates than their alternative models H1<sub>Oe</sub> and H1<sub>Ac</sub> (Table 1). The log difference between H0 and H1 for *Oeceoclades* was 31.5 natural log units, whereas that for *Acrolophia* was 11.5—both considerably above the threshold of 5. Therefore, the Bayes factor test provided strong evidence in favour of a monophyletic origin of *Oeceoclades* and *Acrolophia*. Finally, we could also reject the monophyletic hypothesis for species formerly assigned to the genus *Lissochilus* (likelihood estimates not shown). These species indeed appeared to be scattered across the *Eulophia* s.str. clade (indicated in Fig. 2 with asterisks).

## DISCUSSION

Our results convincingly show that the monophyletic genera *Acrolophia* and *Oeceoclades* are nested within *Eulophia* as currently circumscribed, thus rendering *Eulophia* paraphyletic. In order to maintain an evolutionarily meaningful classification, we are thus faced with the decision of either including *Oeceoclades* and *Acrolophia* in an enlarged *Eulophia*, or splitting *Eulophia* into two separate genera and thereby keeping *Acrolophia* and *Oeceoclades* virtually unchanged. Although there is a trend to recognise larger genera (Humphreys & Linder, 2009), we argue below that the best option in this case is to retain *Acrolophia* and *Oeceoclades* and to split *Eulophia* into

two genera on the basis that each of these four clades is genetically and morphologically distinct.

**Acrolophia.** — All recent authors (e.g., Hall, 1965; Linder & Kurzweil, 1999; Pridgeon & al., 2009) have accepted *Acrolophia* as a well-circumscribed and morphologically distinct genus. Our comprehensive sampling confirms that it is indeed a monophyletic entity that is embedded within *Eulophia* s.l. and sister to *Eulophia* s.str. The seven species of *Acrolophia* share some unique characteristics amongst the Eulophiinae. In particular, the inflorescence is apical and often branched (Fig. 3G), whereas it is lateral and usually simple in both *Eulophia* s.l. (Fig. 3B) and *Oeceoclades*. The leaves are equitant, distichous and fan-like (Fig. 3G), which is not the case in *Eulophia* s.l. and *Oeceoclades*. Furthermore, the typical perennating organs of Eulophiinae (i.e., pseudobulb, corm, or swollen rhizome) are absent in *Acrolophia* and the stem is reduced to such an extent that the leaves appear to be directly connected to the roots.

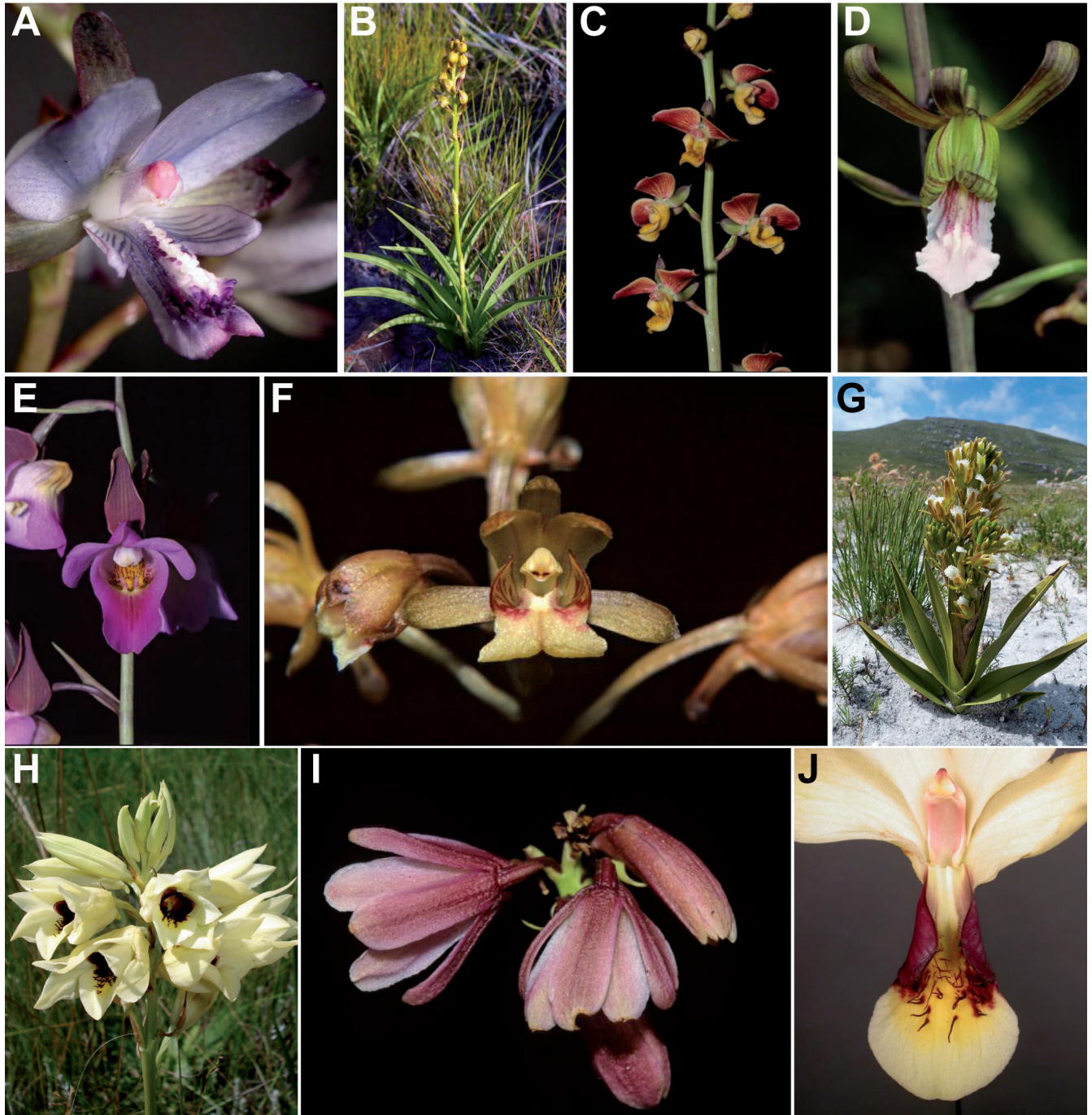
**Oeceoclades.** — As is the case for *Acrolophia*, all recent authors (e.g., Cribb, 1989; La Croix & Cribb, 1998; Du Puy & al., 1999; Hermans & al., 2007), except Geerinck (1992), have also accepted *Oeceoclades* as a distinct genus. Our analysis indicates that it indeed forms a clade, although we only sampled 5 out of 39 species. *Oeceoclades* is morphologically distinct from *Eulophia*. Species of *Oeceoclades* share a quadrilobed labellum with two short calli at the base (Fig. 3F). The lip lacks long keels and hairlike outgrowths (Fig. 3F). The spur is short and often swollen. The pseudobulbs are heteroblastic, and the leaves are petiolate and conduplicate (Summerhayes, 1957; Garay & Taylor, 1976).

Garay & Taylor (1976) considered the heteroblastic pseudobulbs and conduplicate leaves as important taxonomic characters and consequently did not include *Eulophia pulchra* in *Oeceoclades* because it has homoblastic pseudobulbs and plicate leaves. Despite the fact that the vegetative characteristics of *E. pulchra* resemble those of *Eulophia*, its floral morphology is typical of *Oeceoclades* (Thomas, 1996). Because of this ambiguity, some authors have assigned it to *Eulophia* (Thomas, 1996; La Croix & Cribb, 1998; Hermans & al., 2007), whereas others thought it was better placed in *Oeceoclades* (Clements & Cribb, 1989; Cribb, 1989). In our analysis, *E. pulchra* is sister to the rest of *Oeceoclades* and therefore would be better placed in *Oeceoclades*, or in a separate genus altogether. Since our sampling of *Oeceoclades* is as yet limited, we suggest the use of the name *Oeceoclades pulchra* (Thouars) P.J.Cribb & M.A. Clem. for the time being and until a more extensive analysis will show whether this species is nested within *Oeceoclades* or is truly sister to all other members of the genus. In the latter case, a new generic name might be more appropriate for this taxon.

**Eulophia s.str., Pteroglossaspis and the reinstatement of Orthochilus.** — *Acrolophia* and *Oeceoclades* are long-established and morphologically well-circumscribed genera. It would therefore be preferable, in our opinion, to keep these genera and split the currently paraphyletic *Eulophia* into two genera, particularly in view of the fact that clear morphological differences exist between *Eulophia* s.str. and the segregate clade (Fig. 3A–J). The latter clade was identified by A.V. Hall (1963,

1965) in a phenetic analysis of the South African species of *Eulophia* based on 93 characters as the morphologically most distinct group. In Hall's "*Eulophia nigricans* aggregate" all species shared the following characters: petals usually as wide as sepals; leaves usually erect and plicate; sepals usually not

marked with brown or purple; leaf sheaths about halfway along the scape usually more than half the length of the internode they cover; distal crests usually papillose (Hall, 1965). Cribb (1989), La Croix & al. (1991) and La Croix & Cribb (1998), agreed with Hall's conclusion that all species in which the petals and



**Fig. 3.** Morphological synapomorphies for: **A–E**, *Eulophia* s.str.; **F**, *Oeoeclades*; **G**, *Acrolophia*; **H–J**, *Orthochilus*. **A**, *E. zeyheriana* Sond. showing fleshy verrucose ridges on the mid-lobe of the labellum; **B**, *E. parviflora* (Lindl.) A.V.Hall showing the lateral inflorescence; **C**, *E. tuberculata* Bolus showing the lax inflorescence; **D**, *E. petersii* (Rchb.f.) Rchb.f. and **E**, *E. cucullata* (Afzel. ex Sw.) Steud. showing petals and sepals of different size, shape or colour; **F**, *O. maculata* (Lindl.) Lindl. showing the quadrilobed labellum; **G**, *A. lamellata* (Lindl.) Pfitzer showing the terminal, branched inflorescence; **H**, *O. mechowii* Rchb.f. showing the dense inflorescence clustered near the apex; **I**, *O. vinosus* (McMurtry & G.McDonald) Bytebier showing petals and sepals similar in size, shape and colour; **J**, *O. welwitschii* Rchb.f. showing papillae on mid-lobe of the labellum. — All pictures by the authors, except G reproduced with kind permission of H. Staerker.

sepals are similar in shape, colour and size, and the flowers are bell-shaped, form a distinct group within *Eulophia* (Fig. 3H–I). Cribb in Pridgeon & al. (2009: 103) went as far as to suggest that this group should be accorded the rank of section. We propose, on the basis of the current phylogenetic analysis and its morphological synapomorphies, to raise it to the rank of genus.

The correct name for this newly circumscribed genus would be *Orthochilus*, since *Orthochilus abyssinicus* ( $\equiv$  *Eulophia abyssinica*) is part of this clade and is the oldest available name. *Eulophia abyssinica*, *E. aurantiaca* Rolfe, *E. carsonii* Rolfe, *E. euantha* Schltr., *E. subulata* Rendle, *E. thomsonii* Rolfe, *E. welwitschii* (Rchb.f.) Rolfe and *E. mechowii* (Rchb.f.) T. Durand & Schinz form a group of very closely related species, two of which, namely *E. welwitschii* and *E. mechowii*, were included in our sampling. Geerinck (1992) considered the latter two species as conspecific with *E. abyssinica*, although he later changed his opinion on this matter (Geerinck, 2005).

Species assigned to the genus *Pteroglossaspis* (recently considered as synonymous with *Eulophia*; see Pridgeon & al., 2009: 103) form part of the *Orthochilus* and not the *Eulophia* s.str. clade (indicated in Fig. 2 with diamond). This is not totally surprising, as, apart from the fact that they lack a column foot and a spur, which are the diagnostic characters for *Pteroglossaspis*, they are similar in all other morphological aspects to the remainder of *Orthochilus*. We were not able to sample *Pteroglossaspis eustachya*, the type of the genus, but there seems little doubt that this species is closely related to *Eulophia ruwenzoriensis* Rendle, which is included in our phylogeny and is placed within the *Orthochilus* clade.

We have taken a conservative approach in our taxonomic treatment and so far assigned only 35 taxa to *Orthochilus*. There are potentially a few more species that could be part of this genus, but until their DNA has been sampled and/or a long-awaited revision of *Eulophia* has been done, we prefer to keep them in *Eulophia* rather than create more names that would potentially end up in synonymy. By and large, and based on morphology, we do not expect a substantial increase of the *Orthochilus* clade, and we believe it to be largely restricted to the continent of Africa, with three species occurring in the Americas.

The reinstatement of *Orthochilus* and *Oeceoclades pulchra* reduces the size of *Eulophia* from 201 to 165 species, of which we only sampled 31 species (19%). Furthermore, our sampling is biased towards southern Africa. For these reasons we refrain from making inferences that would impact on the classification of *Eulophia* s.str. until more extensive sampling has been achieved.

*Eulophia* s.str. still contains a considerable amount of morphological variation. For instance, different forms of perennating organs (i.e., aerial pseudobulbs, underground corms, and rhizomes) are all represented in this clade. Some species show a great variation in size and colour between petals and sepals, whereas others do much less so (Fig. 3A–E). The former species were often grouped into a separate genus, *Lissochilus*, in which at least 206 epithets have been coined. Summerhayes (1936) pointed out that *Eulophia* and *Lissochilus* could not be kept separate and most authors have followed his objections against the use of *Lissochilus*. Perrier de la Bâthie (1941) was probably

the last author to keep them separate. Hall (1963, 1965), on the basis of a phenetic study, also presented evidence why the two should not be upheld. Our work corroborates the views of Summerhayes (1936), Hall (1963, 1965), and several other authors, as the species formerly assigned to *Lissochilus* failed a test for monophyly (results not shown) and appear scattered across the *Eulophia* clade (Fig. 2).

*Eulophia callichroma* presents a conundrum. It was first described by Reichenbach (1881) who pointed out that it was closely related to *Eulophia tristis* (L.f.) Spreng. (now a synonym of *Acrolophia capensis* (P.J.Bergius) Fourc.). Cribb (1977) re-described it in the genus *Acrolophia* as *A. paniculata* P.J.Cribb. Indeed, the inflorescence in this species is a terminal panicle and therefore closely resembles the habit of *Acrolophia* (seen in Fig. 3G). However, based on the fact that it is hysteranthous, that the leaves are not fan-like, and that it has pseudobulbs, most authors thought it better placed in *Eulophia* (Williamson, 1977; Cribb, 1989; La Croix & al., 1991; La Croix & Cribb, 1998; Linder & Kurzweil, 1999). Our phylogenetic analysis confirms that it does not belong to *Acrolophia*. Nevertheless, the phylogenetic position of *E. callichroma* remains somewhat ambiguous as the chloroplast (Fig. 1B) and concatenated datasets (Fig. 2) place it sister to *Eulophia* s.str., whereas the limited nuclear dataset seems to suggest that it is related to *Oeceoclades* (Fig. 1A). Morphologically, however, *E. callichroma* certainly does not fit within the concept of *Oeceoclades*. Consequently we suggest to retain *E. callichroma* within *Eulophia*. The DNA sequences for the various loci of *E. callichroma* appear quite divergent from those of its closest relatives, which suggests that *E. callichroma* may belong to a branch in the phylogeny for which sampling is underrepresented due to collection bias or extinctions.

## ■ TAXONOMIC TREATMENT

### Artificial key to the genera of *Eulophiinae*

(modified from Cribb in Pridgeon & al., 2009: 94)

1. Plants lacking chlorophyll, leaves absent or reduced to scales ..... 460. ***Eulophia*** (in part)
  1. Plants with one or more green leaves ..... 2
  2. Inflorescence erect but recurved apically so that the apex points towards the ground ..... 462. ***Geodorum***
    2. Inflorescence not as above ..... 3
    3. Plants terrestrial with subterranean tubers, swollen rhizomes or epigeous pseudobulbs, often born in strings, rarely lacking pseudobulbs, tubers or fleshy rhizomes .. 4
    3. Plants epiphytic with pseudobulbs, clustered or remote; rarely terrestrial and then with an elongate rhizome and lacking pseudobulbs ..... 8
    4. Stems usually pseudobulbous, heteroblastic and naked or rarely homoblastic and covered by leaf sheaths; labellum usually distinctly four-lobed or if apparently trilobed then the midlobe emarginate and with 2 lobules when flattened ..... 464. ***Oeceoclades***
      4. Stems cylindrical, tuberous, rhizomatous or pseudobul-



- bous, usually several-noded, often covered by leaf bases, rarely lacking pseudobulbs, swollen rhizomes or tubers; labellum trilobed ..... 5
5. Plants lacking pseudobulbs, swollen rhizomes or tubers 6
5. Plants with pseudobulbs, swollen rhizomes or tubers... 7
6. Inflorescence often branched; sepals spreading; pollinia 2, on stipe ..... 457. *Acrolophia*
6. Inflorescence simple; sepals connivent; pollinia 4, sessile ..... 458. *Cyanaeorchis*
7. Inflorescence usually lax; petals and sepals of different size, shape or colour ..... 460. *Eulophia* (in part)
7. Inflorescence usually dense and often clustered near the apex; flowers campanulate, petals and sepals similar in size, shape and colour ..... 460a. *Orthochilus*
8. Pseudobulbs angular; sepals more than 20 mm long; petals porrect; labellum entire ..... 463. *Grammangis*
8. Plants with prominent, elongate stout rhizomes, often lacking pseudobulbs; flowers with white, rose-purple, pink, green or pale green sepals and petals ..... 9
9. Flowers more or less rotate, pinkish white to rose-purple ..... 461. *Eulophiella*
9. Flowers strongly bilaterally symmetrical, green, often marked with red or black on labellum ..... 10
10. Labellum spurred at base ..... 465. *Paralophia*
10. Labellum lacking a spur at base ..... 459. *Cymbidiella*

*Eulophia* R.Br. in Bot. Reg. 7: ad t. 573. Oct 1821 (“*Eulophus*”), nom. et orth. cons. – Type: *E. guineensis* Lindl., typ. cons. = *Wolfia* Dennst., Schlüssel Hortus Malab.: 38. 1818, non Schreb. 1791, nom. illeg. – Type: *W. spectabilis* Dennst. (≡ *Eulophia spectabilis* (Dennst.) Suresh).

= *Lissochilus* R.Br. in Bot. Reg. 7: t. 573. Oct. 1821, nom. rej. – Type: *L. speciosus* R.Br. (≡ *Eulophia speciosa* (R.Br.) Bolus).

= *Cyrtopera* Lindl., Gen. Sp. Orchid. Pl.: 189. 1833 – Type: *C. woodfordii* (Sims) Lindl. (≡ *Cyrtopodium woodfordii* Sims; = *Eulophia alta* (L.) Fawc. & Rendle). Cribb (in Pridgeon & al., Gen. Orchid. 5(2): 100. 2009) indicated that a type has not been selected, but Farr & al. (Index Nom. Gen. (Pl.) 1 (= in Regnum Veg. 100): 482. 1979) state that the genus was typified with *C. woodfordii* (Sims) Lindl. by A. Richard (in Orbigny, Dict. Univ. Hist. Nat. 4: 561. 1844).

= *Thysanochilus* Falc. in Proc. Linn. Soc. London 1: 14. 1839 – Type: not designated.

= *Hypodematium* A.Rich., Tent. Fl. Abyss. 2: 286. 1850, non Kunze 1833 nec A.Rich. 1848, nom. illeg. – Type: *H. abyssinicum* A.Rich. (= *Eulophia streptopetala* Lindl. var. *streptopetala*).

= *Platypus* Small & Nash in Small, Fl. S.E. U.S.: 329. 1903 – Type: *P. papilliferus* Small & Nash (= *Eulophia alta* (L.) Fawc. & Rendle).

= *Donacopsis* Gagnep. in Bull. Mus. Natl. Hist. Nat., sér. 2, 4: 593. 1932 – Type: *D. laotica* Gagnep. (= *Eulophia pauciflora* Guillaumin).

= *Semiphajus* Gagnep. in Bull. Mus. Natl. Hist. Nat., sér. 2, 4: 598. 1932 – Type: not designated.

Terrestrial or less commonly lithophytic *herbs*, autotrophic or mycoheterotrophic. *Roots* basal, often with well-defined white velamen. *Perennating organ* stem-like or pseudobulbous when above ground, rhizomatous or tuberous when subterranean, cylindrical, fusiform, conical or ovoid, homoblastic. *Leaves* linear, lanceolate, ovate or elliptic, acute to acuminate, coriaceous, articulate or not to a sheathing base; rarely lacking chlorophyll and scale-like in mycoheterotrophic species. *Inflorescence* lateral, simple or rarely branching, generally lax; bracts persistent. *Flowers* green or brown to coloured, occasionally bicoloured. *Dorsal sepal* free, oblong, elliptic, lanceolate or oblanceolate, reflexed, erect or porrect; *lateral sepals* oblique at base and decurrent on column foot, otherwise similar to dorsal sepal. *Petals* free, dissimilar to sepals, often larger, broader and distinctly coloured compared to sepals. *Labellum* free to base or fused to base of column, trilobed, generally spurred at base, lateral lobes free or fused to base of column, midlobe flat or convex, callus with two or three ridges or papillose. *Column* usually with a foot; pollinia two, globose; stipe solitary, triangular to oblong; viscidium oblong, elliptic to lunate. *Ovary* cylindrical, grooved. (description modified from Cribb in Pridgeon & al., 2009: 100).

*Distribution*. – Most diverse in sub-Saharan Africa, with substantial diversity elsewhere only in Madagascar and tropical Asia. Extending to Yemen and Socotra, Réunion, tropical and subtropical America, temperate central Asia; northwestern Australia and the southwestern Pacific Islands.

*Etymology*. – From the Greek *eu* “well, good” and *lophos* “a crest, plume” in reference to the crest on the labellum of some species (Quattrocchi, 2000).

*Orthochilus* Hochst. ex A.Rich., Tent. Fl. Abyss. 2: 284. 1850 – Type: *O. abyssinicus* (Rchb.f.) Hochst. ex A.Rich.

= *Pteroglossaspis* Rchb.f., Otia Bot. Hamburg. 1: 67. 1878 – Type: *P. eustachya* Rchb.f.

= *Triorchos* Small & Nash in Small, Fl. S.E. U.S.: 329. 1903 – Type: *T. ecristatus* (Fernald) Small.

= *Smallia* Nieuwl. in Amer. Midl. Naturalist 3: 158. 1913, nom. nov. pro *Triorchos* Small & Nash.

Terrestrial *herbs*. *Perennating organs* subterranean, tuberous, irregularly shaped, in chains, with slender roots mostly from the new growth. *Leaves* 1–3 [5], mostly erect, plicate, linear to lanceolate, acute to acuminate, often with 2–3 basal sheaths. *Inflorescence* lateral, simple, produced before or with young leaves, sometimes few but more often many-flowered, sometimes lax but more often dense to subspherical; peduncle slender to stout with several papery sheaths; bracts persistent, often conspicuous, erect to spreading or reflexed. *Flowers* mostly subnutant, not opening widely, concolorous, variously coloured, sometimes with a conspicuous and differently coloured disc or papillae on the labellum. *Dorsal sepal* oblong, elliptic, ovate, lanceolate or linear, acute to acuminate; *lateral sepals* similar to dorsal sepal, often oblique at base. *Petals* similar in shape and colour to the sepals, but usually slightly broader and shorter. *Labellum* trilobed, mostly porrect, midlobe flat, sometimes reflexed at tip, generally larger than the side lobes; callus of 2 [3–7] papillose ridges in basal half,

often ending in short or long papillae on the midlobe, or calli of scattered warts on midlobe; *spur* cylindrical to clavate, or absent. *Column* with or without a foot; pollinia two, subglobose to globose; stipe solitary, triangular to oblong; viscidium oblong, elliptic to lunate. *Ovary* cylindrical, grooved. *Fruit* pendent.

*Distribution.* – Sub-Saharan Africa, Madagascar, tropical and subtropical America.

*Etymology.* – From the Greek *orthos* “upright, straight” and *cheilos* “a lip” the long claw (Quattrocchi, 2000).

***Orthochilus abyssinicus*** (Rchb.f.) Hochst. ex A.Rich., Tent. Fl. Abyss. 2: 284. 1850 ≡ *Eulophia abyssinica* Rchb.f. in Linnaea 22: 866. 1850 ≡ *Graphorkis abyssinica* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 662. 1891 – Holotype: ETHIOPIA. Adde Schum Eschet, 25 Jul 1840, *Schimper 1700 sectio tertia* (W n.v.; isotypes: BR barcode BR000008419248!, K barcodes K000078600!, K000078598 [fragment and drawing]!, P barcodes P00359045!, P00359046!, P00359047!, S No. S07-5002!).

***Orthochilus aculeatus*** (L.f.) Bytebier, **comb. nov.** ≡ *Satyrium aculeatum* L.f., Suppl. Pl.: 402. 1782 ≡ *Serapias aculeata* (L.f.) Thunb., Prodr. Pl. Cap.: 3. 1794 ≡ *Cymbidium aculeatum* (L.f.) Sw. in Nova Acta Regiae Soc. Sci. Upsal. 6: 77. 1799 ≡ *Epidendrum aculeatum* (L.f.) Poir. in Lamarck, Encycl., Suppl. 1: 376. 1810 ≡ *Eulophia aculeata* (L.f.) Spreng., Syst. Veg. 3: 720. 1826 – Holotype: SOUTH AFRICA. Cape of Good Hope [Caput Bona Spei], *Thunberg 291* (LINN No. 1055.2!).

***Orthochilus aculeatus* subsp. *huttonii*** (Rolfe) Bytebier, **comb. nov.** ≡ *Eulophia huttonii* Rolfe in Harvey, Fl. Cap. 5(3): 52. 1912 ≡ *Eulophia aculeata* subsp. *huttonii* (Rolfe) A.V.Hall in J. S. African Bot., Suppl. 5: 183. 1965 – Lectotype (designated by Hall in J. S. African Bot., Suppl. 5: 187. 1965): SOUTH AFRICA. Eastern Cape, Katberg, *Hutton s.n.* (K barcode K000410474 [excl. foliis!]).

***Orthochilus adenoglossus*** (Lindl.) Bytebier, **comb. nov.** ≡ *Cymbidium adenoglossum* Lindl. in J. Proc. Linn. Soc., Bot. 6: 134. 1862 ≡ *Eulophia adenoglossa* (Lindl.) Rchb.f., Otia Bot. Hamburg.: 66. 1878 – Holotype: NIGERIA. Nupe, 1859, *Barter s.n.* (K barcode K000078602!).

***Orthochilus albobrunneus*** (Kraenzl.) Bytebier, **comb. nov.** ≡ *Eulophia albobrunnea* Kraenzl. in Bot. Jahrb. Syst. 33: 69. 1902 – Holotype: ETHIOPIA. Diddah, 27 Jul 1900, *Ellenbeck 1510* (B†; record of holotype: K barcode K000078630 [flower and photo!]).

***Orthochilus aurantiacus*** (Rolfe) Bytebier, **comb. nov.** ≡ *Eulophia aurantiaca* Rolfe in Oliver, Fl. Trop. Afr. 7: 67. 1897 ≡ *Eulophia abyssinica* var. *aurantiaca* (Rolfe) Geerinck, Fl. Afr. Centr., Sperm., Orch.(2): 679. 1992 ≡ *Eulophia welwitschii* subsp. *aurantiaca* (Rolfe) Geerinck in Taxonomania 14: 12. 2004 – Syntypes: TANZANIA. Tanganyika Plateau, 1889, *Carson s.n.* (K barcode

K000078607!); TANZANIA. Lake Tanganyika, Sep 1893, *Carson 104* (K barcode K000078607!); TANZANIA. Between Lakes Tanganyika and Malawi [Nyassa], Apr 1890, *Johnston s.n.* (K barcode K000078608!).

***Orthochilus carsonii*** (Rolfe) Bytebier, **comb. nov.** ≡ *Eulophia carsonii* Rolfe in Oliver, Fl. Trop. Afr. 7: 64. 1897 ≡ *Eulophia welwitschii* subsp. *carsonii* (Rolfe) Geerinck in Taxonomania 16: 9. 2005 – Holotype: ZAMBIA. Tanganyika Plateau, Fwambo, 1889, *Carson s.n.* (K barcode K000078609!).

***Orthochilus chloranthus*** (Schltr.) Bytebier, **comb. nov.** ≡ *Eulophia chlorantha* Schltr. in Bot. Jahrb. Syst. 20(Beibl. 50): 9. 1895 – Lectotype (designated by Hall in Linder & Kurzweil, Orch. S. Afr.: 392. 1999): SWAZILAND. Havelock Concession, Sep 1889, *Saltmarsh* in herb. *Galpin 652* (BOL n.v.).

***Orthochilus clandestinus*** (Börge Pett.) Bytebier, **comb. nov.** ≡ *Pteroglossaspis clandestina* Börge Pett. in Garcia de Orta, Sér. Bot. 6: 79. 1984 ≡ *Eulophia clandestina* (Börge Pett.) Bytebier in Strelitzia 22: 190. 2008 – Holotype: ANGOLA. Cuando-Cubango, Menogue, Vila Serpa Pinto, valley of the Cambumbé, 27 Feb 1960, *Mendes 2778* (LISC barcode LISC003336!; isotypes: C barcode C10001090!, COI barcode COI00005853!, ?EA n.v., K barcodes K000306605!, K000306606 [fragment and photocopy of holotype]!, LMU n.v., LUAI n.v., M n.v., MO n.v., SRGH n.v., UPS n.v., ?WAG n.v.).

***Orthochilus corymbosus*** (G.Will.) Bytebier, **comb. nov.** ≡ *Pteroglossaspis corymbosa* G.Will. in Pl. Syst. Evol. 134: 68. 1980 – Holotype: ZAMBIA. Mwinilunga, River Kasompa, 31 Oct 1937, *Milne-Redhead 3028* (K barcode K000306604!).

***Orthochilus distans*** (Summerh.) Bytebier, **comb. nov.** ≡ *Pteroglossaspis distans* Summerh. in Kew Bull. 13: 82. 1958 – Holotype: SIERRA LEONE. Bonthe, Taigbe SE of Bendu, 15 Oct 1946, *Adames 92* (K barcode K000306603!).

***Orthochilus ecristatus*** (Fernald) Bytebier, **comb. nov.** ≡ *Cyrtopodium ecristatum* Fernald in Bot. Gaz. 24: 433. 1897 ≡ *Triorchos ecristatus* (Fernald) Small, Fl. S.E. U.S.: 329. 1903 ≡ *Eulophia ecristata* (Fernald) Ames in Contr. Ames Bot. Lab. 1: 19. 1904 ≡ *Pteroglossaspis ecristata* (Fernald) Rolfe in Orchid Rev. 12: 136. 1904 – Syntypes: U.S.A. Florida, Duval, near Jacksonville and borders of Indian River, *Curtiss 2808* (AMES No. 82164 [now GH barcode 00098728]!), AMES No. 87532 [now GH barcode 00098729]!, AMES No. 82166 [now GH barcode 00098730!]).

The Oakes Ames Orchid Herbarium contains three sheets of *Curtiss 2808*. Specimens 82164 and 87532 were both collected in August and can be considered as duplicates. Specimen 82166, however, was collected in June. Because these three sheets are the results of two botanical collection events, AMES

Nos. 82164, 87532 and 82166 should be considered syntypes, despite the fact that they have the same collector name and number.

***Orthochilus ensatus*** (Lindl.) Bytebier, **comb. nov.** ≡ *Eulophia ensata* Lindl. in Bot. Reg. 14: t. 1147. 1828 ≡ *Graphorkis ensata* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 662. 1891 – Lectotype (designated by Hall in J. S. African Bot., Suppl. 5: 202. 1965): SOUTH AFRICA. Cape of Good Hope, *Lindley t. 1147* (illustration in Bot. Reg. 14: tab. 1147!).

***Orthochilus euanthus*** (Schltr.) Bytebier, **comb. nov.** ≡ *Eulophia euantha* Schltr. in Bot. Jahrb. Syst. 53: 586. 1915 ≡ *Eulophia abyssinica* var. *euantha* (Schltr.) Geerinck, Fl. Afr. Centr., Sperm., Orch.(2): 680. 1992 – Holotype: TANZANIA. Rungwe, Masukulu [Mwasukulu] Forest, Dec 1906, *Stolz 197* (B†; record of holotype: K barcode K000078610!).

(K000078610!, K000078611!, L0061223!, L0061224!, M0103426!, WAG0114789! all have the same collector number and have therefore been indicated as isotypes, but are either from a different locality or were collected at a later date.)

***Orthochilus eustachyus*** (Rchb.f.) Bytebier, **comb. nov.** ≡ *Pteroglossaspis eustachya* Rchb.f., Otia Bot. Hamburg.: 67. 1878 ≡ *Eulophia eustachya* (Rchb.f.) Geerinck, Fl. Rwanda 4: 572. 1988 – Holotype: ETHIOPIA. Tigre and Begemder, 1863–1868, *Schimper 1235* (miscited by Reichenbach as *1735*) (W n.v.; isotypes: CGE barcode CGE00093!, K barcodes K000306613!, K000306614 [fragment, drawing and tracing of holotype!]).

***Orthochilus foliosus*** (Lindl.) Bytebier, **comb. nov.** ≡ *Cyrtopera foliosa* Lindl. in Compan. Bot. Mag. 2: 203. 1837 ≡ *Eulophia foliosa* (Lindl.) Bolus in J. Linn. Soc., Bot. 19: 337. 1882 – Lectotype (designated by Hall in J. S. African Bot., Suppl. 5: 180. 1965): SOUTH AFRICA. Eastern Cape, between Bashee and Umtata [inter Basche et Omtala], *Drège s.n.* (K [drawing] n.v.).

***Orthochilus holubii*** (Rolfe) Bytebier, **comb. nov.** ≡ *Eulophia holubii* Rolfe in Oliver, Fl. Trop. Afr. 7: 60. 1897 – Lectotype (designated by Hall in Linder & Kurzweil, Orch. S. Afr.: 370. 1999): BOTSWANA. Leshumo Valley, Jan 1876, *Holub s.n.* (K barcode K000410163!).

In the protologue, Rolfe lists two specimens as follows: “Northern Bechuanaland: Leshumo Valley, *Holub!*; Near the Zambesi River, N.W of Shesheke, *Holub!*.” These were thus to be treated as syntypes (see for instance Geerinck, 1992: 674). At Kew there are two sheets referable to the protologue. One of these, K000410163, bears a label “Leshumo Valley, Jan 76, Northern Bechuanaland”; the other, K000078612!, bears two labels “13 M. NNW from Shesheke on the Zambesi River,? 76” and “Leshumo Valley, Feb 76”. Hall (1999: 370) lectotypified this species as follows “Botswana, Leshumo Valley, *Holub* (K!, lecto.)”, which could apply to both sheets. Although sheet K000078612, bears a conf. slip by Hall (with no indication to the type status of this specimen), we assume that the

lectotypification refers to the other sheet, K000410163, that bears only a “Leshumo Valley” label.

***Orthochilus leontoglossus*** (Rchb.f.) Bytebier, **comb. nov.** ≡ *Eulophia leontoglossa* Rchb.f. in Flora 64: 329. 1881 – Lectotype (designated by Hall in Linder & Kurzweil, Orch. S. Afr.: 394. 1999): SOUTH AFRICA. Mpumalanga [Transvaal], chiefly near Lydenburg, Dec 1873–Jan 1874, *Atherstone s.n.* (K barcode K000410469!; isolectotype: W n.v.).

***Orthochilus litoralis*** (Schltr.) Bytebier, **comb. nov.** ≡ *Eulophia litoralis* Schltr. in Bot. Jahrb. Syst. 26: 338. 1899 – Holotype: SOUTH AFRICA. Western Cape, Caledon, Hawston, 28 Nov 1896, *Schlechter 9468* (B†; isotypes: BOL barcode BOL149993!, BM barcode BM000525657!, BR barcode BR0000008811974!, GRA barcode GRA0000799-0!, HBG barcode HBG-501701!, K barcode K000410481!, L barcode L0061226!, P barcode P00365264!, PH barcodes PH00013316!, PH00013317!, PRE barcodes PRE0057153-0!, PRE0588835-0!, PRE0588836-0!, S No. S07-5055!, W n.v., WAG barcode WAG0002531!, Z barcode Z-000016429!).

***Orthochilus mechowii*** Rchb.f. in Flora 65: 532. 1882 ≡ *Eulophia mechowii* (Rchb.f.) T.Durand & Schinz, Consp. Fl. Afric. 5: 23. 1894 – Holotype: ANGOLA. Malange, Oct/Nov 1879, *von Mechow 300* (W n.v.; isotypes: K [fragment and drawing], Z000016431!).

***Orthochilus milnei*** (Rchb.f.) Bytebier, **comb. nov.** ≡ *Eulophia milnei* Rchb.f., Otia Bot. Hamburg.: 116. 1881 ≡ *Graphorkis milnei* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 662. 1891 – Holotype: ?CAMEROON/GABON/EQUATORIAL GUINEA. Nimbo River, Benito Ground, *Milne s.n.* (W n.v.; record of holotype: K barcode K000410405!).

***Orthochilus montis-elgonis*** (Summerh.) Bytebier, **comb. nov.** ≡ *Eulophia montis-elgonis* Summerh. in Bull. Misc. Inform. Kew 1932: 509. 1932 – Holotype: KENYA. Mount Elgon, May–Jun 1931, *Lugard 663* (K barcodes K000078633 [sheet I]!, K000078632 [sheet II]!).

***Orthochilus nuttii*** (Rolfe) Bytebier, **comb. nov.** ≡ *Eulophia nuttii* Rolfe in Oliver, Fl. Trop. Afr. 7: 63. 1897 – Holotype: ZAMBIA. Fwambo, 1896, *Nutt s.n.* (K barcode K000078634!).

***Orthochilus odontoglossus*** (Rchb.f.) Bytebier, **comb. nov.** ≡ *Eulophia odontoglossa* Rchb.f. in Linnaea 19: 373. 1846 ≡ *Graphorkis odontoglossa* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 662. 1891 – Holotype: SOUTH AFRICA. Durban [Port Natal], *Gueinzus* (W n.v.).

***Orthochilus pottsii*** (P.M.Br. & DeAngelis) Bytebier, **comb. nov.** ≡ *Pteroglossaspis pottsii* P.M.Br. & DeAngelis in N. Amer. Native Orchid J. 13: 31. 2007 – Holotype: U.S.A. Florida, Citrus, Potts Preserve, 20 Oct 2006, *DeAngelis s.n.* (FLAS n.v.).

*Orthochilus rarus* (Schltr.) Bytebier, **comb. nov.** ≡ *Eulophia rara* Schltr. in Bot. Jahrb. Syst. 53: 582. 1915 – Holotype: TANZANIA. Rungwe, Mulinda Forest, Jan 1913, *Stolz 1815* (B†; record of holotype: K n.v.).

*Orthochilus rutenbergianus* (Kraenzl.) Bytebier, **comb. nov.** ≡ *Eulophia rutenbergiana* Kraenzl. in Abh. Naturwiss. Vereins Bremen 7: 255. 1882 ≡ *Graphorkis rutenbergiana* (Kraenzl.) Kuntze, Revis. Gen. Pl. 2: 662. 1891 ≡ *Lissochilus kranzlinii* H. Perrier in Fl. Madag. 49(2): 13. 1941 – Holotype: MADAGASCAR. Nähe von Antananarivo, 18 Dec 1877, *Rutenberg s.n.* (B†) – Neotype: MADAGASCAR. Imerina, Jan 1881, *Hildebrandt 3842* (K n.v.; isoneotype: BM n.v., M barcode M0103415!, P barcode P00108964!, W n.v.).

The description of this species by Kraenzlin was based on one specimen collected by Rutenberg in Madagascar. Rutenberg's material was originally deposited at Bremen and the type specimens were expropriated by Soviet troops and are thought to be at CSR (Dorr, 1997). Kraenzlin's types were mostly in his own herbarium, which was acquired by B in 1907 and destroyed during the bombing of B at the end of WWII. Under these circumstances, it is not clear whether type material is still extant. Hermans & al. (2007), assume that the type has been destroyed at B, and designated *Hildebrandt 3482* as a "lectotype". Since no other material than the Rutenberg specimen collected on 18 Dec 1877 was mentioned by Kraenzlin, *Hildebrandt 3482* should be considered a neotype (Art. 9.7 of the *Melbourne Code*) and not a lectotype.

*Orthochilus ruwenzoriensis* (Rendle) Bytebier, **comb. nov.** ≡ *Eulophia ruwenzoriensis* Rendle in J. Bot. 33: 166. 1895 ≡ *Pteroglossaspis ruwenzoriensis* (Rendle) Rolfe in Oliver, Fl. Trop. Afr. 7: 100. 1897 – Syntypes: UGANDA. Ruwenzori (eastern side), Apr–May 1894, *Scott Elliot 7813* (BM barcode BM000911528!; isosytype: K barcode K000306611!), *Scott Elliot 7859* (BM barcode BM000525768!; isosytype: K barcode K000306610!), *Scott Elliot 7551* (BM barcode BM000911529!).

*Orthochilus subulatus* (Rendle) Bytebier, **comb. nov.** ≡ *Eulophia subulata* Rendle in J. Bot. 33: 167. 1895 – Holotype: UGANDA. Katonga River South of Uganda (Victoria Region), 26 Feb 1894, *Scott Elliot 7417* (BM n.v.; isotype: K barcode K000410218!).

*Orthochilus tabularis* (L.f.) Bytebier, **comb. nov.** ≡ *Satyrium tabulare* L.f., Suppl. Pl.: 402. 1782 ≡ *Serapias tabularis* (L.f.) Thunb., Prodr. Pl. Cap.: 3. 1794 ≡ *Cymbidium tabulare* (L.f.) Sw. in Nova Acta Regiae Soc. Sci. Upsal. 6: 77. 1799 ≡ *Epidendrum tabulare* (L.f.) Poir. in Lamarck, Encycl., Suppl. 1: 376. 1810 ≡ *Eulophia tabularis* (L.f.) Bolus in Trans. S. African Philos. Soc. 5(1): 108. 1888 – Holotype: SOUTH AFRICA. Western Cape, Cape Peninsula, Table Mountain, *Thunberg s.n.* (UPS-THUNB n.v.), but see comments by Hall (1965: 191–192).

*Orthochilus thomsonii* (Rolfe) Bytebier, **comb. nov.** ≡ *Eulophia thomsonii* Rolfe in Oliver, Fl. Trop. Afr. 7: 66. 1897 – Holotype: TANZANIA. Between Lakes Tanganyika and Malawi [Nyassa], *Thomson s.n.* (K barcode K000078621!).

*Orthochilus trilamellatus* (De Wild.) Bytebier, **comb. nov.** ≡ *Eulophia trilamellata* De Wild. in Bull. Jard. Bot. État Bruxelles 6: 127. 1919 – Holotype: D.R. CONGO. Région de Lualaba (Katanga), Valée de la Kapanda, Dec 1912, *Homblé 978* (BR barcode BR0000008813879!, isotype: BR barcode BR0000008813541!).

There are two duplicates of *Homblé 978* at BR. Neither De Wildeman in the protologue, nor Geerinck in *Flore d'Afrique Centrale* (1992: 697), indicate which one of the two is the holotype. However, there are clear indications on specimen BR0000008813879 that this was used to prepare the drawings which are part of the protologue and therefore this specimen should be considered the holotype.

*Orthochilus vinosus* (McMurtry & G.McDonald) Bytebier, **comb. nov.** ≡ *Eulophia vinosus* McMurtry & G.McDonald, Field Guide Orch. N. South Africa Swaziland: 467. 2008 – Holotype: SOUTH AFRICA. Mpumalanga, Dullstroom, east of village, *McMurtry 4072* (PRE n.v.).

*Orthochilus walleri* (Rchb.f.) Bytebier, **comb. nov.** ≡ *Cyrtopera walleri* Rchb.f., Otia Bot. Hamburg.: 117. 1881 ≡ *Eulophia walleri* (Rchb.f.) Kraenzl. in Engler, Pflanzenw. Ost-Afrikas, C: 157. 1895 – Holotype: MALAWI. Manganja Hills, 1865, *Waller s.n.* (K barcode K000078622!, isotype: W n.v.).

*Orthochilus welwitschii* Rchb.f. in Flora 48: 186. 1865 ≡ *Eulophia welwitschii* (Rchb.f.) Rolfe in Bol. Soc. Brot. 7: 236. 1889 – Holotype: ANGOLA. Huilla, Proteatorum de Monine, Jan 1860, *Welwitsch 720* (W n.v.; isotypes BM barcode BM000529534!, C barcode C10001057!, HBG barcode HBG-501719 [fragment from holotype]!, K barcodes K000078623!, K000078624 [drawing]!, LISU barcodes LISU221619!, LISU221620!).

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#### Appendix 1. Taxa included in this study.

**Taxon name** including authority: country, largest political subdivision, locality, collection date, *collector and collector number* (herbarium acronym), GenBank accession numbers in the order ITS, *rbcL*, *trnK-matK*, *rpl32-trnL*, and *trnQ-5'rps16*. A dash (–) denotes missing sequence; an asterisk (\*) denotes species for which taxonomic changes (transfer to the genera *Orthochilus* or *Oeoeclades*) are proposed.

*Acrolophia bolusii* Rolfe: South Africa, Western Cape, Groot Hagelkraal, 7 Nov 2001, *Bytebier 2120* (BR, K, NBG, NY), KF318909, KF358051, KF358114, KF363835, KF358146; South Africa, Western Cape, Houw Hoek, 14 Oct 2011, *Staerker s.n.* (NU [photographs]), KF318933, KF358055, KF358115, KF363899, KF358193. *Acrolophia capensis* (P.J.Bergius) Fourc.: South Africa, Eastern Cape, Joubertina, Oct 2011, *Staerker s.n.* (NU [photographs]), KF318958, KF358001, KF358074, KF363914, KF358167. *Acrolophia cochlearis* (Lindl.) Schltr. & Bolus: South Africa, Eastern Cape, Langkloof Valley, Oct 2012, *Thornton Smith AC1* (NU), KF318947, KF358029, KF358059, KF363915, KF358212; South Africa, KwaZulu-Natal, Umtamvuna N.R., 28 Sep 2011, *Staerker s.n.* (NU [photographs]), –, KF358000, KF358097, KF363880, KF358137. *Acrolophia lamellata* (Lindl.) Pfitzer: South Africa, Western Cape, Groot Hagelkraal, 7 Nov 2001, *Bytebier 2125* (BR, K, NBG), KF318964, KF358002, KF358063, KF363896, KF358174. *Acrolophia lunata* (Schltr.) Schltr. & Bolus: South Africa, Eastern Cape, Langkloof Valley, Oct 2011, *Thornton Smith ALL* (NU), KF318965, KF358006, KF358129, KF363871, KF358176. *Acrolophia micrantha* (Lindl.) Pfitzer: South Africa, Western Cape, Betty's Bay, 14 Oct 2011, *Staerker s.n.* (NU [photographs]), KF318913, KF358019, KF358111, KF363833, KF358173. *Acrolophia* sp. aff. *cochlearis*: South Africa, Eastern Cape, Langkloof Valley, Oct 2011, *Thornton Smith AM1* (NU), KF318912, KF358003, KF358116, KF363840, KF358163. *Acrolophia ustulata* (Bolus) Schltr. & Bolus: South Africa, Western Cape, Robinson Pass, 27 Nov 2012, *Vlok 2891* (NU), KF318963, KF358027, KF358121, KF363911, KF358152. *Ansellia africana* Lindl.: South Africa, KwaZulu-Natal, UKZN Botanical Garden, 23 Sep 2011, *Martos 748* (NU), KF318915, KF358009, KF358098, KF363854, KF358189. *Eulophia aculeata* (L.f.) Spreng.\*: South Africa, Eastern Cape, Grahamstown, Rabbits Wood, 29 Nov 2001, *Peter 431* (NU), KF318949, –, KF358077, KF363872, KF358147. *Eulophia acutilabra* Summerh., Tanzania, Ruvuma, Mkuju river project area, 4 Dec 2011, *McClelland 790* (BNRH), KF318954, KF358035, KF358103, KF363875, KF358150. *Eulophia angolensis* (Rchb.f.) Summerh.: South Africa, Mpumalanga, Witklopdam, 30 Dec 2002, *Bytebier 2480* (BR, K, NBG, NY), KF318932, KF358031, KF358075, KF363905, KF358139. *Eulophia calanthoides* Schltr.: South Africa, KwaZulu-Natal, Wairoonga Farm, 8 Feb 2001, *Peter 357* (NU), KF318896, –, KF358107, KF363844, KF358175. *Eulophia callichroma* Rchb.f.: South Africa, Mpumalanga, Songimvelo N.R., 22 Nov 2012, *Staerker s.n.* (NU), KF318903, KF358041, KF358058, KF363904, –, *Eulophia chlorantha* Schltr.\*: Swaziland, Hhohho, Mbabane, 4 Nov 2011, *Staerker s.n.* (NU), KF318939, KF358025, KF358124, KF363848, KF358140. *Eulophia clitellifera* (Rchb.f.) Bolus: South Africa, KwaZulu-Natal, Pietermaritzburg, Wembley, 17 Nov 2000, *Peter 296* (NU), –, –, KF358056, KF363879, KF358184. *Eulophia coeloglossa* Schltr.: South Africa, KwaZulu-Natal, Umtamvuna N.R., 6 Dec 2012, *Staerker s.n.* (NU), KF318961, KF358016, KF358071, KF363873, KF358182. *Eulophia cucullata* (Afzel. ex Sw.) Steud.: South Africa, KwaZulu-Natal, Mabibi N.R., 15 Nov 2001, *Peter 418* (NU), KF318946, KF358047, KF358106, KF363865, KF358145. *Eulophia ensata* Lindl.\*: South Africa, KwaZulu-Natal, Thornville, 30 Dec 2002, *Peter 4035* (form cream) (GRA), KF318956, KF358021, KF358117, KF363851, KF358136; South Africa, KwaZulu-Natal, Amatigulu, 15 Dec 2001, *Peter s.n.* (form cream) (GRA), KF318931, –, KF358073, KF363870, KF358172; South Africa,

## Appendix 1. Continued.

KwaZulu-Natal, Thornville, 30 Dec 2002, *Peter 4033* (form yellow) (GRA), KF318957, –, KF358082, KF363887, KF358156. *Eulophia flavopurpurea* (Rchb.f.) Rolfe, Cameroon, Littoral, Melon, 8 Mar 2007, *Bytebier 2742* (YA, BR), KF318930, –, KF358069, KF363838, KF358181. *Eulophia foliosa* (Lindl.) Bolus\*: South Africa, Mpumalanga, Long Tom Pass, 31 Dec 2002, *Bytebier 2484* (BR, K, NBG), –, –, KF358101, KF363858, KF358142; South Africa, KwaZulu-Natal, Himeville, 17 Dec 2000, *Peter 338* (NU, NH), KF318920, KF358034, KF358113, KF363888, KF358179. *Eulophia graminea* Lindl.: Singapore, South Keppel, Sentosa, 16 Nov 2011, *Peter 7598* (GRA), KF318890, KF358040, KF358078, KF363897, –, *Eulophia guineensis* Lindl.: Kenya, Western, Kakamega Forest, 12 Feb 2009, *Odhiambo 36* (EA), KF318960, KF358028, KF358080, KF363849, KF358209. *Eulophia hereroensis* Schltr.: South Africa, KwaZulu-Natal, Ashburton, 4 Nov 2000, *Peter 302* (NU), KF318940, –, KF358066, KF363906, KF358138. *Eulophia hians* Spreng. var. *hians*: South Africa, Mpumalanga, Lydenburg, 26 Sep 2011, *Staerker s.n.* (NU), KF318959, KF358052, KF358112, KF363913, KF358151; South Africa, Eastern Cape, Port Elizabeth, Bridgemead, 1 Nov 2003, *Peter 5277* (GRA), KF318892, KF358024, KF358060, KF363831, KF358166; South Africa, KwaZulu-Natal, Umtamvuna N.R., 9 Nov 2011, *Grieve 476* (NU), KF318950, –, KF358096, KF363874, KF358190. *Eulophia hians* var. *inaequalis* (Schltr.) S. Thomas: South Africa, KwaZulu-Natal, Pietermaritzburg, Ukilinga Farm, 28 Aug 2012, *Bytebier 3464* (NU), KF318942, KF358015, KF358104, KF363892, KF358154; South Africa, KwaZulu-Natal, Wagendrift Dam, 3 Oct 2002, *Peter 3774* (GRA), KF318902, –, KF358100, KF363881, –, *Eulophia hians* var. *nutans* (Sond.) S. Thomas: Malawi, Northern Region, Nyika Plateau, 4 Feb 2003, *Peter 4183* (GRA), KF318928, –, KF358135, KF363898, KF358171. *Eulophia horsfallii* (Bateman) Summerh.: South Africa, KwaZulu-Natal, Palm Beach, 14 Jan 2001, *Peter 5496* (GRA), KF318922, –, –, KF363902, KF358160; Tanzania, Ruvuma, Mkuju river project area, 7 Dec 2011, *McClelland 793* (BNRH), KF318926, KF358018, KF358109, KF363876, KF358191. *Eulophia huttonii* Rolfe\*: South Africa, KwaZulu-Natal, Garden Castle, 1 Dec 2001, *Peter 434* (NU), KF318910, –, –, KF363912, –, *Eulophia leontoglossa* Rchb.f.\*: South Africa, KwaZulu-Natal, Cobham, 6 Jan 2002, *Peter 448* (NU), KF318941, KF357998, KF358132, KF363882, KF358198. *Eulophia litoralis* Schltr.\*: South Africa, Western Cape, Jonkershoek, 9 Dec 2009, *Bytebier 3163* (NU), KF318901, KF358043, KF358085, KF363863, KF358194. *Eulophia livingstoneana* (Rchb.f.) Summerh., Tanzania, Ruvuma, Mkuju river project area, 4 Dec 2011, *McClelland 792* (BNRH), KF318943, –, KF358057, KF363846, KF358161. *Eulophia longisepala* Rendle, Tanzania, Ruvuma, Mkuju river project area, 29 Nov 2011, *McClelland 788* (BNRH), KF318918, KF358010, KF358086, KF363843, KF358188. *Eulophia macowanii* Rolfe: South Africa, Eastern Cape, Umtata, UNITRA campus, 28 Nov 2001, *Peter 429* (NU), KF318904, –, KF358120, KF363842, KF358144. *Eulophia mechowii* (Rchb.f.) T. Durand & Schinz\*: Angola, Huila, Upper Zootechnica, 16 Jan 2009, *Bellstedt 1197* (NU), KF318914, KF358013, KF358102, KF363868, KF358157. *Eulophia meleagris* Rchb.f.: South Africa, Mpumalanga, Dullstroom, 20 Feb 2012, *Martos 797* (NU), KF318936, KF357999, KF358083, KF363859, KF358162. *Eulophia milnei* Rchb.f.\*: South Africa, KwaZulu-Natal, Umtamvuna N.R., 6 Dec 2012, *Staerker s.n.* (NU), KF318923, KF358049, –, KF363860, KF358195. *Eulophia odontoglossa* Rchb.f.\*: Tanzania, Njombe, Njombe, 19 Feb 2003, *Bytebier 2551* (EA), KF318951, KF358044, KF358105, KF363841, KF358158; Tanzania, Njombe, Njombe, 19 Feb 2003, *Bytebier 2546* (BR, DSM, EA, K, NY), KF318935, KF358038, KF358089, KF363855, KF358200. *Eulophia ovalis* var. *bainesii* (Rolfe) P.J.Cribb & La Croix, Malawi, Northern Region, Nyika Plateau, 4 Feb 2003, *Peter 4182* (GRA), KF318905, KF358020, KF358064, KF363909, KF358153. *Eulophia ovalis* Lindl. var. *ovalis*: South Africa, Mpumalanga, Agnes Mine, 29 Dec 2002, *Bytebier 2476* (BR, K, NBG), KF318908, KF357997, KF358125, KF363857, KF358164; South Africa, KwaZulu-Natal, Wahroonga Farm, 8 Feb 2001, *Peter 358* (GRA, NU), KF318929, –, KF358087, KF363853, KF358186. *Eulophia parviflora* (Lindl.) A.V.Hall: South Africa, KwaZulu-Natal, Vernon Crookes NR, 16 Jul 2011, *Martos 738* (form long spur) (NU), KF318966, KF358046, KF358070, KF363886, KF358168; South Africa, KwaZulu-Natal, Harburg Eagle View, 17 Dec 2011, *Johnson s.n.* (form long spur) (NU), –, KF358017, KF358062, KF363866, KF358185; South Africa, Eastern Cape, Port Elizabeth, Skoenmaakerskop, 14 Nov 2006, *Peter 5959f* (form Port Elizabeth) (GRA), KF318895, KF358030, KF358065, KF363890, KF358202; South Africa, Eastern Cape, Grahamstown, Dassie Krantz, 8 Nov 2006, *Peter 5943* (form short spur) (GRA), KF318893, –, KF358122, KF363850, KF358159. *Eulophia parvilabris* Lindl.: South Africa, KwaZulu-Natal, Springside N.R., 28 Jan 2001, *Peter s.n.* (GRA), KF318927, –, KF358130, KF363878, KF358178. *Eulophia petersii* (Rchb.f.) Rchb.f.: South Africa, Mpumalanga, Lowveld Botanical Gardens, Nelspruit, 6 Dec 2000, *Peter s.n.* (GRA), KF318906, –, KF358128, KF363895, KF358143; Kenya, Nyanza, Mfangano Island, 7 Aug 2000, *Kirika 528* (EA), KF318897, KF358012, KF358067, KF363837, KF358155. *Eulophia platypetala* Lindl.: South Africa, Western Cape, 30 Apr 2005, *Peter 5635* (GRA), –, KF358004, KF358088, KF363877, KF358197. *Eulophia pulchra* (Thouars) Lindl.\*: Reunion, Saint Philippe, Basse Vallée, 8 Feb 2011, *Martos 732* (REU), KF318919, KF358022, KF358081, KF363847, KF358165; Tanzania, Iringa, Udzungwa Mountain NP, 8 Nov 1997, *Luke 5010* (EA, K), KF318911, KF358042, KF358079, KF363891, KF358170; Reunion, Entre-Deux, Bayonne Dimitile, 21 Jan 2011, *Pailler s.n.* (REU), KF318938, KF358053, KF358090, KF363862, KF358180. *Eulophia ruwenzoriensis* Rendle\*: Tanzania, Mbeya, Kitulo Plateau, 13 Mar 2005, *Van der Niet 407* (NU), KF318894, KF358032, KF358072, KF363883, KF358211. *Eulophia? schnel-liae* L.Bolus: South Africa, KwaZulu-Natal, Port Edwards, 27 Feb 2011, *Church s.n.* (NU), KF318891, KF358045, KF358126, KF363864, KF358187. *Eulophia schweinfurthii* Kraenzl.: South Africa, KwaZulu-Natal, Port Edwards, 27 Feb 2011, *Church s.n.* (NU), KF318924, –, KF358133, KF363834, –, *Eulophia speciosa* (R.Br.) Bolus: South Africa, KwaZulu-Natal, St Lucia, 12 Nov 2011, *Martos 763* (NU), KF318967, KF358023, KF358123, KF363884, KF358183. *Eulophia stachyodes* Rchb.f.: Kenya, Western, Kakamega Forest, 19 Feb 2009, *Odhiambo 213* (EA), KF318953, KF358050, KF358094, KF363839, KF358199. *Eulophia streptopetala* var. *stenophylla* (Summerh.) P.J.Cribb: Kenya, Nairobi, Nairobi Arboretum, 16 Mar 1995, *Bytebier 494* (EA), KF318925, KF357996, KF358093, KF363869, KF358201. *Eulophia streptopetala* Lindl. var. *streptopetala*: South Africa, Eastern Cape, Port Alfred, 21 Oct 2006, *Peter 5933* (GRA), KF318921, –, KF358134, KF363889, KF358192; D.R. Congo, Orientale, Mongbwalu, 21 Jan 2011, *Bytebier 3239* (BR, EA, EPU, NU), KF318934, KF358048, KF358110, KF363901, KF358207; Kenya, Central, Lake Ol Bolossat, 27 Jun 2007, *Odhiambo 34* (EA), KF318898, KF358011, KF358131, KF363903, KF358208. *Eulophia stricta* Rolfe: Kenya, Coast, Kinango Kwale, 15 Dec 2007, *Odhiambo 84* (EA), KF318955, –, KF358127, KF363908, –, *Eulophia tabularis* (L.f.) Bolus\*: South Africa, Western Cape, Table Mountain, 10 Dec 2010, *Staerker s.n.* (GRA), KF318907, KF358014, KF358092, KF363894, KF358169. *Eulophia tenella* Rchb.f.: South Africa, Eastern Cape, Grahamstown, 16 Jan 2002, *Peter 455* (NU), KF318900, KF358007, KF358119, KF363910, KF358196. *Eulophia tuberculata* Bolus: South Africa, Eastern Cape, Grahamstown, Ecce Pass Wild Flower Reserve, 22 Dec 2006, *Peter 5961* (GRA), KF318945, KF358037, KF358076, KF363856, KF358210. *Eulophia vinosa* McMurtry & G.McDonald\*: South Africa, KwaZulu-Natal, Balgowan, 19 Sep 2001, *Peter s.n.* (GRA), KF318952, –, –, KF363852, –, *Eulophia welwitschii* (Rchb.f.) Rolfe\*: South Africa, KwaZulu-Natal, Far Away Farm, 6 Jan 2010, *Bytebier 3167* (BR, NU), –, –, KF358095, KF363832, KF358141. *Eulophia zeyheriana* Sond.: South Africa, KwaZulu-Natal, Cobham, 6 Jan 2002, *Peter 447* (NU), KF318948, KF358026, KF358091, KF363916, KF358148. *Oeoclaudes bernetii* J.-B.Castillon: Reunion, Saint Denis, Ilet à Guillaume, 12 Mar 1992, *Jubault s.n.* (REU), KF318937, KF358039, KF358068, KF363836, KF358206; Reunion, Saint Joseph, Plaine des Grègues, 4 Apr 2010, *Pailler s.n.* (REU), –, –, –, KF363893, –, *Oeoclaudes maculata* (Lindl.) Lindl.: Kenya, Western, Kakamega Forest, 7 Oct 2009, *Odhiambo 10* (EA), KF318917, KF358036, KF358084, KF363845, KF358177; Reunion, Saint Pierre, Piton Monvert, Mar 2011, *Pailler s.n.* (REU), KF318968, KF358008, KF358118, KF363867, KF358204. *Oeoclaudes saundersiana* (Rchb.f.) Garay & P.Taylor: Kenya, Coast, Mwach, 26 Nov 1997, *PCP 2* (EA), KF318916, KF358033, KF358108, KF363907, KF358203; Kenya, Western, Kakamega Forest, 19 Feb 2009, *Odhiambo 212* (EA), KF318962, KF358005, KF358061, KF363900, KF358205. *Oeoclaudes sp.*: Madagascar, Southern, –, –, *Peter 5497* (GRA), KF318944, –, –, KF363861, –, *Oeoclaudes ugandae* (Rolfe) Garay & P.Taylor: Kenya, Western, Kakamega Forest, 7 Oct 2009, *Odhiambo 4* (EA), KF318899, KF358054, KF358099, KF363885, KF358149.