



Lankesteriana International Journal on
Orchidology

ISSN: 1409-3871

lankesteriana@ucr.ac.cr

Universidad de Costa Rica
Costa Rica

Williams, Norris H.; Whitten, W. Mark; Dressler, Robert L.
MOLECULAR SYSTEMATICS OF TELIPOGON (ORCHIDACEAE: ONCIDIINAE) AND
ITS ALLIES: NUCLEAR AND PLASTID DNA SEQUENCE DATA
Lankesteriana International Journal on Orchidology, vol. 5, núm. 3, diciembre, 2005, pp.
163-184
Universidad de Costa Rica
Cartago, Costa Rica

Available in: <http://www.redalyc.org/articulo.oa?id=44339809001>

- How to cite
- Complete issue
- More information about this article
- Journal's homepage in redalyc.org

redalyc.org

Scientific Information System

Network of Scientific Journals from Latin America, the Caribbean, Spain and Portugal
Non-profit academic project, developed under the open access initiative

MOLECULAR SYSTEMATICS OF *TELIPOGON* (ORCHIDACEAE: ONCIDIINAEE) AND ITS ALLIES: NUCLEAR AND PLASTID DNA SEQUENCE DATA

NORRIS H. WILLIAMS^{1,3}, W. MARK WHITTEN¹, AND ROBERT L. DRESSLER^{1,2}

¹Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA

²Jardín Botánico Lankester, Universidad de Costa Rica, apdo. 1031-7050, Cartago, Costa Rica

³Author for correspondence: orchid@flmnh.ufl.edu

ABSTRACT. Phylogenetic relationships of *Telipogon* Kunth, *Ornithocephalus* Hook. and related genera (Orchidaceae: Oncidiinae) were evaluated using parsimony analyses of data from the internal transcribed spacers of nuclear ribosomal (nrITS DNA) and three plastid regions (*matK*, *trnL-F*, and the *atpB-rbcL* intergenic spacer region). In addition to an analysis of 81 OTU's for ITS only, we used a matrix of 30 taxa for combined nuclear and plastid analyses. *Stellilabium* is embedded within *Telipogon* and should be merged with the latter genus. *Telipogon* consists of two South American clades and a Central American clade. One *Stellilabium* clade is sister to the Central American clade of *Telipogon*, and the second *Stellilabium* clade is sister to all of the Central American species of *Telipogon* and *Stellilabium*. *Hofmeisterella* is a member of the *Telipogon* alliance. The genus *Dipterostele* is not supported by this work. Nomenclatural changes are made transferring *Stellilabium* to *Telipogon*.

RESUMEN. Se evaluaron las relaciones filogenéticas de *Telipogon*, *Ornithocephalus* y géneros afines (Orchidaceae: Oncidiinae) mediante análisis de parsimonia de datos de espaciadores de ADN ribosomal nuclear (nrITS) y de tres regiones de ADN de plastidios (*matK*, *trnL-F* y la región espaciadora intergénica *atpB-rbcL*). Además de un análisis de 81 OTU con ITS, se usó una matriz de 30 taxa para realizar análisis combinados de ADN nuclear y de plastidios. *Stellilabium* aparece anidado dentro de *Telipogon*. Éste presenta dos cladogramas sudamericanos y uno centroamericano. Un clado de *Stellilabium* es hermano del clado centroamericano de *Telipogon*; el segundo clado de *Stellilabium* es hermano de todas las especies centroamericanas de *Telipogon* y *Stellilabium*. *Hofmeisterella* es un miembro del grupo de *Telipogon*. El género *Dipterostele* como tal no se justifica, según este estudio. Se realizan cambios nomenclatoriales para transferir las especies de *Stellilabium* a *Telipogon*.

KEY WORDS / PALABRAS CLAVE: *Hofmeisterella*, *Ornithocephalus*, *Stellilabium*, *Telipogon*, Oncidiinae, Orchidaceae

The phylogenetic placements of *Telipogon* Kunth and its relatives (formerly in subtribe Telipogoninae), *Ornithocephalus* Hook. and its relatives (formerly in subtribe Ornithocephalinae), *Pachyphyllum* Kunth and *Fernandezia* Ruiz & Pav. (formerly in subtribe Pachyphyllinae), and *Lockhartia* Hook. (formerly in subtribe Lockhartiinae) have been unclear for many years, although most authors now agree that these taxa belong in Maxillarieae (Dressler 1993) and are related to subtribe Oncidiinae (*sensu* Dressler 1993). Telipogoninae and Ornithocephalinae have been separated from Oncidiinae on the basis of four pollinia versus two in the Oncidiinae. Dressler (1993) included *Pachyphyllum*, *Fernandezia*, and *Lockhartia* in the Oncidiinae. Our earlier analyses (Whitten *et al.* 2000) showed that these groups all belong within the Oncidiinae, and we later reported on 10 species in these alliances, which we analyzed using a combined matrix

of ITS/*matK/trnL-F* for a total of 79 species (Williams *et al.* 2001a). The species studied here represent a broad sampling of species from both Central America (primarily Panama and Costa Rica) and northern South America (primarily Ecuador).

The relationships of the *Telipogon* - *Pachyphyllum* - *Ornithocephalus* alliances were demonstrated in our earlier study, but the systematic position of *Lockhartia* was not satisfactorily resolved at that time (Williams *et al.* 2001a,b). The *Telipogon* - *Pachyphyllum* - *Ornithocephalus* alliances are sister groups embedded within the Oncidiinae. In those studies *Lockhartia* was an isolated group within the Oncidiinae, but the three-gene analysis did not resolve its closest relatives. Here we expand on that study, discuss the *Telipogon* alliance in more detail, and present some preliminary data on the *Ornithocephalus* alliance. Our larger analyses of the Oncidiinae (634 species for ITS, 252 species for

ITS/*matK/trnL-F*) show that *Lockhartia* is sister to the *Telipogon - Pachyphyllum - Ornithocephalus* alliance (Williams & Whitten 2003, and unpublished in prep.).

The systematic position of *Hofmeisterella* Rchb.f. has been disputed in the past. Szlachetko (1995) placed *Hofmeisterella* with *Chytroglossa*, *Eloyella*, *Hintonella*, and *Phymatidium* in subtribe Hintonellinae of his tribe Ornithocephaleae, whereas Dressler (1993) placed *Hofmeisterella* with *Telipogoninae*, and Dodson (pers. comm.) also considered inclusion within *Telipogoninae*. We address this question by analyzing a range of species in both alliances.

MATERIALS AND METHODS

Specimens – Table 1 list taxa examined, vouchers, and GenBank numbers for all sequences. Samples for DNA extraction were taken from wild collected plants, cultivated plants, or from herbarium material.

Molecular techniques – DNA extraction, purification, PCR amplifications, sequencing, alignments, primers, etc. were the same as in Williams *et al.* (2001a), except as described below. All data matrices are available upon request from NHW (orchid@flmnh.ufl.edu).

The PCR protocol for the *atpB-rbcL* intergenic spacer was 94 °C for 2 min, 94 °C for 45 sec, 62 °C 1 min, 72 °C for 75 sec, 32 cycles, and a final extension of 72 °C 2 min. The primer sequences used are given in Table 2. The original *atpB-rbcL* intergenic spacer primers used for this group were those of Chiang *et al.* (1998), but later modified as shown in Table 2.

Data matrices – Two data matrices were used: 1) an 81-OTU matrix was analyzed for ITS alone which included ITS 1 and ITS 2, the included 5.8S region, and portions of the flanking 18s and 26s regions; and 2) a 30-taxon subset of that matrix was used for both ITS analyses and individual and combined analyses of *matK*, *trnL-F*, and the *atpB-rbcL* intergenic spacer. We were unable to obtain useable sequence data for *Phymatidium* for the *trnL-F* study and for *Telipogon ariasii* for the *atpB-rbcL* intergenic spacer region, so those two matrices contain only 29 taxa.

Outgroup choice – Outgroup choice was determined by our analyses of *Oncidiinae* (Williams *et al.* 2001a, b, Williams & Whitten 2003) and by our expanded analysis of 634 taxa for ITS alone and 252 taxa for ITS/*matK/trnL-F*. We used *Lockhartia* as the outgroup in the large ITS only matrix and *Fernandezia tica* and *Pachyphyllum* sp. as the outgroup in the combined nuclear and plastid analyses.

Data analysis – PAUP* 4.0b10 (Swofford 2000) was

used on a PowerMac G4 computer for all analyses with the following search strategies under Fitch parsimony (unordered characters, equal weight to all changes, Fitch 1971): 1000 replicates random taxon entry, MULTTREES on, and SPR swapping holding only 10 trees/replicate to reduce time spent in swapping on large numbers of trees in each replicate. After completing the random replicates, all shortest trees found were then used as the starting trees in a search with a limit of 10 000 trees with swapping to completion on these trees. Tree statistics for the analyses are given in Table 3. We performed the following analyses: individual analyses of 30 taxa for ITS, *matK*, *trnL-F*, and the *atpB-rbcL* intergenic spacer; a combination of the three plastid regions; a combined ITS + plastid dataset; and an individual analysis for the 81 OTU ITS only matrix. Support was determined by bootstrap analysis performed in PAUP* and by Bayesian analysis performed in MrBayes 3.0B (Huelsenbeck & Ronquist 2001) on the combined plastid + ITS matrix. The parameters for the Bayesian analysis were as follows: lset nst=2 rates=equal; set autoclose=yes; mcmc ngen=2,000,000 printfreq=100 samplefreq=10 nchains=4 savebrlens=yes; mcmc; sumt; burnin=200,000 contype=halfcompat. The analysis was repeated with rates=gamma. In each case the first 10 000 trees were omitted and the majority rule consensus tree obtained in PAUP* from the remaining trees. The two Bayesian analyses yielded the same topologies, identical to those of parsimony analyses.

RESULTS

Analysis of individual matrices—ITS — The ITS analysis included 795 characters, of which 375 were variable and 301 (38%) potentially parsimony informative, resulting in eight trees of 914 steps [CI=0.58 (0.54 with uninformative characters excluded), RI=0.79]. Figure 1 is one tree with branch lengths and bootstrap support (BS).

Telipogon alliance: The ITS analysis of a moderately supported (75%BS) *Telipogon* alliance has a basal polytomy with *Hofmeisterella*, the *Trichoceros* clade (100%BS), the *Telipogon ariasii-pulcheraldstromii* clade (100%BS), and the strongly supported remainder of the group with 100%BS. This latter branch comprises the *Telipogon nervosus-vargasii* clade (100%BS), sister to a weakly supported clade (74%BS) of South American *Stellilabium* (100%BS) + a weakly supported (78%BS) clade of Central American *Stellilabium* (100%BS) + Central American *Telipogon* (98%BS). Within the Central American *Telipogon* clade, *T. butcheri* is sister to a strongly

supported (100%BS) clade of five additional species from Central America.

***Ornithocephalus* alliance:** Within the strongly supported *Ornithocephalus* alliance (99%BS), *Phymatidium* is sister to a moderately supported clade (84%BS) consisting of two clades each with 100%BS support: one clade of *Zygostates alleniana* + *Dipteranthus grandiflorus* and a second clade of *Eloyella* sister to a weakly supported (59%BS) clade of *Hintonella* sister to a 100%BS clade of *Ornithocephalus inflexus* + *Sphyrastylis dalstromii*.

Analysis of individual matrices—*trnL-F* — This analysis had 1252 characters, 298 were variable and 149 (12%) were potentially parsimony informative, and yielded 1458 trees with a length of 425 steps [CI=0.80 (0.68 with uninformative characters excluded), RI=0.84]. Figure 2 is one tree with branch lengths and bootstrap values.

***Telipogon* alliance:** The *trnL-F* only analysis shows a strongly supported (93%BS) *Telipogon* alliance with a weakly supported (68%BS) clade of *Hofmeisterella* and *Trichoceros* sister to the strongly supported (94%BS) remaining ingroup. The ingroup consists of a strongly supported (100%BS) *Telipogon ariasii-pulcher-dalstromii* clade and a weakly supported clade (56%BS) comprising a strongly supported (100%BS) South American *Stellilabium* clade of three species sister to a weakly supported (50%BS) clade consisting of a strongly supported (100%BS) *Telipogon nervosus-vargasii* clade, and a moderately supported (76%BS) Central American clade which consists of a strongly supported (97%BS) *Stellilabium* clade of four species and a strongly supported (99%BS) *Telipogon* clade of six species. In this analysis *T. butcheri* is within the clade of the other Central American species of *Telipogon*.

***Ornithocephalus* alliance:** The *trnL-F* analysis produced a strongly supported (100%BS) *Ornithocephalus* alliance consisting of two clades: a strongly supported clade of (96%BS) *Zygostates alleniana* + *Dipteranthus grandiflorus* and a moderately supported (77%BS) clade of *Eloyella* sister to a weakly supported (59%BS) clade of *Ornithocephalus inflexus* + *Sphyrastylis dalstromii* + *Hintonella mexicana*.

Analysis of individual matrices—*matK* — The individual *matK* analysis consisted of 1331 included characters, 284 were variable and 151 (11%) were potentially parsimony informative, and yielded four trees of 434 steps [CI=0.76 (0.64 with uninformative characters excluded), RI=0.83]. Figure 3 is one tree

with branch lengths and bootstrap values.

***Telipogon* alliance:** In this analysis the *Telipogon* alliance is weakly supported (62%BS) with *Hofmeisterella* sister to a weakly supported (53%BS) remainder of the alliance. The strongly supported (100%BS) *Trichoceros* clade is sister to the moderately supported (88%BS) remainder of the alliance. The remainder of the alliance consists of a strongly supported (100%BS) *Telipogon ariasii-pulcher-dalstromii* clade + a strongly supported (99%BS) clade consisting of a weakly supported (66%BS) South American clade of three species of *Stellilabium* with 100%BS support sister to a strongly supported (99%BS) *Telipogon nervosus-vargasii* clade. The Central American clade with 83%BS support consists of a strongly supported (100%BS) clade of four species of Central American *Stellilabium* and the strongly supported (100%BS) clade of six species of Central American *Telipogon*. In this analysis, as in the *trnL-F* analysis, *T. butcheri* was not resolved from the other Central American species of *Telipogon*.

***Ornithocephalus* alliance:** The *Ornithocephalus* alliance (99%BS) consists of a trichotomy of *Phymatidium* + a strongly supported clade (99%BS) of *Zygostates alleniana* + *Dipteranthus grandiflorus* and a strongly supported (98%BS) unresolved clade of *Eloyella*, *Hintonella* and a moderately supported (84%BS) clade of *Ornithocephalus inflexus* + *Sphyrastylis dalstromii*.

Analysis of individual matrices—*atpB-rbcL* intergenic spacer — The individual *atpB-rbcL* intergenic spacer analysis consisted of 1499 included characters, of which 530 were variable and 220 (15%) were potentially phylogenetically informative [CI=0.81 (0.65 with uninformative characters excluded), RI=0.75], and yielded three trees of 761 steps. Figure 4 shows one tree with branch lengths above the lines and bootstrap values below the lines.

***Telipogon* alliance:** The analysis of this intergenic spacer region yielded two clades: a weakly supported (68%BS) *Telipogon* alliance and a moderately supported (88%BS) *Ornithocephalus* alliance. *Hofmeisterella* + *Trichoceros* (98%BS) forms a trichotomy with a weakly supported (81%BS) remaining *Telipogon* + *Stellilabium* clade. This large ingroup has the following groups: a strongly supported (100%BS) *Telipogon pulcher-dalstromii* clade sister to the weakly supported remaining species (56%BS) consisting of a polytomy consisting of a strongly supported (100%BS) South American clade of three species of *Stellilabium* sister to a strongly supported (100%BS) *Telipogon nervosus-*

vargasii clade; a moderately supported (65%BS) Central American clade of four species of *Stellilabium* with *S. bullpenense* sister to a moderately supported (78%BS) clade of the other three species from Central America; and a strongly supported (100%BS) clade of the six Central American species of *Telipogon*. Within the Central American *Telipogon* clade, *T. parvulus* is sister to a moderately supported (82%BS) clade of *T. biolleyi-butcheri-caulescens-seibertii-panamensis*, and within that clade is a weakly supported (70%BS) yet unresolved polytomy of *T. biolleyi-butcheri-caulescens-seibertii*.

Ornithocephalus alliance: This alliance with 88 % bootstrap support consists of a strongly supported (96%BS) *Zygostates alleniana* + *Dipteranthus grandiflorus* sister to a moderately supported (75%BS) clade of *Hintonella* sister to a moderately supported (85%BS) clade of a polytomy of *Eloyella* + *Sphyrastylis dalstromii* and a weakly supported (76%BS) *Ornithocephalus inflexus* + *Phymatidium falcifolium*.

Analysis of the combined plastid matrix of *matK/trnL-F/atpB-rbcL* intergenic spacer — The combined matrix consisted of 4082 characters, of which 1112 were variable and 520 (13%) were potentially parsimony informative. The analysis yielded four trees of 1634 steps [CI=0.79 (0.65 with uninformative characters excluded), RI=0.80]. The combined matrix yielded a tree which most resembles the *matK* only results, but with better resolution and stronger support for several clades. Figure 5 shows one tree with branch lengths above the lines and bootstrap values below the lines.

Telipogon alliance: The *Telipogon* alliance is strongly supported (94%BS) with *Hofmeisterella* + the *Trichoceros* clade (100%BS) sister to the strongly supported (100%BS) remainder of the alliance, which forms two strongly supported clades: a strongly supported (100%BS) *Telipogon ariasii-pulcher-dalstromii* clade, and the strongly supported (100%BS) remainder. The latter clade has two supported clades: a weakly supported clade (59%BS) consisting of the strongly supported (100%BS) South America clade of three species of *Stellilabium* + the strongly supported (100%BS) *Telipogon nervosus-vargasii* clade; and the moderately supported (86%BS) Central American two groups of *Telipogon* (100%BS) and *Stellilabium* (100%BS). Within the Central American *Telipogon* clade, *T. parvulus* is sister to the moderately supported (79%BS) other five species, and within that five species group only *T. panamensis* is resolved. Within the Central American *Stellilabium* clade, *S. bullpenense* is

sister to the strongly supported (96%BS) clade of *S. aciculare* + (*S. barbozae* + *S. monteverdense* 96%BS).

Ornithocephalus alliance: This strongly supported alliance (100%BS) has two major clades: *Zygostates alleniana* + *Dipteranthus grandiflorus* with 100%BS support is sister to a strongly supported (96%BS) clade within which *Phymatidium* is sister to a moderately supported (83%BS) trichotomous clade of *Eloyella* + *Hintonella* + a moderately supported (71%BS) clade of *Ornithocephalus inflexus* + *Sphyrastylis dalstromii*.

Analysis of the combined ITS/plastid data set — The combined nuclear and plastid matrix had 4859 characters, of which 1487 were variable and 821 (17%) were potentially parsimony informative. The analysis yielded 30 trees of 2568 steps [CI=0.71 (0.59 with uninformative characters excluded), RI=0.79]. Figure 6 shows one of the trees obtained.

Telipogon alliance: The strongly supported (98%BS) *Telipogon* alliance consists of *Hofmeisterella* and the *Trichoceros* clade (100%BS) forming a polytomy with the strongly supported (97%BS) remainder of the alliance, which has two major clades: the *Telipogon ariasii-pulcher-dalstromii* clade with 100%BS and the remainder of the alliance with 100%BS. The *Telipogon nervosus-vargasii* clade (100%BS), the clade of three South American species of *Stellilabium* (100%BS) and the strongly supported (94%BS) Central American *Stellilabium* clade (100%BS) + Central American *Telipogon* clade (100%BS) form a trichotomy. The Central American *Stellilabium* clade has *S. bullpenense* sister to a weakly supported (67%BS) three species clade, within which is the strongly supported (100%BS) *S. barbozae-monteverdense* clade. The Central American *Telipogon* clade has *T. butcheri* sister to the strongly supported (96%BS) remaining five unresolved species.

Ornithocephalus alliance: This strongly supported (100%BS) alliance consists of *Phymatidium* sister to a weakly supported (57%BS) clade of the remainder which consists of a strongly supported (100%BS) *Zygostates alleniana* + *Dipteranthus grandiflorus* sister to a strongly supported (100%BS) trichotomy of *Eloyella* + *Hintonella* + a strongly supported (100%BS) clade of *Ornithocephalus inflexus* + *Sphyrastylis dalstromii*.

Bayesian analysis of the combined ITS/plastid data set — Figure 7 is the tree obtained by Bayesian analysis of the combined plastid and ITS data sets. The monophyly of the *Telipogon* and *Ornithocephalus* alliances is supported by 100% posterior probability

of each alliance. Strongly supported clades within the *Telipogon* alliance, as indicated by 100% posterior probability, are: *Trichoceros*; *Telipogon* + *Stellilabium*; the *Telipogon ariasii-pulcher-dalstromii* clade; the *Telipogon nervosus-vargasii* clade; the South American *Stellilabium* clade; the Central American *Stellilabium* clade; and the Central American *Telipogon* clade. The *Ornithocephalus* alliance shows 100% posterior probability support for *Ornithocephalus inflexus* + *Sphyrastylis dalstromii* as well as for *Eloyella* + *Hintonella* + *Ornithocephalus* + *Sphyrastylis* and for *Zygostates alleniana* + *Dipteranthus grandiflorus*.

Expanded ITS analysis of 81 taxa in *Telipogon*, *Ornithocephalus*, *Pachyphyllum* alliances — The ITS only matrix had 682 characters, of which 414 were variable and 352 (52%) were potentially parsimony informative. The analysis yielded 251 trees of 1333 steps [CI=0.49 (0.46 with uninformative characters excluded), RI=0.89]. Figure 8 shows one tree with bootstrap values and branch lengths. This expanded ITS analysis includes an additional eleven species of the *Ornithocephalus* alliance and allows us to place *Hofmeisterella* with the *Telipogon* alliance and not with the *Ornithocephalus* alliance with more confidence. The bootstrap analysis, with *Lockhartia* as the outgroup, shows a strongly supported (100%BS) group of three clades: the strongly supported (96%BS) *Ornithocephalus* alliance; the strongly supported (100%BS) *Pachyphyllum* alliance; and the moderately supported (78%BS) *Telipogon* alliance. The *Telipogon* alliance has three parts: 1) a strongly supported (100%BS) *Trichoceros* clade; 2) a moderately supported (90%BS) *Telipogon* clade of South American species; and 3) a moderately supported (78%BS) clade of *Hofmeisterella* sister to a strongly supported (100%BS) clade comprised of *Stellilabium* and the remaining species of *Telipogon*.

The first clade, *Trichoceros*, is still under study and will not be discussed further at this time. The second clade, the *Telipogon venustus-T. ariasii* group, is strictly South American. Two accessions of *T. venustus* are sister to polytomy of *T. valenciae* and the *T. ariasii-T. falcatus* clade. Within this latter clade (with 86%BS), *T. falcatus* is sister to a strongly supported clade (100%BS) of eight species. *Telipogon ariasii-T. frymirei* have 91 %BS and *T. chrysocrates-T. andicola* have 87%BS.

This third clade consists of a strongly supported (100%BS) South American clade of *Telipogon klotzscheanus-nervosus-vargasii* sister to a clade with moderate support (74%BS) consisting of a strongly

supported (100%BS) South American *Stellilabium* clade and a moderately supported (84%BS) clade of two Central American groups: a strongly supported (100%BS) clade of *Stellilabium* species and a strongly supported (98%BS) clade of *Telipogon* species. The Central American *Stellilabium* clade of six species consists of a strongly supported clade (100%BS) of *S. aciculare*, *S. smaragdinum*, and a species from the Dominican Republic (*Stellilabium* sp. n660, recently described by Ackerman, 2004, as a new species of *Telipogon*) sister to a weakly supported (63%BS) clade of (*S. barbozae* + *monteverdense* 100%BS) + *S. bullpenense*. The Central American *Telipogon* clade consists of *T. butcheri* sister to a strongly supported (100%BS) clade of the remaining 18 species of *Telipogon*. Within the large clade of 18 species, the only groups resolved are the following: two accessions of *T. parvulus* with 99%BS; *T. griesbeckii* (two accessions) + *T. olmosii* with 58%BS; and a six species group with 64%BS which includes a weakly supported (63%BS) two species clade of *T. panamensis* and *T. personatus*.

***Ornithocephalus* alliance:** This expanded ITS analysis of the *Ornithocephalus* alliance with 96%BS support has two accessions of *Phymatidium falcifolium* sister to a moderately supported (90%BS) remainder of the alliance. This group includes a strongly supported (100%BS) clade of *Eloyella*, *Hintonella*, and *Chytroglossa* sister to a strongly supported (100%BS) clade of *Ornithocephalus* and *Sphyrastylis* species. This latter clade has *Sphyrastylis* embedded within *Ornithocephalus*. The second major clade in this alliance is the strongly supported (99%BS) *Zygostates* + *Dipteranthus* clade. Within this clade, *D. pellucidus* is sister to a clade with 70%BS of *D. grandiflorus* sister to a strongly supported (100%BS) *D. obliquus* + *Z. lunata* + *Z. alleniana* clade.

DISCUSSION

Molecular analyses — An analysis of 634 species in the Oncidiinae for ITS and 252 species for ITS/*matK*/*trnL-F* (Williams *et al.* 2001a,b, Williams & Whitten 2003, and unpublished) established that the *Telipogon* – *Pachyphyllum* – *Ornithocephalus* – *Lockhartia* alliances are sister groups embedded within the Oncidiinae. These earlier works and data reported here establish that *Hofmeisterella* is a part of the *Telipogon* alliance.

Taxonomic implications in the *Telipogon* alliance — Garay and Romero (1998) reinstated the genus *Dipterostele* Schltr. for a number of species of *Stellilabium*. We sampled one of those species, *S.*

hystrix, which Dressler (1999) places in *Stellilabium* sect. *Dipterosteles*. The molecular data (100% bootstrap support for four genes, 100% posterior probability from Bayesian analysis) place *S. hystrix* as sister to a clade with *Stellilabium pogonostalis*, a species Dressler places in *Stellilabium* sect. *Stellilabium* and which Garay and Romero do not place in *Dipterosteles*. Furthermore, the large analysis of ITS places *S. hystrix* within a clade containing *S. boliviense* and *S. pogonostalis* (Fig. 8) and five Ecuadorian species, which shows that *Stellilabium* section *Dipterosteles* is not monophyletic. Dressler (1999) discusses a number of characters that distinguish these two sections of *Stellilabium*, and if *Dipterosteles* were recognized, then the South American species of *Stellilabium* would have to be placed in at least three distinct genera. *Stellilabium* is not monophyletic (Figs. 1-8) and is embedded within *Telipogon*. Unless *Telipogon* is broken into three genera and *Stellilabium* into at least two genera representing the Central American clade and the South American clade (many more if *Dipterosteles* is recognized), there is no way to have a monophyletic group without merging all of these groups into *Telipogon*. Dressler's *Stellilabium* sect. *Taeniorhachis* is not monophyletic and has *Stellilabium* sect. *Rhamphosteles* embedded within it. At this time, more taxa are needed to resolve relationships of species usually placed in *Stellilabium*, but the "Stellilabium habit," which is essentially small flowers and a tendency to leaflessness at maturity, has arisen at least twice, once in South America and once in Central America, possibly from two different groups of *Telipogon*.

Braas and Lückel (1982) based their genus *Darwiniella* on *Trichoceros bergoldii* Garay & Dunst. (Dunsterville & Garay 1972), and Dressler (1999) states that it "is surely a robust member of this group", referring to *Stellilabium* sect. *Stellilabium*. Material of this species has not been available, but Dodson (2004) considers *Darwiniella* a synonym of *Stellilabium*.

The species listed as *Stellilabium* sp. D. Dod 168 from the Dominican Republic in the 81 OTU ITS analysis was initially identified as *S. minutiflorum* (Kraenzl.) Garay, but Ackerman has concluded that it is a new species and has named it *Telipogon niri* Ackerman in a separate publication (Ackerman 2004). This is the only species of the *Telipogon* alliance known from the Caribbean area.

Telipogon consists of three groups: 1) a Central American clade from Panama and Costa Rica; 2) one South American clade of *Telipogon klotzschianus-nervosus-vargasii*; and 3) a second South American clade of *T. venustus* and the *T. ariasii*-va-

lenciae complex. The combined plastid/ITS analysis places *Hofmeisterella* sister to all of the combined *Telipogon* + *Stellilabium* clades, with *Trichoceros* sister to this group (Fig. 6). If *Stellilabium* is combined with *Telipogon*, *Hofmeisterella* must also be placed in *Telipogon*. Although *Trichoceros* is vegetatively distinct from the other members of the *Telipogon* alliance, the flowers are an extreme manifestation of the pseudocopulation / mimicry pollination complex of characters. We prefer to maintain it as a separate genus because of the distinctive vegetative morphology and easily recognized field characters, such as the distinctive gray-green sheen of the succulent leaves, the distinct pseudobulbs, and the rambling, vine-like habit.

At this time we make formal transfers below of species of *Stellilabium* to *Telipogon*. Ackerman has already made one such combination in naming *Telipogon niri* Ackerman in a separate publication (Ackerman 2004) for a species from the Dominican Republic shown in Fig. 8 as *Stellilabium* sp. D. Dod 168. In essence, most of the species of *Stellilabium* are just small versions of *Telipogon* that often become leafless at maturity.

Nomenclatural Changes

Telipogon acicularis (Dressler) N.H. Williams & Dressler, *comb. nov.*

Basionym: *Stellilabium aciculare* Dressler, Harvard Pap. Bot. 4(2): 471-472, f. 1E-F. 1999.

Telipogon alticola (Dodson & R. Escobar) N.H. Williams & Dressler, *comb. nov.*

Basionym: *Stellilabium alticolum* Dodson & R. Escobar, Orquideología 20(1): 48. 1998.

Telipogon anacristinae (Pupulin) N.H. Williams & Dressler, *comb. nov.*

Basionym: *Stellilabium anacristinae* Pupulin, Harvard Pap. Bot. 8(1): 30, f. 1A-G. 2003.

Telipogon andinus (L.O. Williams) N.H. Williams & Dressler, *comb. nov.*

Stellilabium andinum (L.O. Williams) Garay & Dunst., Orchids Venezuela: 1004. 1979.

Basionym: *Cordanthera andina* L.O. Williams, Lilloa 6: 244. 1941.

Telipogon astroglossus Rchb. f., Xenia Orchid. 1: 16, t. 7, f. II, 12-19. 1854.

= *Stellilabium astroglossum* (Rchb. f.) Schltr., Die Orchideen 530. 1914.

The epithet *atropurpurea* is occupied in *Telipogon* by *Telipogon atropurpurea* D.E. Benn. & Ric. Fernández, Publ. Mus. Hist. Nat. Univ. Nacion. Mayor San Marcos, Bot. 36: 9 (1992), and/or by *Telipogon atropurpurea* D.E. Benn. & Ric. Fernández, Orquideophilo 5: 27 (1997). Either way, a new name is needed for the species known as *Stellilabium atropurpureum* P. Ortiz, Orquideologia 23(1): 24 (31), (2004), and we publish here the following name for this species:

Telipogon ortizii* N.H. Williams & Dressler, *nom. nov.

The epithet honors Pedro Ortiz, who named the species originally.

Telipogon barbozae* (J.T. Atwood & Dressler) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium barbozae* J.T. Atwood & Dressler, Selbyana 16(2): 239, f. 1. 1995.

Telipogon bennettii* (Dodson & R. Escobar) N.H. Williams & Dressler, *comb. nov.

Stellilabium bennettii (Dodson & R. Escobar) Christenson, Icon. Orchid. Peruvianum pl. 773. 2001.

Basionym: *Trichoceros bennettii* Dodson & R. Escobar, Icon. Pl. Trop. II (2): t. 195. 1989.

Telipogon bergoldii* (Garay & Dunst.) N.H. Williams & Dressler, *comb. nov.

Stellilabium bergoldii (Garay & Dunst.) Carnevali & G.A. Romero, in G.A. Romero & G. Carnevali, Orchids Venezuela, ed. 2: 1147. 2000.

Darwiniella bergoldii (Garay & Dunst.) Braas & Lückel, Die Orchidee 33(5): 169. 1982, *nom. illeg.*

Darwiniera bergoldii (Garay & Dunst.) Braas & Lückel, Die Orchidee 33 (6): 212. 1982.

Basionym: *Trichoceros bergoldii* Garay & Dunst., Venez. Orchids Ill. 5: 310. 1972.

Telipogon boliviensis* (R. Vásquez & Dodson) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium boliviense* R. Vásquez & Dodson, Icon. Pl. Trop. 6: t. 592. 1982.

Telipogon boylei* (J.T. Atwood) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium boylei* J.T. Atwood, Icon. Pl. Trop. 14: t. 1392. 1989.

Dipterostele boylei (J.T. Atwood) Garay & G.A.

Romero, Harvard Pap. Bot. 3: 57. 1998.

Telipogon bullpenensis* (J.T. Atwood) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium bullpenense* J.T. Atwood, Icon. Pl. Trop. 14: t. 1393. 1989.

The epithet *butcheri* is occupied in *Telipogon* by *Telipogon butcheri* Dodson & R. Escobar, Orquideologia 18: 278 (1993) and the species known as *Stellilabium butcheri* Dressler, Harvard Pap. Bot. 4(2): 472-473, f. 1G (1999) needs a new name. *Telipogon chiriquensis* is already taken and *T. panamensis* is taken. We publish here the following name for the species known as *Stellilabium butcheri* Dressler:

Telipogon butchii* N.H. Williams & Dressler, *nom. nov.

The specific epithet refers to the affectionate nickname used by everyone who knew Henry Butcher.

Telipogon campbelliorum* (J.T. Atwood) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium campbelliorum* J.T. Atwood, Icon. Pl. Trop. 14: t. 1394. 1989.

Telipogon distantiflorus* (Ames & C. Schweinf.) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium distantiflorum* Ames & C. Schweinf., Sched. Orchid. 8: 70. 1925.

Dipterostele distantiflorum (Ames & C. Schweinf.) Garay & G.A. Romero, Harvard Pap. Bot. 3: 57. 1998.

Telipogon erratus* (Dressler) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium erratum* Dressler, Lankesteriana: 2: 11-13, f. 1. 2001.

Telipogon fortuneae* (Dressler) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium fortuneae* Dressler, Harvard Pap. Bot. 4(2): 473, f. 1B-D. 1999.

The epithet *frymirei* is occupied in *Telipogon* by *Telipogon frymirei* Dodson, Icon. Pl. Trop. 10: t. 991 (1984), and the species known as *Stellilabium frymirei* Dodson, Icon. Pl. Trop. 5: t. 495 (1982) needs a new name. We publish here the following name for this species:

Telipogon embreei* N.H. Williams & Dressler, *nom. nov.

The epithet honors the late Alvin Embree, who accompanied us on many field trips, found numerous new species of orchids, and was present at the collection of the type specimen of this species.

Dipterosteale frymirei (Dodson) Garay & G.A. Romero, Harvard Pap. Bot. 3: 57. 1998.

Telipogon helleri* (L.O. Williams) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium helleri* L.O. Williams, Brittonia 14: 443. 1962.

Dipterosteale helleri (L.O. Williams) Garay & G.A. Romero, Harvard Pap. Bot. 3: 57. 1998.

The epithet *hirtzii* is occupied in *Telipogon* by *Telipogon hirtzii* Dodson & R. Escobar, Icon. Pl. Trop. II (6): t. 590 (1989) and the species known as *Stellilabium hirtzii* Dodson, Icon. Pl. Trop. 10: pl. 982 (1984) needs a new name. We publish here the following name for this species:

Telipogon alexii* N.H. Williams & Dressler, *nom. nov.

The epithet honors the same person.

Telipogon hystrix* (Dodson) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium hystrix* Dodson, Icon. Pl. Trop. 5: t. 496. 1982.

Dipterosteale hystrix (Dodson) Garay & G.A. Romero, Harvard Pap. Bot. 3: 57. 1998.

Telipogon ibischii* (R. Vásquez) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium ibischii* R. Vásquez, Lindleyana 13(2): 61. 1998.

Telipogon jostii* (Dodson) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium jostii* Dodson, Nat. Ecuad. Orch. 5: 1180. 2004.

Telipogon lankesteri Ames, Sched. Orchid. 3: 23. 1923.

Stellilabium lankesteri (Ames) Dressler, Novon 7(2): 124. 1997.

Dipterosteale lankesteri (Ames) Garay & G.A. Romero, Harvard Pap. Bot. 3: 57. 1998.

The epithet *lueri* is occupied in *Telipogon* by

Telipogon lueri Dodson & D.E. Benn., Icon. Pl. Trop. II(2): t. 190 (1989), and the species known as *Stellilabium lueri* Dodson & R. Vásquez, Icon. Pl. Trop. II(4): t. 381 (1989) needs a new name. We publish here the following name for this species:

Telipogon calueri* N.H. Williams & Dressler, *nom. nov.

The epithet refers to the first two initials of the name of the same person, Carl A. Luer.

Dipterosteale lueri (Dodson & R. Vásquez) Garay & G.A. Romero, Harvard Pap. Bot. 3: 57. 1998.

Telipogon microglossus* (Schltr.) N.H. Williams & Dressler, *comb. nov.

Stellilabium microglossum (Schltr.) Dodson, Icon. Pl. Trop. 4: pl. 334. 1980.

Basionym: *Dipterosteale microglossa* Schltr., Repert. Spec. Nov. Regni Veg. 8: 106. 1921.

Telipogon minutiflorus Kraenzl, Ann. Naturhist. Hofmus. 33: 14. 1920.

Stellilabium minutiflorum (Kraenzl.) Garay, J. Arnold Arbor. 50: 446. 1969.

Dipterosteale minutiflora (Kraenzl.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 70. 1923.

Telipogon monteverdensis* (J.T. Atwood) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium monteverdense* J.T. Atwood, Icon. Pl. Trop. 14: t. 1395. 1989.

Telipogon morganiae* (Dodson) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium morganiae* Dodson, Icon. Pl. Trop. 1: t. 335. 1980.

Dipterosteale morganiae (Dodson) Braas & Lückel, Die Orchidee 33: 175. 1982.

Telipogon morii* (Dressler) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium morii* Dressler, Harvard Pap. Bot. 4(2): 473, fig. 1H. 1999.

Telipogon pampatamboensis* (Dodson & R. Vásquez) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium pampatamboense* Dodson & R. Vásquez, Icon. Pl. Trop. II(4): t. 382. 1989.

Telipogon perlobatus* (Senghas) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium perlobatum* Senghas, J.

Orchideenfreund 1: 172. 1994.

The species known as *Stellilabium peruvianum* D.E. Benn. & Christenson, Lindleyana 13(2): 86-88, f. 30 (1998) needs a new name, as the epithet is used in *Telipogon* already by *Telipogon peruvianus* T. Hashim., Bull. Natl. Sci. Mus., Tokyo, B 16: 21 (1990). We publish here the following name for the species known as *Stellilabium peruvianum* D.E. Benn. & Christenson:

Telipogon selbyanus* N.H. Williams & Dressler, *nom. nov.

The epithet honors the Marie Selby Botanical Gardens, an organization which has promoted the scientific study of orchids for three decades.

Telipogon pogonostalix Rchb.f., *Linnaea* 41: 72. 1876.
Stellilabium pogonostalix (Rchb. f.) Garay & Dunst., Venez. Orchids III. 2: 336. 1961.
Sodirolella ecuadorensis Schltr., Repert. Spec. Nov. Regni Veg. Beih. 8: 108. 1921, is a synonym according to Dodson (1998: 50-51).

Telipogon pseudobulbosus* (D.E. Benn. & Christenson) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium pseudobulbosum* D.E. Benn. & Christenson, Lindleyana 13(2): 88, f. 31. 1998.

Telipogon smaragdinus* (Pupulin & M.A. Blanco) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium smaragdinum* Pupulin & M.A. Blanco, Lankesteriana 5: 28-30. 2002.

Telipogon standleyi Ames, Sched. Orch. 9: 53, f. 9. 1925.

Stellilabium standleyi (Ames) L.O. Williams, Brittonia 14: 46. 1962.

Dipterostele standleyi (Ames) Garay & G.A. Romero, Harvard Pap. Bot. 3: 58. 1998.

Telipogon tanii* (Dodson) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium tanii* Dodson, Icon. Pl. Trop. 1: t. 337. 1980.

Possibly = *Stellilabium astroglossum* (Rchb.f.) Schltr., Orchideen: 530. 1914, *vide* Kew Monocot List

Dipterostele tanii (Dodson) Garay & G.A. Romero, Harvard Pap. Bot. 3: 58. 1998.

Telipogon tsipiriensis* (Pupulin) N.H. Williams & Dressler, *comb. nov.

Basionym: *Stellilabium tsipiriense* Pupulin, Harvard

Pap. Bot. 8(1): 30, f. 2A-H, L. 2003.

The epithet *vasquezii* is occupied in *Telipogon* by *Telipogon vasquezii* Dodson, Selbyana 7: 358 (1984), and the species known as *Stellilabium vasquezii* Dodson, Icon. Pl. Trop. 6: t. 593 (1982) needs a new name. There is already (or will be, see above) a *Telipogon boliviensis*, so we publish here the following name for the species known as *Stellilabium vasquezii* Dodson:

Telipogon roberti* N.H. Williams & Dressler, *nom. nov.

The epithet honors the same person, but refers to his first name, Roberto, latinized as Robertus (Genitive *Roberti*).

Dipterostele vasquezii (Dodson) Garay & G.A. Romero, Harvard Pap. Bot. 3: 58. 1998.

Non Telipogon vasquezii Christenson, Icon. Orchid. Peruv.: t. 784. 2001, *nom. illeg.*

The epithet *vulcanicum* is occupied in *Telipogon* by *Telipogon vulcanicum* Dodson & Hirtz, Nat. Ecuad. Orch. 5: 1186 (2004), thus the species known as *Stellilabium vulcanicum* Dodson & Hirtz, Nat. Ecuad. Orch. 5: 1181 (2004) needs a new name. We publish here the following name for this species:

Telipogon reventadorensis* N.H. Williams & Dressler, *nom. nov.

The epithet refers to the location (Volcán Reventador, Ecuador) where the type was collected.

The work reported here definitely establishes that *Hofmeisterella* is not associated with members of the *Ornithocephalus* alliance as Szlachetko (1995) suggested, but rather is firmly associated with the *Telipogon* alliance in the Oncidiinae. Reichenbach originally placed this species in his genus *Hofmeistera* (*De Pollinis Orchidearum* 30. 1852), but later in the same year apparently decided that this name was too close to *Hofmeisteria* Walp. [published in: *Repertorium Botanices Systematicae* 6: 106. 1846 (“1847”) as a member of the Asteraceae], and renamed it *Hofmeisterella*.

The current work (as well as previous work, Whitten *et al.* 2000, Williams *et al.* 2001 a, b, Whitten *et al.* 2005) shows that the *Fernandezia* / *Pachyphyllum* group is associated with these alliances, rather than with *Dichaea* as Szlachetko (1995) suggested. *Fernandezia* and *Pachyphyllum* form a clade with 100%BS in the 81

taxon ITS analysis. A more comprehensive study of the *Fernandezia / Pachyphyllum* group is underway.

Taxonomic implications in the *Ornithocephalus* alliance — Toscano de Brito and Dressler (2000) transferred all species of *Sphyrastylis* to *Ornithocephalus* based on morphological studies, and studies of pollinarium morphology and leaf anatomy also supported this transfer (Toscano de Brito 1994, 1998). The molecular data presented here (Fig. 8) confirm this decision. In the ITS trees *Zygostates* is nested within *Dipteranthus*, but until we have a more comprehensive study of the *Ornithocephalus* alliance we refrain from making these nomenclatural changes.

Biogeographic implications — The Central American *Telipogon* clade (Fig. 8) has very little sequence divergence for ITS, and only moderate sequence divergence for the combined plastid regions. The *Stellilabium* component of this clade has more ITS divergence among species than the *Telipogon* component. The lack of sequence divergence in the *Telipogon* component suggests rapid evolution of this group from a South American introduction.

ACKNOWLEDGMENTS. We thank Mario Blanco, Stig Dalström, Ron Determann, Calaway H. Dodson, Lorena Endara, Günter Gerlach, Cordelia Head, Andres Maduro, Erich Michel, José Portilla, Franco Pupulin, Gustavo Romero, and Jorge Warner for plant specimens and access to collections. We thank Wendy Zomlefer for many constructive comments on the manuscript. This work was supported by NSF grants DEB 9815821 to NHW and DEB 9509071 to WMW, by grants from the American Orchid Society Fund for Education and Research, and the Florida Museum of Natural History.

LITERATURE CITED

- Ackerman, J.D. 2004. Notes on the Caribbean orchid flora. V. New species, combinations and records. *Lankesteriana* 4: 47-56.
- Braas, L.A. & E. Lückel. 1982. *Darwiniella*, eine neue Gattung der Subtribus Telipogoninae Schltr. *Die Orchidee* 33: 167-176.
- Chiang, T.Y., B.A. Schaal & C.I. Peng. 1998. Universal primers for amplification and sequencing a noncoding spacer between the *atpB* and *rbcL* genes of chloroplast DNA. *Bot. Bull. Acad. Sin.* 39: 245-250.
- Dodson, C.H. 1998. New orchid species and combinations from Ecuador-Fascicle 6. *Orquideología* 21: 3-60.
- Dodson, C.H. 2004. Native Ecuadorian Orchids 5: 1014.
- Dressler, R.L. 1993. *Phylogeny and Classification of the Orchid Family*. Dioscorides Press. Portland, OR. 314 p.
- Dressler, R.L. 1999. A reconsideration of *Stellilabium* and *Dipterosteale*. *Harvard Pap. Bot.* 4: 469-473.
- Dunsterville, G.C.K. & L.A. Garay. 1972. Venezuelan Orchids Illustrated 5: 310.
- Fitch, W.M. 1971. Toward defining the course of evolution: minimal change for a specific tree topology. *Syst. Zool.* 20: 406-416.
- Garay, L.A. & G.A. Romero-González. 1998. *Schedulae Orchidum*. *Harvard Pap. Bot.* 3: 53-62.
- Huelsenbeck, J.P. & F. Ronquist. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754-755.
- Sun, Y., D.Z. Skinner, G.H. Liang & S.H. Hulbert. 1994. Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. *Theor. Appl. Genet.* 89: 26-32.
- Swofford, D.L. 2000. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b2. Sinauer Assoc., Sunderland, Mass.
- Szlachetko, D.L. 1995. *Systema Orchidialium*. *Fragm. Flor. Geobot. Suppl.* 3: 1-152.
- Taberlet, P., L. Gielly, G. Pautou & J. Bouvet. 1991. Universal primers of amplification of three non-coding regions of chloroplast DNA. *Pl. Mol. Biol.* 17: 1105-1109.
- Toscano de Brito, A.L.V. 1994. Systematic studies in the subtribe Ornithocephalinae (Orchidaceae). Ph. D. thesis, University of Reading, Reading, England.
- Toscano de Brito, A.L.V. 1998. Leaf anatomy of Ornithocephalinae (Orchidaceae) and related subtribes. *Lindleyana* 13: 234-258.
- Toscano de Brito, A.L.V. & R.L. Dressler. 2000. New combinations in *Ornithocephalus* (Ornithocephalinae: Orchidaceae) and description of a new species from Mesoamerica. *Lindleyana* 15: 252-256.
- Whitten, W.M., N.H. Williams & M.W. Chase. 2000. Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. *Amer. J. Bot.* 87: 1842-1856.
- Whitten, W.M., N.H. Williams, R.L. Dressler, G. Gerlach & F. Pupulin. 2005. Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana* 5: 87-108.

- Williams, N.H., M.W. Chase, T. Fulcher & W.M. Whitten. 2001a. Molecular systematics of the Oncidiinae based on evidence from four DNA sequence regions: expanded circumscriptions of *Cyrtochilum*, *Erycina*, *Otoglossum*, and *Trichocentrum* and a new genus (Orchidaceae). *Lindleyana* 16: 113-139.
- Williams, N.H., M.W. Chase & W.M. Whitten. 2001b. Phylogenetic position of *Miltoniopsis*, *Caucaea*, a new genus, *Cyrtochiloides*, and relationship of *Oncidium phymatochilum* based on nuclear and chloroplast DNA sequence data (Orchidaceae: Oncidiinae). *Lindleyana* 16: 272-285.
- Williams, N.H. & W.M. Whitten. 2003. Molecular phylogenetics and generic concepts in the Maxillarieae (Orchidaceae). *Lankesteriana* 7: 61-62.

Table 1. Vouchers and GenBank accessions.

Table 1. Vouchers and GenBank accessions.						
Taxon	Voucher	Herb.	ITS	<i>trnL-F</i>	<i>matK</i>	<i>atpB-rbcL</i> spacer
<i>Chytroglossa marileoniae</i> Rchb.f.	Whitten 2949	FLAS	DQ315817			
<i>Dipteranthus grandiflorus</i> (Lindl.) Pabst	Chase 103	K	AF350508	AF350666	AF350587	
<i>Dipteranthus obliquus</i> (Schnee) Garay & Dunst.	Gerlach 93/3251	FLAS	DQ315818			
<i>Dipteranthus pellucidus</i> (Rchb.f.) Cogn.	Whitten 2792	FLAS	DQ315819			
<i>Eloyella thienii</i> Dodson	Whitten 1833	FLAS	DQ315820	DQ315916	DQ315888	DQ315792
<i>Fernandezia ionanthera</i> (Rchb.f. & Warsz.) Schltr.	Whitten 97069	FLAS	AF239390	AF239582	AF239486	
<i>Fernandezia</i> sp.	Chase 89096	K	AF350506	AF350664	AF350585	
<i>Fernandezia tica</i> Mora-Ret. & J.B. García	Maduro 240	MO	DQ315821	DQ315917	DQ315889	DQ315793
<i>Hintonella mexicana</i> Ames	Williams s.n.	FLAS	DQ315822	DQ315918	DQ315890	DQ315794
<i>Hofmeisterella eumicroscopica</i> (Rchb.f.) Rchb.f. #1	Chase 112	K	AF350510	DQ315919	AF350589	
<i>Hofmeisterella eumicroscopica</i> (Rchb.f.) Rchb.f. #2	Whitten 2690	FLAS	DQ315823			
<i>Lockhartia amoena</i> Endres & Rchb.f.	Chase 84101	K	AF350515	AF350673	AF350594	
<i>Lockhartia oerstedii</i> Rchb.f.	Whitten s.n.	FLAS	AF350514	AF350672	AF350593	
<i>Ornithocephalus grexanserinus</i> Dressler & Mora-Ret.	UF98009	FLAS	DQ315824			
<i>Ornithocephalus inflexus</i> Lindl.	Blanco 2645	USJ	AF350507	AF350665	DQ315891	
<i>Ornithocephalus iridifolius</i> Rchb.f.	Gerlach 93/904	M	DQ315825			
<i>Ornithocephalus kruegeri</i> Rchb.f.	Gerlach 93/3569	M	DQ315826			
<i>Ornithocephalus myrticola</i> Lindl.	Gerlach 92/3881	M	DQ315827			
<i>Pachyphyllum</i> sp.	Chase 87105	K	DQ315828			
<i>Pachyphyllum</i> sp.	Whitten 2313	FLAS	DQ315829			

<i>Pachyphyllum</i> sp.	Whitten 2453	FLAS	DQ315830			
<i>Pachyphyllum</i> sp.	Whitten 1614	FLAS	DQ315832	DQ315920	DQ315892	DQ315795
<i>Pachyphyllum</i> sp.	Whitten 1703	FLAS	DQ315833			
<i>Pachyphyllum cuencae</i> Rehb.f.	Whitten 2537	FLAS	DQ315831			
<i>Phymatidium falcifolium</i> Lindl.	Whitten 1831	FLAS	DQ315834		DQ315893	DQ315796
<i>Sphyrastylis dalstromii</i> Dodson	Williams s.n.	FLAS	DQ315835	DQ315921	DQ315894	DQ315797
<i>Sphyrastylis escobariana</i> Garay	Whitten 2693	FLAS	AF350509	AF350667	AF350588	DQ315
<i>Sphyrastylis</i> sp.	Dalstrom 2355	SEL	DQ315836			
<i>Stellilabium aciculare</i> Dressler	Dressler 3617	MO	DQ315837	DQ315922	DQ315896	DQ315798
<i>Stellilabium barbozae</i> Atwood & Dressler	Pupulin 4710	USJ	DQ315838	DQ315923	DQ315897	DQ315799
<i>Stellilabium boliviense</i> R.Vásquez & Dodson	Dalstrom 2397	SEL	DQ315839			
<i>Stellilabium bullpenense</i> Atwood	Pupulin 4729	USJ	DQ315840	DQ315924	DQ315898	DQ315800
<i>Stellilabium hystrix</i> Dodson	Whitten 1824	FLAS	DQ315841	DQ315925	DQ315899	DQ315801
<i>Stellilabium monteverdense</i> Atwood	Pupulin 4731	USJ	DQ315842	DQ315926	DQ315900	DQ315802
<i>Stellilabium pogonostalix</i> (Rehb.f.) Garay & Dunst.	Chase 123	K	AF350511	AF350669	DQ315901	
<i>Stellilabium smaragdinum</i> Pupulin & M.A. Blanco	Whitten 2155	FLAS	DQ315844			
<i>Stellilabium</i> sp. = <i>Telipogon niri</i> Ackerman	D. Dod 168	NY	DQ315843			
<i>Stellilabium</i> sp.	Whitten 2530	FLAS	DQ315845			
<i>Stellilabium</i> sp.	Whitten 2531	FLAS	DQ315846			
<i>Stellilabium</i> sp.	Whitten 2532	FLAS	DQ315847			
<i>Stellilabium</i> sp.	Whitten 2533	FLAS	DQ315848			
<i>Stellilabium</i> sp.	Hirtz 7103	QCNE	DQ315849	DQ315927	DQ315895	DQ315803
<i>Telipogon ampliflorus</i> C. Schweinf.	Maduro 253	FLAS	DQ315850			
<i>Telipogon andicola</i> Rehb.f.	Escobar 3603	FLAS	DQ315851			
<i>Telipogon ariasii</i> Dodson & D.E. Benn.	Maduro 235	FLAS	DQ315852	DQ315928	DQ315902	
<i>Telipogon biolleyi</i> Schltr.	Maduro 242	FLAS	DQ315853	DQ315929	DQ315903	
<i>Telipogon bombiformis</i> Dressler	Maduro 138	FLAS	DQ315854			
<i>Telipogon butcheri</i> Dodson & R. Escobar	Maduro 208	FLAS	DQ315855	DQ315930	DQ315904	DQ315805
<i>Telipogon caulescens</i> Dressler #1	Maduro 168	MO	DQ315856	DQ315931	DQ315905	DQ315806

<i>Telipogon caulescens</i> Dressler #2	Gerlach 02/3089	M	DQ315857			
<i>Telipogon chiriquensis</i> Dodson & R. Escobar	Maduro 192	FLAS	DQ315858			
<i>Telipogon chrysocrates</i> Rchb.f.	Escobar 2673	FLAS	DQ315859			
<i>Telipogon costaricensis</i> Schltr.	photo	FLAS	DQ315860			
<i>Telipogon dalstromii</i> Dodson	Maduro 233	FLAS	DQ315861	DQ315932	DQ315906	DQ315807
<i>Telipogon falcatus</i> Linden & Rchb.f.	Escobar 3353	FLAS	DQ315862			
<i>Telipogon frymirei</i> Dodson	Dodson 17390	FLAS	DQ315863			
<i>Telipogon griesbeckii</i> Dressler #1	Maduro 169	MO	DQ315864			
<i>Telipogon griesbeckii</i> Dressler #2	Maduro 169	FLAS	DQ315865			
<i>Telipogon klotzscheanus</i> Rchb.f.	Gerlach 95/3136	FLAS	DQ315866			
<i>Telipogon maduroi</i> Dressler	Maduro 190	MO	DQ315867			
<i>Telipogon medusae</i> Dressler	Maduro 209	MO	DQ315868			
<i>Telipogon monticola</i> L.O. Williams	Maduro 241	MO	DQ315869			
<i>Telipogon nervosus</i> (L.) Druce	Gerlach 94/3958	M	DQ315870	DQ315933	DQ315907	DQ315808
<i>Telipogon olmosii</i> Dressler	Maduro 213	MO	DQ315871		DQ315	DQ315
<i>Telipogon panamensis</i> Dodson & R. Escobar	Maduro 194	MO	DQ315872	DQ315934	DQ315908	DQ315809
<i>Telipogon parvulus</i> C. Schweinf. #1	Williams s.n.	FLAS	DQ315873	DQ315935	DQ315909	DQ315810
<i>Telipogon parvulus</i> C. Schweinf. #2	Maduro 193	PMA	AF350513	AF350671	AF350592	
<i>Telipogon personatus</i> Dressler	Maduro 214	PMA	DQ315874			
<i>Telipogon pulcher</i> Rchb.f.	Gerlach 97-3608	M	DQ315875	DQ315936	DQ315910	DQ315811
<i>Telipogon seibertii</i> Dodson & R. Escobar	Maduro 191	PMA	DQ315876	DQ315937	DQ315911	DQ315812
<i>Telipogon</i> sp.	Whitten 2412	FLAS	DQ315877			
<i>Telipogon</i> sp.	Whitten 2413	FLAS	DQ315878			
<i>Telipogon valenciae</i> Dodson & R. Escobar	Escobar 4015	FLAS	DQ315879			
<i>Telipogon vargasii</i> C. Schweinf.	Gerlach 95/2450	M	DQ315880	DQ315938	DQ315912	DQ315813
<i>Telipogon venustus</i> Schltr. #1	Hirtz <i>et al.</i> 2302	FLAS	DQ315881			
<i>Telipogon venustus</i> Schltr. #2	Gerlach 03/1489	M	DQ315882			
<i>Trichoceros antennifer</i> (Humb. & Bonpl.) Kunth	Whitten 1803	FLAS	DQ315883			
<i>Trichoceros muralis</i> Lindl.	No voucher		DQ315884	DQ315940	DQ315914	DQ315814

<i>Trichoceros parviflorus</i> Kunth	Chase 138	K	AF350512	AF350670	AF350591	DQ315
<i>Trichoceros</i> sp.	Whitten 2353	FLAS	DQ315885	DQ315939	DQ315913	DQ315815
<i>Zygostates alleniana</i> Kraenzl.	Gerlach 95/2428	M	DQ315886	DQ315941	DQ315915	DQ315816
<i>Zygostates lunata</i> Lindl.	Gerlach 92/3883	M	DQ315887			

Table 2. Primers used in this study.

Region	Primer name	Sequence	Reference
ITS forward	17 SE	acgaattcatggtccgggtaagtgttcg	Sun <i>et al.</i> (1994)
ITS reverse	26 SE	tagaattccccggttcgctcgccgttac	Sun <i>et al.</i> (1994)
<i>trnL-F</i> forward	C	cgaaatcggttagacgctacg	Taberlet <i>et al.</i> (1991)
<i>trnL-F</i> reverse	F	attggaactggtgacacgag	Taberlet <i>et al.</i> (1991)
<i>matK</i> forward	56F	acttctctatccgctactcctt	Williams <i>et al.</i> (2001)
<i>matK</i> reverse	1520R	cggataatgtccaataccaata	Williams <i>et al.</i> (2001)
<i>atpB-rbcL</i> intergenic spacer forward	atpBmaxF	agaagtagtgggattgctctc	
<i>atpB-rbcL</i> intergenic spacer reverse	atpBmaxR	tcacaacaacaagggtctactcg	

Table 3. Statistics from PAUP* analyses of separate and combined data matrices for the combined data set of 30 taxa in the *Telipogon* and *Ornithocephalus* alliances and 81 OTU's for the ITS only analysis.

	ITS	<i>trnL-F</i>	<i>matK</i>	<i>atpB-rbcL</i> spacer	Combined plastid	ITS and plastid 30 taxa	ITS only 81 OTU's
# included positions in matrix	795	1252	1331	1499	4082	4859	682
# variable sites	375	298	284	530	1112	1487	414
# phylogenetically informative sites	301	149	151	220	520	821	341
# of trees (Fitch)	8	1458	4	3	4	30	252
# of steps	914	425	434	761	1634	2568	1311
CI	0.58	0.80	0.76	0.81	0.79	0.71	0.49
CI excluding non-informative sites	0.54	0.68	0.64	0.65	0.65	0.59	0.46
RI	0.79	0.84	0.83	0.75	0.80	0.79	0.88
Ave. # of changes per variable site (# steps/# var. sites)	2.44	1.43	1.53	1.44	1.47	1.73	3.17

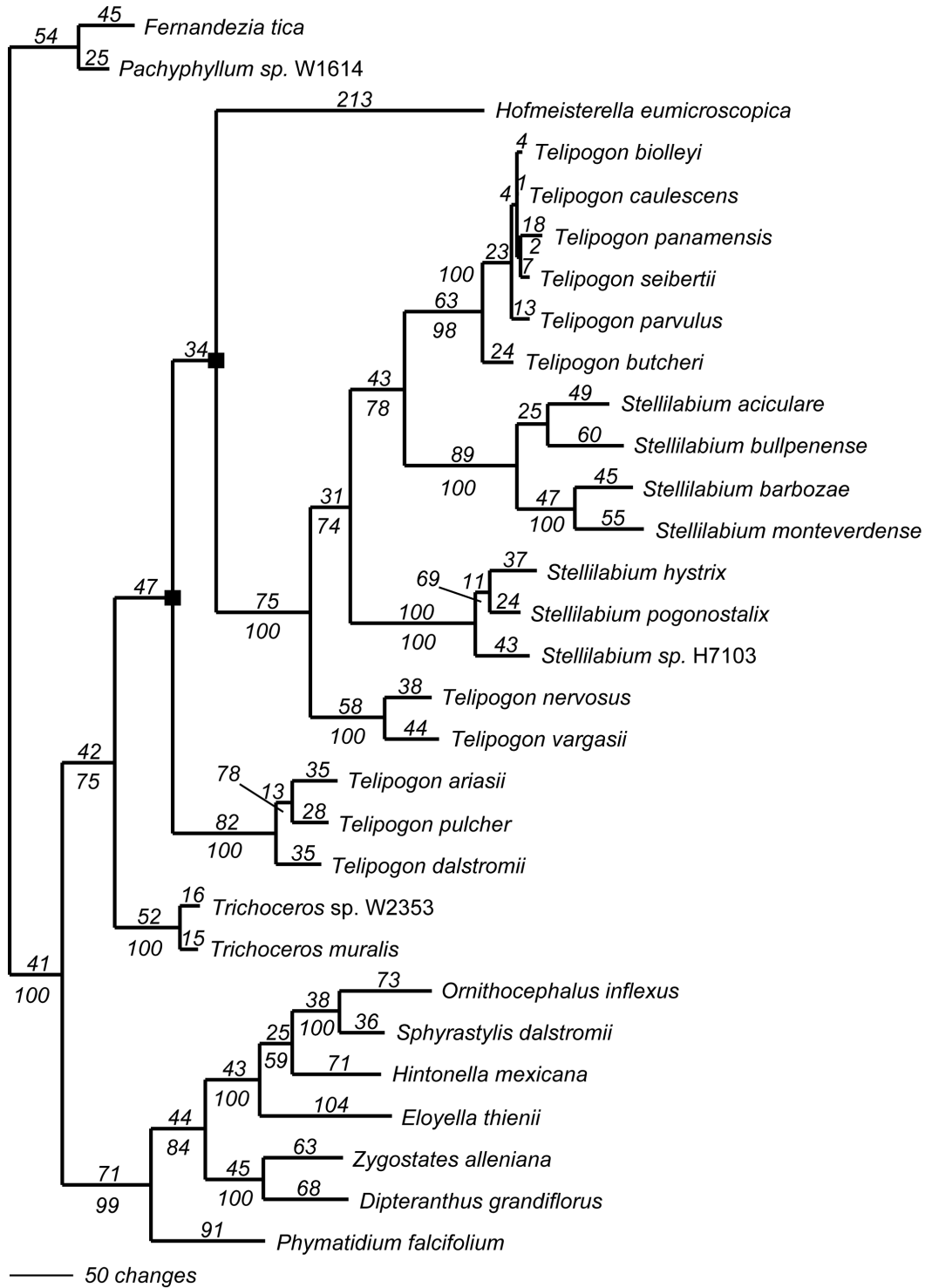


Fig. 1. One of eight trees for the limited ITS only analysis, with branch lengths (ACCTRAN optimization) above lines, bootstrap values below lines. Nodes that collapse in the strict consensus tree are indicated with a small black square.

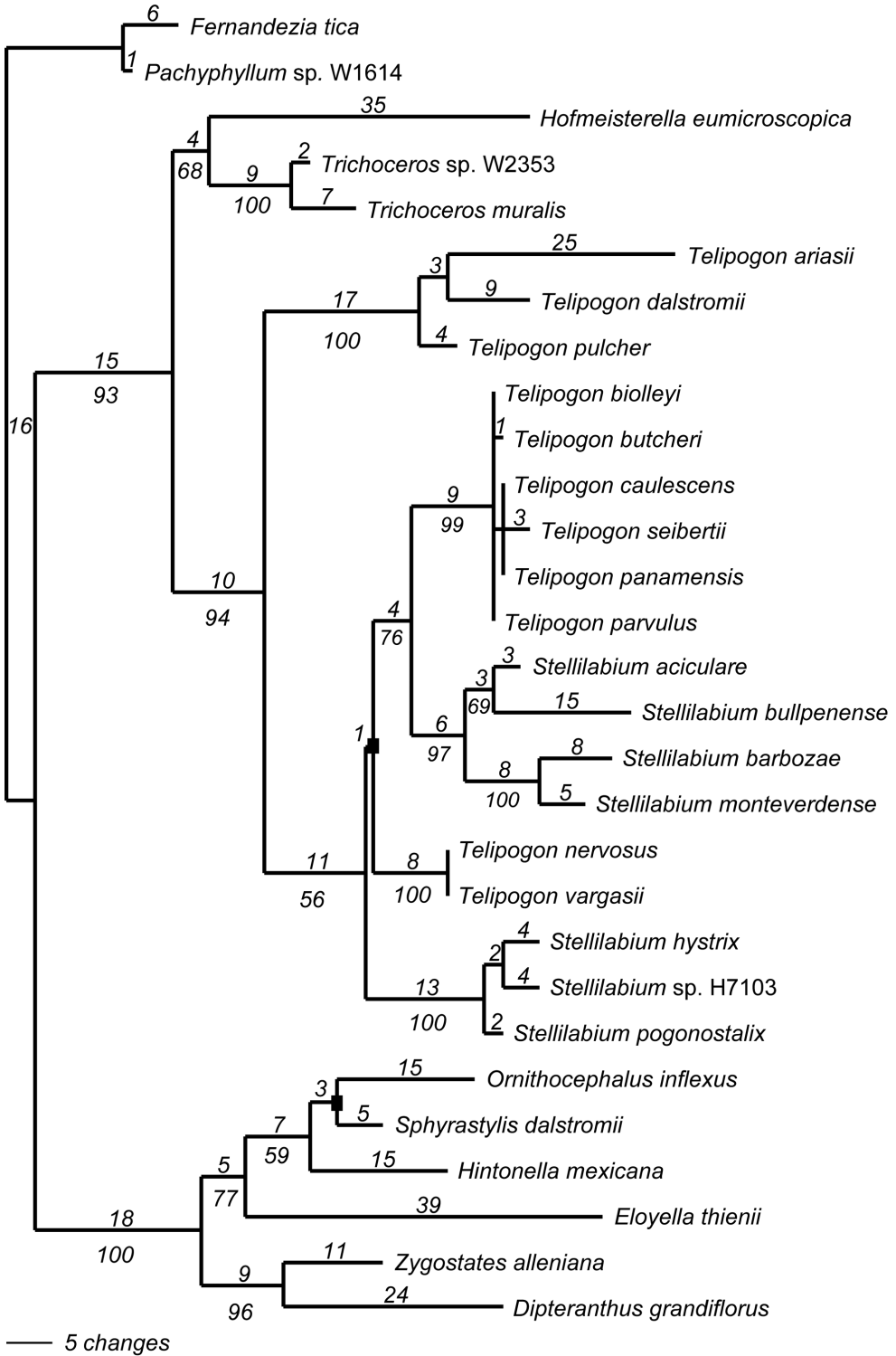


Fig. 2. One of 1458 trees for the limited *trnL-F* only analysis, with branch lengths (ACCTRAN optimization) above lines, bootstrap values below lines. Nodes that collapse in the strict consensus tree are indicated with a small black square.

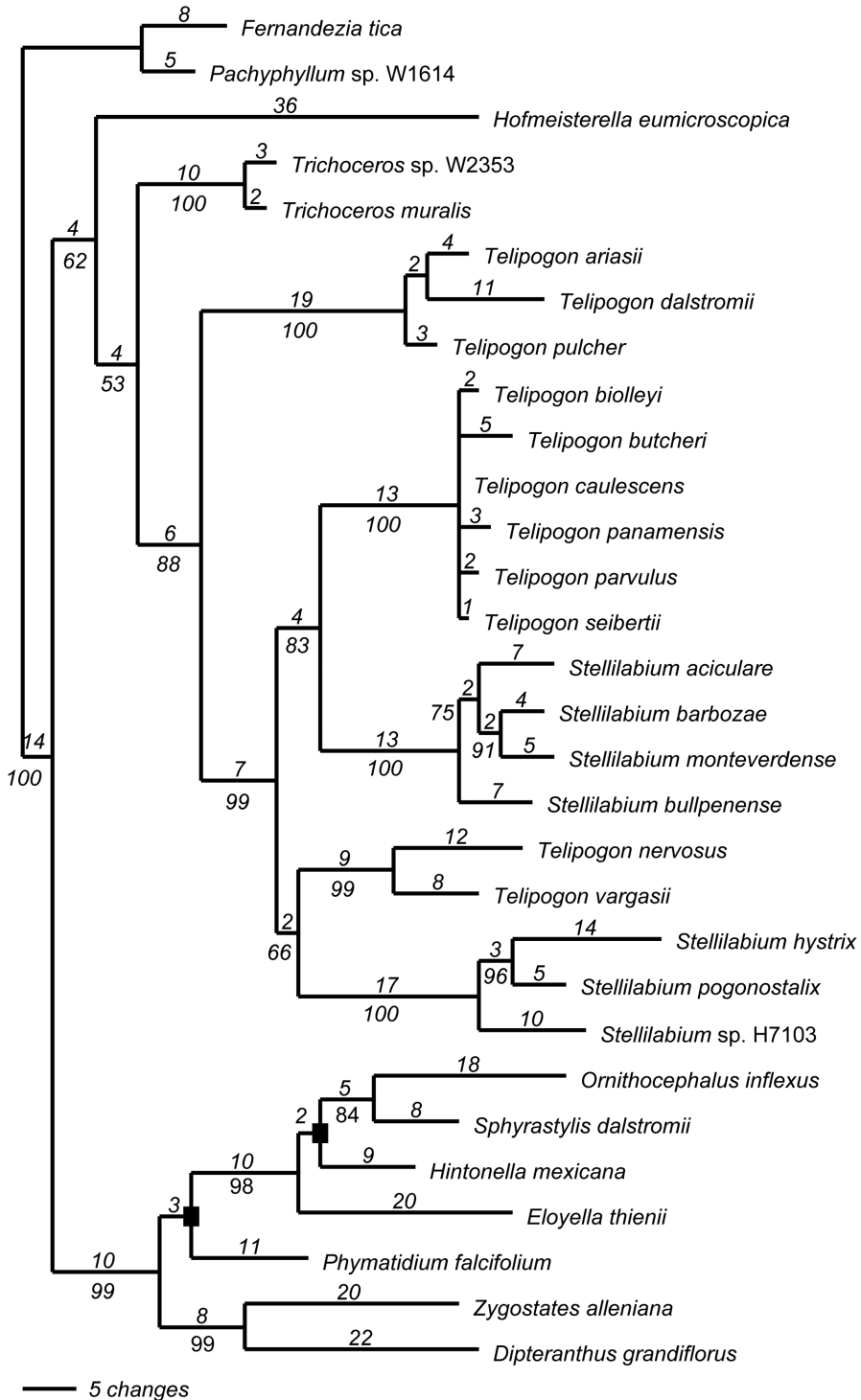


Fig. 3. One of four trees for the limited *matK* only analysis, with branch lengths (ACCTRAN optimization) above lines, bootstrap values below lines. Nodes that collapse in the strict consensus tree are indicated with a small black square.

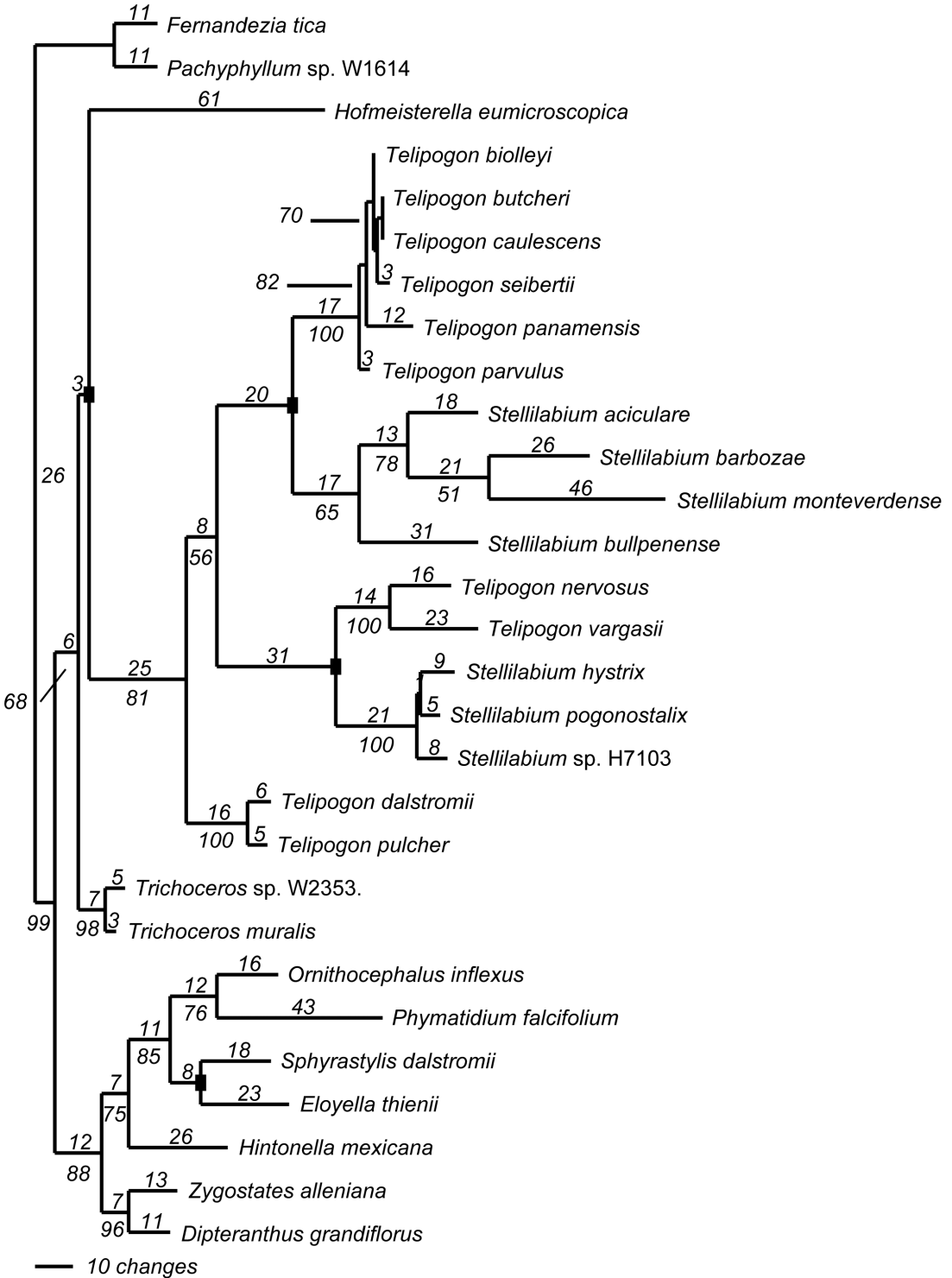


Fig. 4. One of three trees for the limited *atpB-rbcL* intergenic spacer region analysis, with branch lengths (ACCTRAN optimization) above lines, bootstrap values below lines. Nodes that collapse in the strict consensus tree are indicated with a small black square.

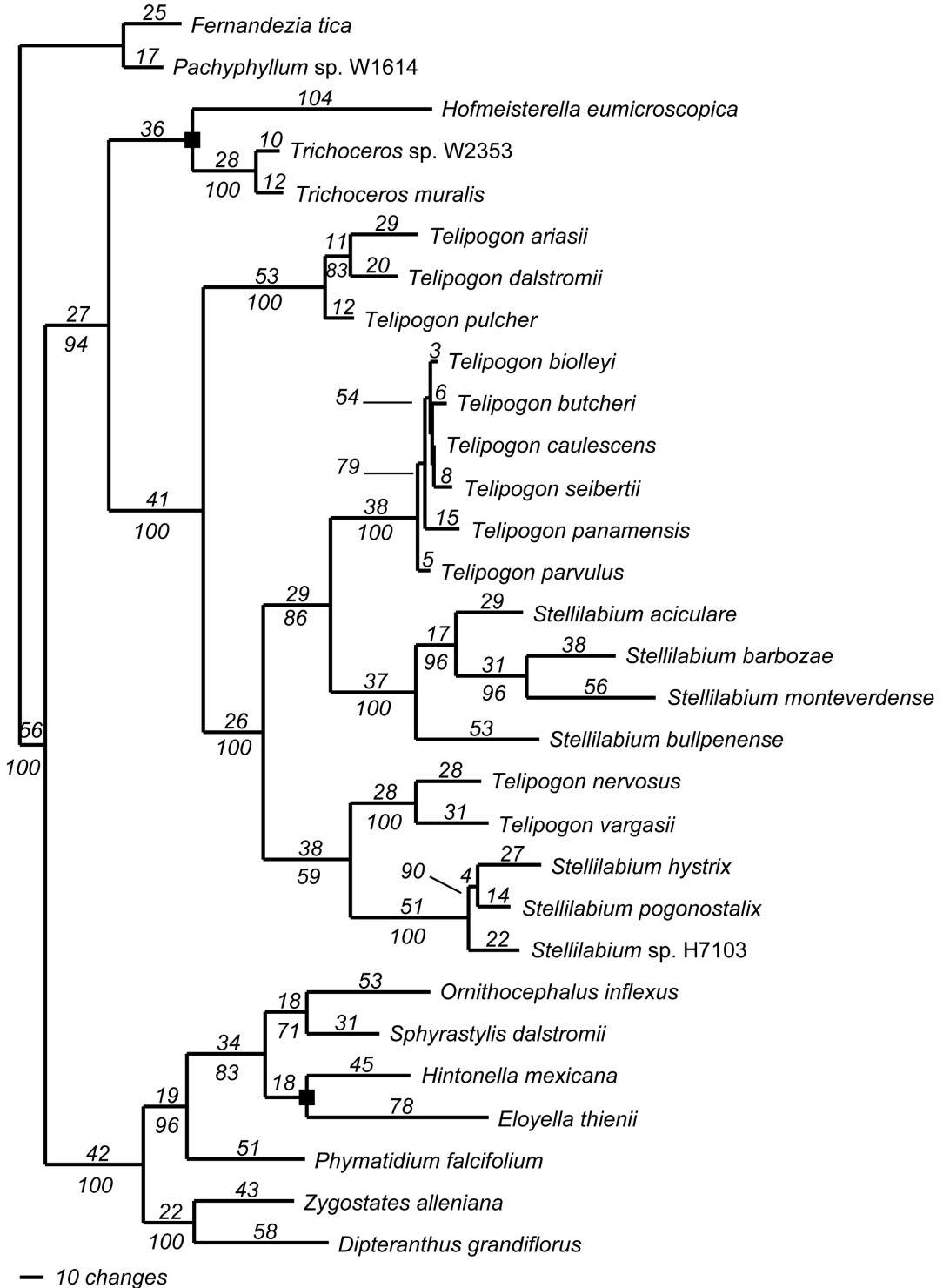


Fig. 5. The one of four trees for the combined plastid data set for the limited analysis, with branch lengths (ACCTRAN optimization) above lines, bootstrap values below lines. Nodes that collapse in the strict consensus tree are indicated with a small black square.

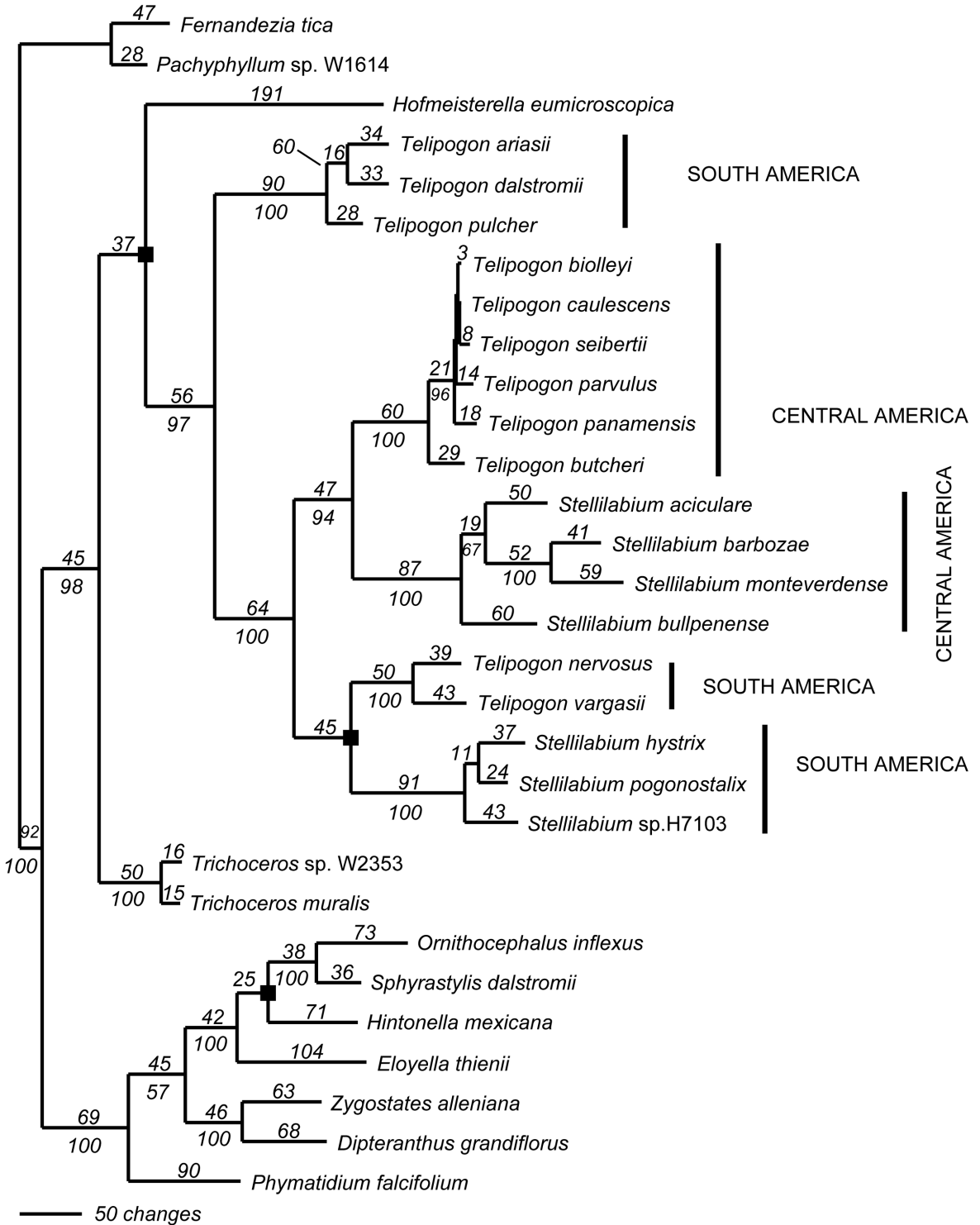


Fig. 6. One of 30 trees for the combined ITS plus plastid data set analysis, with branch lengths (ACCTRAN optimization) above lines, bootstrap values below lines. Nodes that collapse in the strict consensus tree are indicated with a small black square.

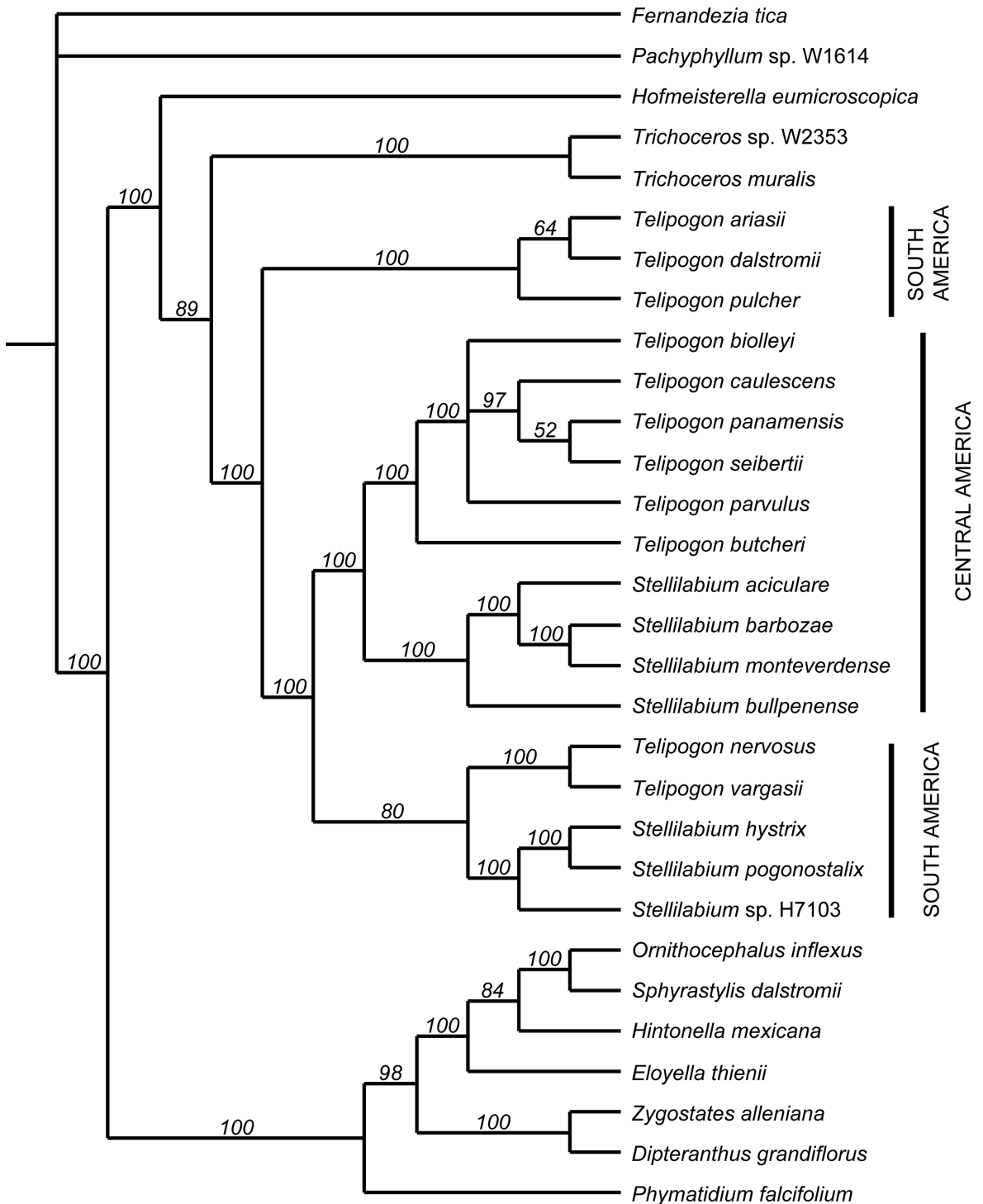


Fig. 7. The majority rule consensus tree for the Bayesian analysis of the combined ITS plus plastid data set with posterior probability values above lines.

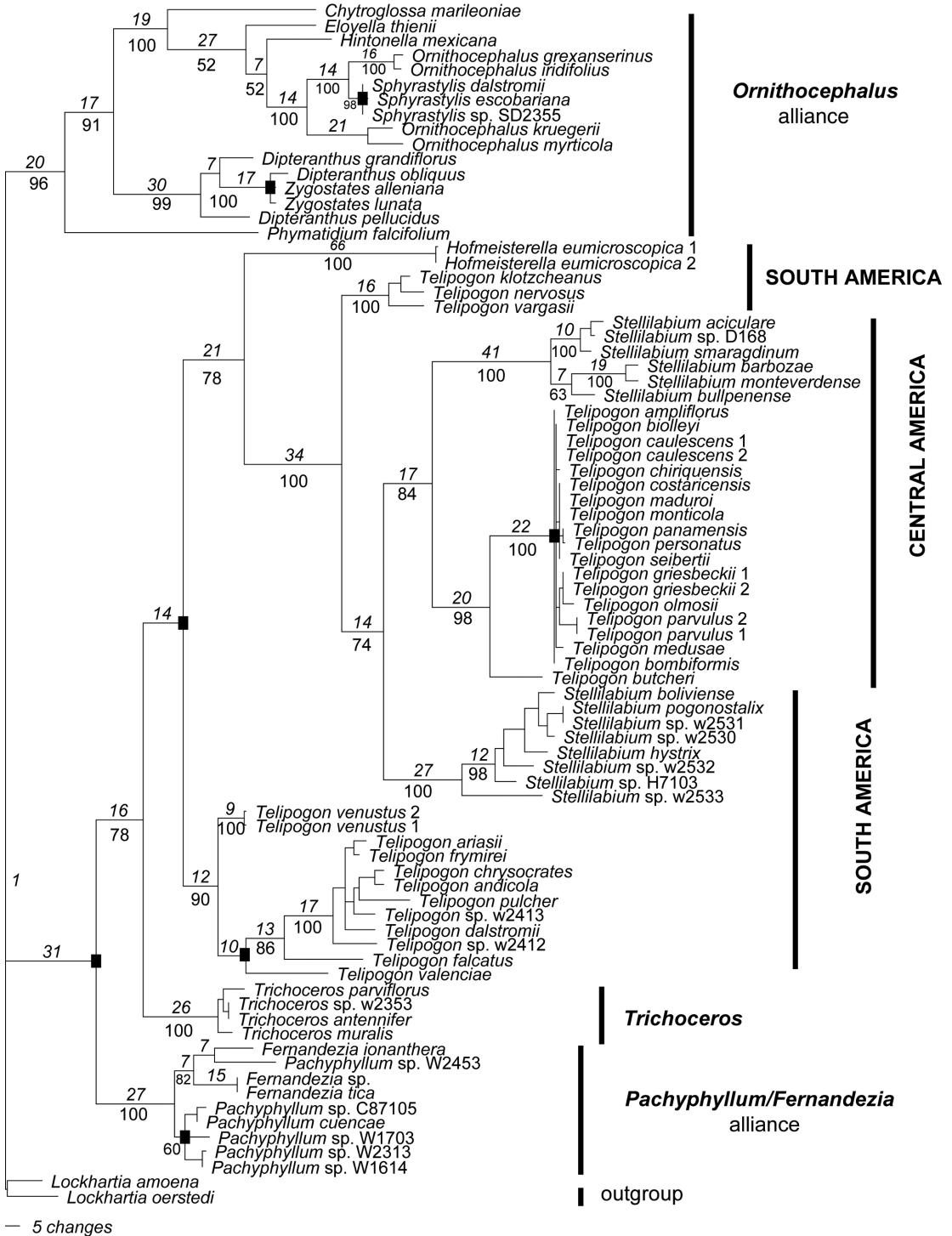


Fig. 8. One of 251 trees for ITS only for 81 taxa, with branch lengths (ACCTRAN optimization) above lines, bootstrap values below lines. Nodes that collapse in the strict consensus tree are indicated with a small black square. Branch lengths for terminal branches and for extremely short (<7) branches omitted for clarity. See text for bootstrap values for the South American *Stellilabium* clade and the *T. ariasii*-*T. venustus* clade.