



Identifying the generic limits of the Cheilanthoid genus *Doryopteris*

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Abstract

Morphology-based delimitation of genera in the Cheilanthoid ferns has proved to be problematic and understanding of the phylogeny and relationships amongst Cheilanthoid ferns based on morphological characters has posed even further difficulties, owing perhaps in large part to adaptation by many taxa to xeric habitats, as well as convergent evolution. It is only now with the application of DNA sequence data that relationships of species and genera are becoming clear. Here, we present results of cpDNA sequence data from species that have been traditionally placed in the genus *Doryopteris* and, based on both these results, and morphological and distribution data, this study helps clarify the concept of the genus *Doryopteris* its position within the Cheilanthoid ferns and the status of *Lytoneuron*. As a result, three genera are redefined: *Doryopteris*, *Lytoneuron* and *Ormopteris*.

Key words: Cheilanthoid ferns, cpDNA, *Doryopteris*, geographic distribution, *Lytoneuron*, morphology, *Ormopteris*, phylogeny, taxonomy

Introduction

The phylogeny of the cheilanthoid ferns using DNA sequences of plastid genome regions has been studied extensively in recent years (Gastony & Rollo 1995, Gastony & Rollo 1998, Zhang *et al.* 2005, Kirkpatrick 2007, Prado *et al.* 2007, Schuettpelz *et al.* 2007, Zhang *et al.* 2007, Rothfels *et al.* 2008, Windham *et al.* 2009, Beck *et al.* 2010, Bouma *et al.* 2010, Yesilyurt & Schneider 2010, Eiserhardt *et al.* 2011, Lehtonen 2011, Link-Perez *et al.* 2011, Sigel *et al.* 2011, Li *et al.* 2012, Grusz & Windham 2013, Prado *et al.* 2013). These studies have provided not only new insights in the evolution of xeric ferns, such as the evolution of convergences, but also cytological and morphological evidence concerning the generic classification of these unusual ferns. Comparison of the results of these studies with the most recent pre-cladistic classification (Tryon *et al.* 1990) reveals several trends. Firstly, some genera, *Cheilanthes* Swartz (1806: 126) and *Pellaea* Link (1841: 59) as defined in Tryon *et al.* (1990), were found to be polyphyletic (Gastony & Rollo 1995, Gastony & Rollo 1998, Kirkpatrick *et al.* 2007, Prado *et al.* 2007, Schuettpelz *et al.* 2007, Zhang *et al.* 2007, Windham *et al.* 2009, Eiserhardt *et al.* 2011). In turn, the segregation of *Argyrochosma* (Smith 1841: 50) Windham (1987: 38) and *Notholaena* Brown (1810: 145), which was not accepted by Tryon *et al.* (1990), was confirmed (Rothfels *et al.* 2008, Sigel *et al.* 2011). Some previously recognized genera, such as *Adiantopsis* Fée (1852: 145) (Link-Perez *et al.* 2011) and *Notholaena* (Rothfels *et al.* 2008), required relatively minor re-circumscription, whilst other genera were either re-established, such as *Allosorus* Bernhardt (1805: 36) (Christenhusz 2012) and *Myriopteris* Fée (1852: 148) (Grusz and Windham 2013), or introduced, such as *Calciphlopteris* Yesilyurt & Schneider (2010: 52) and *Gaga* Pryer, F.W.Li & Windham in Li *et al.* (2012: 855). In summary, the classification of these ferns has changed substantially as a result of these studies.

Relatively little attention has been given so far to the genus *Doryopteris* Smith (1841: 404), despite the existence of several DNA sequence based studies (Prado *et al.* 2007, 2013, Zhang *et al.* 2007, Eiserhardt *et al.* 2011). These studies found evidence for polyphyly of the genus as defined in the past. Consequently, the *Doryopteris ludens* (Wallich ex Hooker 1858: 210) Smith (1875: 289) group (Yesilyurt 2004, Schuettpelz *et al.* 2007, Windham *et al.* 2009) was

excluded and placed into the new genus *Calciphlopteris* (Yesilyurt & Schneider 2010). Two other species, *Doryopteris pedatoides* (Desvaux 1827: 293) Kuhn (1879: 63) and *D. pilosa* (Poiret 1804: 717) Kuhn (1879: 63), were reported to be more closely related to several species of *Pellaea* occurring in Afro-Madagascar (Eiserhardt *et al.* 2011).

Tryon (1942) mentioned that he was not able to place these taxa with confidence but, so far, the species have not been formally excluded from *Doryopteris*. Despite these changes, the studies recovered most species previously treated as *Doryopteris* (Tryon 1942, Tryon & Tryon 1982) to be nested in a well-supported clade (Prado *et al.* 2007, Eiserhardt *et al.* 2011), composed mainly of species occurring in the Brazilian geographic centre of cheilanthoids (Tryon & Tryon 1973). However, this clade also included the segregate *Ormopteris* (Smith ex Smith 1875: 281), and thus *Doryopteris* was found to be paraphyletic (Prado *et al.* 2007, Eiserhardt *et al.* 2011). In the classification of Tryon *et al.* (1990), *Ormopteris* was considered as *Pellaea* sect. *Ormopteris* (Smith 1875: 281) Tryon & Tryon 1981: 135) (see also Tryon & Tryon 1982). As mentioned above, *Pellaea* was found to be polyphyletic (Kirkpatrick *et al.* 2007, Prado *et al.* 2007, Schuettpelez *et al.* 2007, Windham *et al.* 2009, Eiserhardt *et al.* 2011). In this context it is interesting to note the different fate of the four sections of *Pellaea* (Tryon & Tryon 1982). Section *Ormopteris* was found to be monophyletic and not closely related to sect. *Pellaea* (1841: 59), whereas the sect. *Platyloma* (Smith: 1875: 164) Hooker & Baker (1867: 151) was found to be nested in sect. *Pellaea*, and sect. *Holcochlaena* (Hooker & Baker 1867: 153) was found to be polyphyletic (Kirkpatrick 2007, Eiserhardt *et al.* 2011).

The clade comprising *Doryopteris* and *Ormopteris* was found to be nested in a clade comprising the Neotropical genus *Adiantopsis* (see also Link-Perez *et al.* 2011), the genus *Trachypteris* Andre ex Christ (1899: 150) and various species previously assigned either to *Cheilanthes* or *Pellaea*. The *Doryopteris-Ormopteris* clade itself was found to be divided into three clades, of which two include species previously recognized as species of *Doryopteris*, and one clade comprised exclusively of species previously recognized as belonging to *Ormopteris* (Prado *et al.* 2007, Eiserhardt *et al.* 2011). These results reiterate the conflicting interpretation of the relationships of these plants in the past (Prantl 1882, Copeland 1947).

In this study, we address the relationship of these ferns using the most exhaustive taxon sampling to date that incorporates data from the PhD thesis of Yesilyurt (2004) and the master thesis of Barbará (2003). Particular care was given to a comprehensive sampling of the two sections recognized, sect. *Doryopteris* and sect. *Lytoneuron* Klotzsch (1847: 343) (Tryon 1942; Tryon & Tryon 1982). Special care was also taken to include samples of the type species of sect. *Doryopteris* (*D. pedata* var. *palmata* (Willdenov 1810: 357) Smith (1841: 163) and sect. *Lytoneuron* (*D. lomariacea* Klotzsch (1847: 343)). With *D. triphylla* (Lamarck 1783: 41) Christ (1902: 546), the sampling also included the type of the putative segregate *Cassebeera* Kaulfuss (1824: 216) (de la Sota & Giudice 2004). All species of *Ormopteris* were included although this was not achieved for *Doryopteris*. Following Tryon's (1942) concept for *Doryopteris*, where 12 taxa have been referred for the section *Lytoneuron*, nine for the section *Doryopteris*, and seven under "Miscellaneous Species", seven taxa from each section and four from "Miscellaneous Species" have been sampled here. However, seven more taxa have been explored and added to this final study. Our conclusions are based on the reconstruction of phylogenetic relationships using plastid genome sequence data and on comparative study of morphological evidence including scanning electron microscopy of spore ornamentation and karyological evidence.

Materials and Methods

Comparative morphological studies were carried out by studying herbarium specimens held at the following institutions (abbreviations as given in Index Herbariorum): B, BHBC, BM, BOLO, BR, C, FI, G, GH, GUA, K, L, M, MO, NY, PACA, PR, RB, S, SP, SPF, U, UC, US. These studies included macromorphology and spore morphology using scanning electron microscopy. The study also included chromosome counts of selected species of *Doryopteris* prepared using protocols described in Manton (1950). The study covered ca. 210 names referred to the genus *Doryopteris* and, whenever possible, types (alongside with their protologues) were sought and analysed to clarify their taxonomic and nomenclatural status. A full systematic account of the genus will be published elsewhere.

The phylogenetic relationships of the taxa were explored by assembling two datasets. The first dataset is based on the plastid coding region *rbcL*. The dataset included one specimen of each species of cheilanthoid fern available in GenBank (<http://www.ncbi.nlm.nih.gov/GenBank/>) at December 25th 2013 (Table 1). To this dataset, we added the *rbcL* sequences previously generated by Yesilyurt (2004) and Barbará (2003). In the case of the *Doryopteris* clade, more than one specimen per species was included if data were available. The second dataset is based on a smaller sampling focused on the *Doryopteris* clade. In this dataset we combined the *rbcL* region and the plastid *trnL-trnF* region. The integration of these two regions was obtained to improve the resolution of the phylogenetic relationships.

Previously unpublished DNA sequences were generated by extracting whole DNA from silica gel-dried leaf tissue using a modified CTAB protocol (Rogers & Bendich 1985, Doyle & Doyle 1987) or by using DNeasy Plant Mini Kit following the manufacturers protocol (Qiagen, Venlo, Netherlands). Amplification of *rbcL* including primer regions and PCR protocols followed the reports in Gastony & Rollo (1995). The *trnL-trnF* region was amplified using the primers given in Taberlet *et al.* (1991) and Trewick *et al.* (2002). DNA sequencing was carried out using big-dye chemistry and an ABI capillary sequencer (Applied Biosystems, Foster City, California, USA). Newly generated sequences were assembled using Lasergene (DNASTAR, Madison, Wisconsin, USA) and submitted to GenBank (see Table 2).

TABLE 1. Sequences downloaded from GenBank (www.ncbi.nlm.nih.gov/GenBank) and used in this study (with the exception of a few accessions cited in Table 2). Taxa are ordered according to the presented phylogeny. Taxon names are used as throughout the text. We followed the most recent taxonomic treatments available. For each taxon, the *rbcL* accession number is provided. The *trnLF* sequence is provided as a second accession if the sequence was available. In a few cases, more than one specimen was incorporated marked as smp 1, smp 2, and smp 3.

	Taxon	Voucher
Outgroup	<i>Calciophilopteirs ludens</i>	EF452150, DQ432686
Bommeria clade	<i>Bommeria ehrenbergiana</i>	U19497
	<i>Bommeria elegans</i>	U27729
	<i>Bommeria hispida</i>	EF452142
Myriopteris clade	<i>Myriopteris alabamensis</i>	EF452143, DQ914220
	<i>Myriopteris allosuroides</i>	U27239
	<i>Myriopteris aurea</i>	EU268780
	<i>Myriopteris covillei</i>	EU268782, DQ914221
	<i>Myriopteris lanosa</i>	U27205, DQ914227
	<i>Myriopteris lendigera</i>	EU268784, DQ914228
	<i>Myriopteris myriophylla</i>	EU268786
	<i>Myriopteris newberryi</i>	EU268787, EU831188
	<i>Myriopteris pringlei</i>	HM003031, EU831189
	<i>Myriopteris rawsonii</i>	GU935520, GU935615
	<i>Myriopteris rufa</i>	EF452144
	<i>Myriopteris scabra</i>	U27448
	<i>Myriopteris wrightii</i>	HM003030, DQ914233
Argyrochosma clade	<i>Argyrochosma dealbata</i>	HQ846421
	<i>Argyrochosma delicatula</i>	HQ846420
	<i>Argyrochosma fendleri</i>	HQ846447, DQ914209
	<i>Argyrochosma formosa</i>	HQ846419
	<i>Argyrochosma incana</i>	HQ846452, EU831181
	<i>Argyrochosma jonesii</i>	HQ846454, DQ914210
	<i>Argyrochosma limitanea</i> subsp. <i>limitanea</i>	HQ846456, DQ914211
	<i>Argyrochosma limitanea</i> subsp. <i>mexicana</i>	HQ846418
	<i>Argyrochosma lumholtzii</i>	HQ846424
	<i>Argyrochosma microphylla</i>	HQ846443
	<i>Argyrochosma nivea</i> var. <i>flava</i>	HQ846450
	<i>Argyrochosma nivea</i> var. <i>nivea</i>	HQ846449, DQ914212
	<i>Argyrochosma nivea</i> var. <i>tenera</i>	HQ846446
	<i>Argyrochosma pallens</i>	HQ846415
	<i>Argyrochosma palmeri</i>	HQ846458
	<i>Argyrochosma peninsularis</i>	HQ846457
<i>Argyrochosma pilifera</i>	HQ846427	
Astrolepis clade	<i>Astrolepis cochisensis</i> subsp. <i>cochisensis</i>	EU268774, EU831183
	<i>Astrolepis sinuata</i> subsp. <i>sinuata</i>	JQ855927, DQ914218;
Pellaea clade	<i>Pellaea andromedifolia</i>	U19501, EU831157
	<i>Pellaea atropurpurea</i>	EF452162, EU831158
	<i>Pellaea breweri</i>	EU268808, EU831161
	<i>Pellaea calidirupium</i>	GU136793
	<i>Pellaea cordifolia</i>	U28253
	<i>Pellaea falcata</i>	GU136794, DQ914182
	<i>Pellaea glabella</i>	KF186501, DQ914185
<i>Pellaea intermedia</i>	EF452163, DQ914186	

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TABLE 1. (Continued)

	Taxon	Voucher
	<i>Pellaea pringlei</i>	U28787
	<i>Pellaea rotundifolia</i>	GU136795, DQ914181
	<i>Pellaea rufa</i>	GU935521, GU935616
	<i>Pellaea truncata</i>	EF452164, EU831176
	<i>Paragymnopteris bipinnata</i>	DQ423656, DQ914204
	<i>Paragymnopteris delavayi</i>	HQ846422, DQ432683
	<i>Paragymnopteris marantae</i>	EF452161, DQ914205
	<i>Paragymnopteris sargentii</i>	DQ432653, DQ914207
	<i>Paragymnopteris vestiata</i>	DQ432652, DQ914208
Mildella clade	<i>Mildella intramarginalis</i>	U29449
Notholaena clade	<i>Notholaena aliena</i>	EU268790
	<i>Notholaena aschenborniana</i>	EF452159
	<i>Notholaena aurantiaca</i>	EU268777
	<i>Notholaena brachypus</i>	EU268781
	<i>Notholaena bryopoda</i>	EU268791
	<i>Notholaena californica</i>	EU268792
	<i>Notholaena candida</i>	EU268793
	<i>Notholaena copelandii</i>	JQ855931
	<i>Notholaena grayi</i> subsp. <i>grayi</i>	EU268794
	<i>Notholaena grayi</i> subsp. <i>sonorensis</i>	EU268795
	<i>Notholaena greggii</i>	EU268796
	<i>Notholaena lemmonii</i> var. <i>lemmonii</i>	EU268797
	<i>Notholaena meridionalis</i>	JQ855932
	<i>Notholaena montieliae</i>	JQ855933
	<i>Notholaena nealleyi</i>	JQ855934
	<i>Notholaena rigida</i>	EU268799
	<i>Notholaena rosei</i>	EU268800
	<i>Notholaena schaffneri</i>	EU268801
	<i>Notholaena standleyi</i>	EU268804
	<i>Notholaena sulphurea</i>	EU268806
	<i>Notholaena trichomanoides</i>	EU268807
Bolborrhiza clade	<i>Cheilanthes bolborrhiza</i>	JQ855928
	<i>Cheilanthes leucopoda</i>	EU268785
Pentagramma clade	<i>Pentagramma triangularis</i>	JX313531
Allosorus clade	<i>Aleuritopteris albofusca</i>	U19498, DQ432677
	<i>Aleuritopteris albomarginata</i>	AY266411, DQ432665
	<i>Aleuritopteris argentea</i>	EF452137, DQ432667
	<i>Aleuritopteris dalhousiae</i>	DQ432646, DQ432673
	<i>Aleuritopteris duclouxii</i>	U27447
	<i>Aleuritopteris farinosa</i>	KF992450
	<i>Aleuritopteris formosana</i>	DQ432643, DQ432671
	<i>Aleuritopteris grisea</i>	AY299653, DQ432673
	<i>Aleuritopteris krameri</i>	AB574809
	<i>Aleuritopteris kuhnii</i> var. <i>brandtii</i>	AB574807
	<i>Aleuritopteris kuhnii</i> var. <i>kuhnii</i>	AY266412
	<i>Aleuritopteris linkiangensis</i>	DQ432645, DQ432668
	<i>Aleuritopteris niphobola</i>	AY266409, DQ432670
	<i>Aleuritopteris squamosa</i>	DQ432642
	<i>Aleuritopteris subvillosa</i>	JQ855926
	<i>Aleuritopteris tamburii</i>	DQ432644, DQ432666
	<i>Allosorus guanchicus</i>	GU937504, GU935580
	<i>Allosorus fragilis</i>	GU935503
	<i>Allosorus pteridioides</i>	GU935505
	<i>Cheilanthes chinensis</i>	DQ432651, DQ432679
	<i>Cheilanthes christii</i>	DQ432640, DQ432664
	<i>Cheilanthes chusana</i>	AB574808
	<i>Cheilanthes insignis</i>	AY266413, DQ432676

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TABLE 1. (Continued)

	Taxon	Voucher
	<i>Cheilanthes nitidula</i>	DQ432638, DQ432662
	<i>Cheilanthes patula</i>	DQ432641, DQ432663
	<i>Cheilanthes trichophylla</i>	DQ432639, DQ432661
<i>Cheilanthes</i> clade	<i>Cheilanthes capensis</i>	GU935511, GU935536
	<i>Cheilanthes contracta</i>	GU935519, GU935593
	<i>Cheilanthes deltoidea</i>	GU935512, GU935608
	<i>Cheilanthes depauperata</i>	GU035516, GU935590
	<i>Cheilanthes dinteri</i>	GU935506, GU935582
	<i>Cheilanthes distans</i>	GU136791
	<i>Cheilanthes eckloniana</i>	GU935513, GU935585
	<i>Cheilanthes lasiophylla</i>	HM003032
	<i>Cheilanthes hastata</i>	GU935509, GU935612
	<i>Cheilanthes hirta</i>	GU035514, GU935589
	<i>Cheilanthes marlothii</i>	GU935514, GU935587
	<i>Cheilanthes micropteris</i>	EF452145
	<i>Cheilanthes parviloba</i>	GU935517, GU935591
	<i>Cheilanthes robusta</i>	GU935507, GU935609
	<i>Cheilanthes rufopunctata</i>	JX313528
	<i>Cheilanthes sieberi</i>	GU136792, EU831190
<i>Hemionitis</i> clade	<i>Hemionitis arifolia</i>	JX313529
	<i>Hemionitis levyi</i>	U27725
	<i>Hemionitis palmata</i>	KC984525
	<i>Hemionitis rufa</i>	AY357707
	<i>Hemionitis tomentosa</i>	EF473696
<i>Pellaeopsis</i> clade	<i>Doryopteris pedatoides</i>	KF992477, JN122022
	<i>Doryopteris pilosa</i>	KF992478, JN22023
	<i>Pellaea angulosa</i>	KF992507
	<i>Pellaea boivinii</i>	U29132
	<i>Pellaea dura</i>	GU935490, GU935579
<i>Gaga</i> clade	<i>Gaga angustifolia</i>	JN647779
	<i>Gaga apiacea</i>	JN647783
	<i>Gaga arizonia</i>	JN647785, DQ914219
	<i>Gaga chaerophylla</i>	JN647790
	<i>Gaga complanata</i>	JN647792
	<i>Gaga cuneata</i>	JN647794
	<i>Gaga decomposita</i>	JN647797
	<i>Gaga decurrens</i>	JN647800
	<i>Gaga germanotta</i>	JX313546
	<i>Gaga harrissii</i>	JN647803
	<i>Gaga hintoniorum</i>	JN647806
	<i>Gaga kaulfussii</i>	JN647810
	<i>Gaga lerstenii</i>	JX313536
	<i>Gaga membranacea</i>	JN647821
	<i>Gaga marginata</i>	JN647819
	<i>Gaga monstraparva</i>	JX313547
	<i>Gaga pellaepsis</i>	JN647822
	<i>Gaga purpusii</i>	JN647825
<i>Aspidotis</i> clade	<i>Aspidotis californica</i>	JX313525, DQ914213
	<i>Aspidotis densa</i>	JX313526
	<i>Aspidotis meifolia</i>	JX313527
<i>Trachypteris</i> clade	<i>Trachypteris pinnata</i>	U27450
<i>Adiantopsis</i> clade	<i>Adiantopsis flexuosa</i>	JN709722
	<i>Adiantopsis chlorophylla</i>	EF473684
	<i>Adiantopsis dactylifera</i>	JN709759
	<i>Adiantopsis dichotoma</i>	JN709728
	<i>Adiantopsis lindigii</i>	JN709754
	<i>Adiantopsis monticola</i>	JN709729

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TABLE 1. (Continued)

	Taxon	Voucher
	<i>Adiantopsis paupercula</i>	JN709765
	<i>Adiantopsis parvisegmenta</i>	JN709749
	<i>Adiantopsis pedata</i>	JN709748
	<i>Adiantopsis pentagona</i>	JN709749
	<i>Adiantopsis radiata</i>	JN709760
	<i>Adiantopsis reesii</i>	JN709755
	<i>Adiantopsis regularis</i>	JN709726
	<i>Adiantopsis rupicola</i>	JN709753
	<i>Adiantopsis seemannii</i>	JN709731
	<i>Adiantopsis ternata</i>	JN709756
	<i>Adiantopsis timida</i>	JN709758
	<i>Adiantopsis trifurcata</i>	JN709767
	<i>Adiantopsis tweediana</i>	JN709724
	<i>Adiantopsis vincentii</i>	JN709752
<i>Choristosoria</i> grade	<i>Cheilanthes bradei</i>	JN122014, JN122019
	<i>Cheilanthes goyazensis</i>	EF473687, JN122018
	<i>Cheilanthes induta</i>	GU935501, GU935597
	<i>Cheilanthes multifida</i> smp 1	GU935500, GU935596
	<i>Cheilanthes multifida</i> smp 2	GU935398, GU935594
	<i>Cheilanthes namaquensis</i>	GU035393, GU935584
	<i>Cheilanthes quadripinnata</i>	GU935496
	<i>Cheilanthes viridis</i> smp 1	EF452147, GU935603
	<i>Cheilanthes viridis</i> smp 2	GU935494, GU935601
	<i>Cheilanthes viridis</i> smp 3	GU935495, GU935692
	<i>Cheilanthes viridis</i> smp 4	JX455163
	<i>Pellaea calomelanos</i>	GU935497, GU935600
	<i>Pellaea pteroides</i>	GU035502, GU935599
<i>Doryopteris</i> clade	<i>Doryopteris collina</i>	EF473694
	<i>Doryopteris concolor</i> smp 1	U5621
	<i>Doryopteris concolor</i> smp 2	AY266414
	<i>Doryopteris decora</i>	U27446
	<i>Doryopteris lomariacea</i>	EG473689
	<i>Doryopteris nobilis</i>	EG473690
	<i>Doryopteris ornythopus</i>	EG4735691
	<i>Doryopteris paradoxa</i>	EF473692
	<i>Doryopteris pentagona</i>	EF473693
	<i>Doryopteris pedata</i> var. <i>palmata</i>	U27206
	<i>Doryopteris redivia</i>	EF473694
	<i>Doryopteris sagittifolia</i> smp 1	EF462151
	<i>Doryopteris sagittifolia</i> smp 2	EF473695
	<i>Ormopteris cymbiformis</i>	EG473697
	<i>Ormopteris gleichenioides</i>	EF473698
	<i>Ormopteris pinnata</i>	EG473699
	<i>Ormopteris riedelii</i>	EG473700

Alignments were obtained manually in Mesquite 2.75 (Maddison & Maddison 2011). The non-coding regions were visually inspected for ambiguously aligned regions and inversions. They were excluded prior to phylogenetic analyses. Models of sequence evolution were identified using jModeltest 2 (Darriba *et al.* 2012) and implemented as models without parameter values in maximum likelihood and Bayesian phylogenetic inferences.

Maximum parsimony analyses were carried out using PAUP* 4.0 (Swofford 2002) using heuristic searches with 1000 random-starting trees and TBR run to completion. Maximum parsimony bootstrap values (MP-BV) were obtained by running 1000 bootstrap replicates with 10 random starting trees each using the fast bootstrap option. Approximation of Maximum Likelihood was carried out using PhyML 3.0 (Guindon *et al.* 2010) with parameters estimated simultaneously with the phylogeny. Maximum likelihood bootstrap values (ML-BV) were obtained with 1000 bootstrap replicates. Bayesian inference of phylogeny was carried out using MrBayes 2.3 (Ronquist & Huelsenbeck 2003), using the model GTR + inv + gamma, based on AIC selection in MrModeltest with a single partition and

parameters estimated simultaneously with the phylogeny. Bayesian inference was run for 10,000,000 generations and results were analysed using TRACER v. 1.5. (Rambaut *et al.* 2013) and visualised using FIGTREE v. 1.4. (Rambaut 2012). Convergence was reached after 10,000 iterations and trees were sampled at a frequency of 1,000 to avoid autocorrelation among samples.

TABLE 2. Voucher information and GenBank accession numbers of newly generated sequences (*rbcL* and *trnL-trnF* regions) including some previously published sequences generated using the same vouchers.

Taxon	Voucher	Locality	Herbarium	<i>rbcL</i>	<i>trnLF</i>
VOUCHER					
<i>Doryopteris acutiloba</i>	J. C. Yesilyurt 715 & R.N.Cislinski, R. E. Cislinski	PR-Brazil	BM, SP	KP407206	KP407217
<i>Doryopteris collina</i>	J.C. Yesilyurt 552 & J. Prado	SP-Brazil	BM, SP	KP407199	KP407228
<i>Doryopteris concolor</i>	J.C. Yesilyurt, 557 & J. Prado	SP-Brazil	BM, SP	KP407197	KP407222
<i>Doryopteris crenulans</i>	J.C. Yesilyurt 555 & J. Prado	PR-Brazil	BM, SP	KP407207	KP407218
<i>Doryopteris feei</i>	J.C. Yesilyurt 738 & J. Prado	RJ-Brazil	BM, SP	KP407210	KP407221
<i>Doryopteris itatiaiensis</i>	J.C. Yesilyurt 739 & J. Prado	RJ-Brazil	BM, SP	KP407208	KP407219
<i>Doryopteris lomariacea</i>	J.C. Yesilyurt 547 & J. Prado, P.H. Labiak	SP-Brazil	BM, SP	KP407209	JN122020
<i>Doryopteris lorentzii</i>	J.C. Yesilyurt, 527 & R.N. Cislinski, R.E. Cislinski	SC-Brazil	BM, SP	JN122015 KP407213	KP407233
<i>Doryopteris kirkii</i>	D. Bridson 267	Rwanda	BR 830 0805	KP407198	KP407223
<i>Doryopteris leitei</i>	J.C. Yesilyurt 529 & R.N. Cislinski; R. E. Cislinski	SC-Brazil	BM, SP	KP407211	KP407224
<i>Doryopteris majestosa</i>	J.C. Yesilyurt, 564 & J. Prado, P.H. Labiak	RJ-Brazil	BM, SP	KP407202	KP407225
<i>Doryopteris nobilis</i>	J.C. Yesilyurt, 542 & J. Prado, P.H. Labiak	SP-Brazil	BM, SP	KP407204	KP407226
<i>Doryopteris ornithopus</i>	J.C. Yesilyurt 548 & J. Prado, P.H. Labiak	MG-Brazil	BM, SP	KP407212	KP407220
<i>Doryopteris rediviva</i>	J. C. Yesilyurt 732 & J. Prado	RJ-Brazil	BM, SP	KP407200	KP407229
<i>Doryopteris sagittifolia</i>	J.C. Yesilyurt 733 & E. Yesilyurt, V. Cislinski	SP-Brazil	BM, SP	KP407205	KP407232
<i>Doryopteris triphylla</i>	J.C. Yesilyurt 519 & R.N. Cislinski, R.E. Cislinski	RS-Brazil	BM, SP	KP407214	KP407234
<i>Doryopteris varians</i>	J. C. Yesilyurt 563 & J. Prado, P.H. Labiak	RJ-Brazil	BM, SP	KP407201	KP407230
<i>Doryopteris surinamensis</i>	J.P. Schulz 10262	Suriname	GH	KP407215	KP407231
<i>Doryopteris</i> sp. 1	J.C. Yesilyurt 705 & E. Yesilyurt, V. Cislinski	SC-Brazil	BM	KP407203	KP407235
<i>Doryopteris</i> sp. 2	J.C. Yesilyurt 541 & J. Prado, P.H. Labiak	SP-Brazil	SP	KP407216	KP407227
<i>Ormopteris crenata</i>	J. Prado & T. Barbará 1409	MG-Brazil	SP	KM081636	KM435285
<i>Ormopteris cymbiformis</i>	J. Prado & T. Barbará 1404	MG-Brazil	SP	KM081637	KM435286
<i>Ormopteris gleichenioides</i>	J. Prado & T. Barbará 1406	MG-Brazil	SP	KM081638	KM435287
<i>Ormopteris pinnata</i>	J. Prado & T. Barbará 1407	MG-Brazil	SP	KM081639	KM435288
<i>Ormopteris riedelii</i>	J. Prado & T. Barbará 1408	MG-Brazil	SP	KM081640	KM435289

Results

Two data sets were generated, the *rbcL* data set comprising 202 previously published (Table 1) and 20 newly derived sequences (Table 2) from a broad range of cheilanthoid taxa, and a smaller subset of 74 (from both previously published and newly derived sequences) taxa for the combined *rbcL* and *trnLF* analysis. The *rbcL* data set recovered two species of *Doryopteris*, *D. pedatoides* and *D. pilosa*, as closely related to a clade comprising species of the genera *Hemionitis* Linnaeus (1753: 1077) and several Afro-Madagascan *Pellaea* species (Clade H in Fig. 1), whereas all other species were found to be nested in a clade comprising *Doryopteris* and *Ormopteris* (clade DO in Fig. 1). This clade comprised four subclades. One included only species of the genus *Ormopteris*, whereas two clades comprised species previously classified as section *Doryopteris* and sect. *Lytoneuron* respectively (clade DO in Fig. 1). The fourth clade comprised *Doryopteris concolor* (Langsdorff & Fischer 1810: 19) Kuhn (1879: 19) and relatives. *Doryopteris triphylla* was found to be nested in the clade comprising species of the sect. *Doryopteris*, instead of the clade corresponding to sect. *Lytoneuron* (Fig. 2), where it historically was included. The *Lytoneuron* clade was found to be sister to the *Ormopteris* clade, whereas the *Doryopteris concolor* group was found to be sister to sect. *Doryopteris* (Fig. 2).

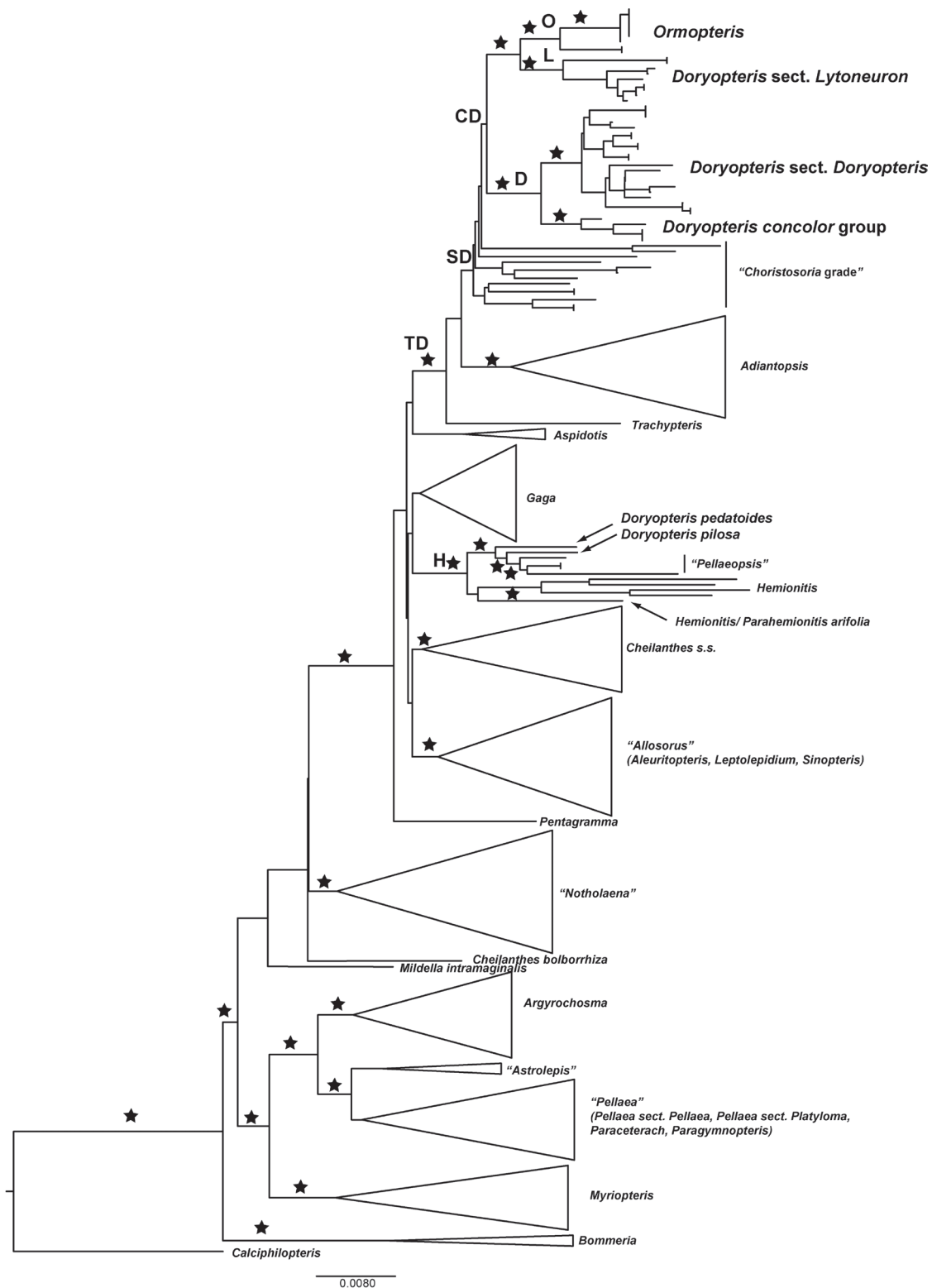


FIGURE 1. Sketch of the phylogeny of cheilanthoid ferns based on *rbcL* sequence data (as available in December 2013). The branch lengths correspond to the reconstructed number of changes in the maximum likelihood reconstruction whereas stars mark clades with a posterior confidence of $p \geq 0.95$ in the consensus tree of the Bayesian inference of the phylogeny. Species of major groups outside of *Doryopteris* and relatives discussed are collapsed. *Doryopteris* is shown as defined in Tryon (1942) with the sect. *Doryopteris* and sect. *Lytoneuron* recognized and *Doryopteris concolor* and relatives assigned as *Doryopteris concolor* group. *Choristosoria* and *Pteridella* are widely ignored generic names that can be attributed to grade/ clades recognized in this study. All other generic names are assigned according to our current understanding. Generic names in “ ” may require redefinition. In some case, putative segregates are named but in general the oldest available generic name is selected. The relationships of *D. pedatoides* and *D. pilosa* are shown. The relationships of *Doryopteris-Lytoneuron-Ormopteris* relatives are outlined but shown in more detail in figure 2. CD = crown group of the *Doryopteris-Lytoneuron-Ormopteris* clade, SD = stem group *Doryopteris-Lytoneuron-Ormopteris* clade, TD = *Trachypteris+Adiantopsis+Doryopteris-Lytoneuron-Ormopteris* clade. D = *Doryopteris* clade, L = *Lytoneuron* clade, O = *Ormopteris* clade.

These clades (DO in Fig. 1) were found to be nested in a clade comprising *Adiantopsis* and several species previously placed in *Cheilanthes* and *Pellaea* (SD clade in Fig. 1). *Trachypteris* was found to be the probable sister of this clade (TD in Fig. 1) and *Adiantopsis* was the putative sister to the rest of this clade (SD in Fig. 1). The remaining species were found to form a grade between *Adiantopsis* and the *Doryopteris*-*Ormopteris* clade.

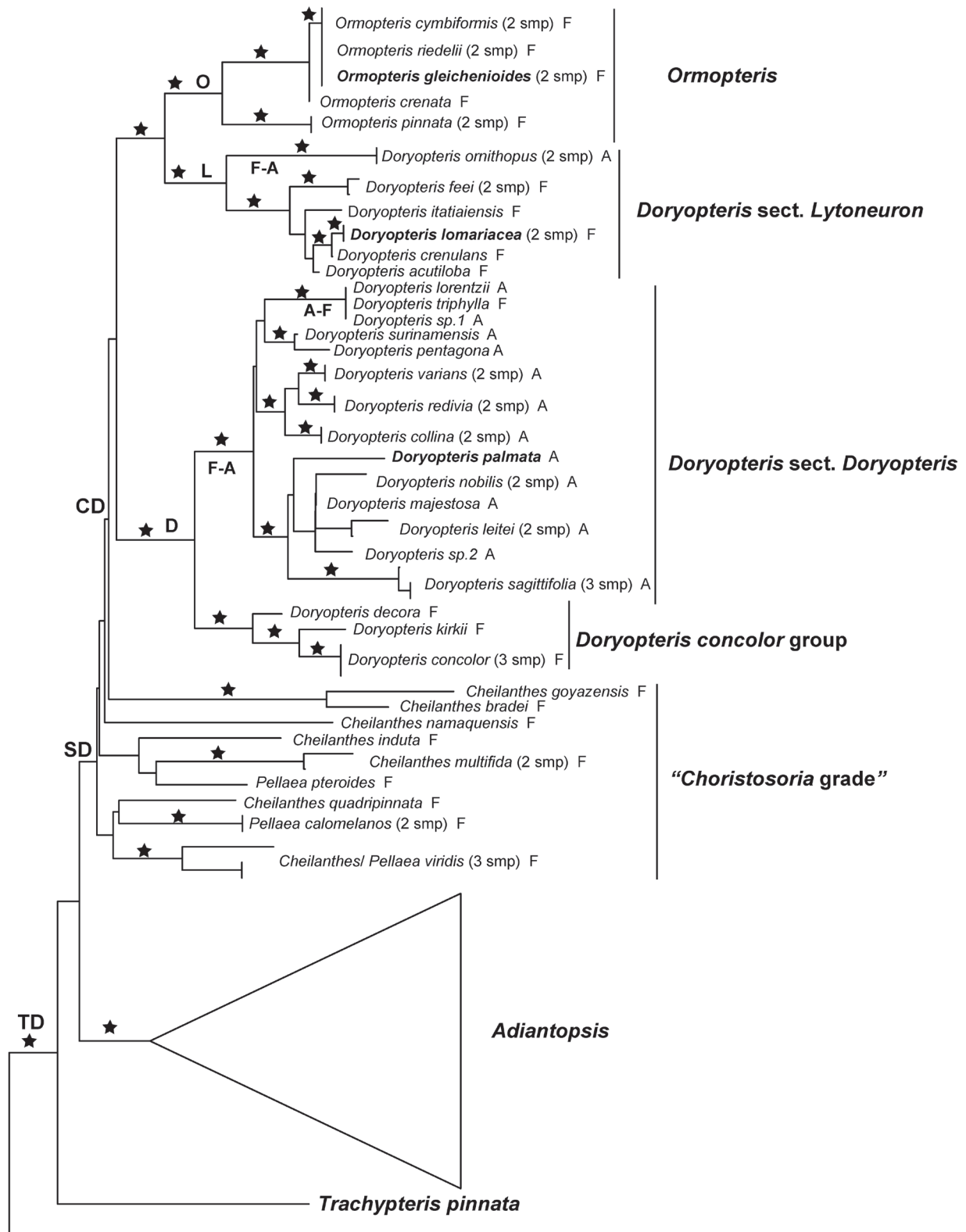


FIGURE 2. Phylogram obtained in the maximum likelihood analyses of the combined *rbcL* and *trnLF* dataset. Stars mark clades with a posterior confidence of $p \geq 0.95$ in the consensus tree of the Bayesian inference of the phylogeny. The *Adiantopsis* clade is collapsed for (Link-Perez *et al.* 2011). All abbreviation and lineage assignments as in Fig. 1. If more than one specimen was investigated, the number is given (e.g., “2 smp”). A = regularly anastomosed venation, F = free or irregularly anastomosed venation. F-A marked transitions from free to regularly anastomosing venation, A-F marked the transition from anastomosing to free venation. Note: The species *Doryopteris palmata* was originally submitted to the GenBank as *D. pedata* var. *palmata*.

Discussion

Exclusion of Doryopteris pedatoides and D. pilosa

Tryon (1942) already expressed some reservation about the placement of these two species and Yesilyurt (2004) excluded these species from the genus *Doryopteris*. The more recent phylogenetic results presented here and previously in Eiserhardt *et al.* (2011) provide further strong evidence that these taxa do not belong in *Doryopteris*. Instead, they are nested in a clade that includes the type species of *Pellaeopsis* Smith (1875: 289) and *Pteridella* Kuhn (1879: 1879). The clade comprises species of quite distinct morphology but all species occur in the Afro-Madagascan region. In turn, this clade is sister to the *Hemionitis* clade, including *Parahemionitis arifolia* (Burman f. 1768: 231) Panigrahi (1993: 90). With its southeast Asian distribution, the latter is the biogeographic exception in the otherwise Neotropical genus *Hemionitis* (Mickel 1974). Thus, these two species may be treated as part of a re-recognized and newly defined *Pellaeopsis* or part of a broadly defined *Hemionitis*. Further studies are required to investigate the position of five species endemic to Madagascar that are currently treated as *Doryopteris*, *D. cordifolia* (Baker 1891: 4) Diels (1899: 270), *D. latiloba* Christensen (1928: 213), *D. kitchingii* (Baker 1880: 327) Bonaparte (1913:16), *D. humbertii* Tardieu (1958: 144), *D. madagascariensis* Tardieu (1958: 148) by Roux (2009) and that were not included here. They may be best considered as *incertae sedis* until this is achieved.

Relationships of Ormopteris

This study confirms the separation of *Ormopteris* from *Pellaea* suggested in previous phylogenetic studies (Barbará 2003, Prado *et al.* 2007, Eiserhardt *et al.* 2011). The group has a rather complex taxonomic history, which illustrates the challenges of tracing relationships of cheilanthoid ferns using morphology alone. In the more recent classifications, *Ormopteris* was considered as a section of *Pellaea* (Tryon & Tryon 1982, Tryon *et al.* 1990) but this definition of *Pellaea* was repeatedly found to represent a polyphyletic taxon (see Prado *et al.* 2007, Zhang *et al.* 2007, Kirkpatrick 2007, Eiserhardt *et al.* 2011). Interestingly, the earliest studies describing species of *Ormopteris* considered close relationships with species belonging to *Doryopteris*, such as *Doryopteris triphylla*. For example, Kaulfuss (1824) recognized the latter together with *Ormopteris pinnata* (Kaulfuss 1824: 217) Lellinger (1972: 6) as members of the genus *Cassebeera*. A similar classification was later accepted in Hooker & Baker (1868), who accepted *Cassebeera* consisting of *Doryopteris triphylla*, *Ormopteris pinnata* (Kaulfuss 1824: 217) (Lellinger 1972: 6), and *Ormopteris gleichenioides* (Gardner 1843: 507) Smith (1875: 281) (see also Christ 1897). Other early studies considered these taxa as belonging to a broadly defined genus *Pellaea* (Link 1841, Prantl 1882). In the classification of Prantl (1882), species now placed in *Doryopteris* or *Ormopteris* were considered to belong to *Pellaea*, which in turn consisted of eight sections. A few years later, Diels (1899) recognized *Cassebeera* including *Doryopteris triphylla*, *Ormopteris gleichenioides* and *O. pinnata* as separate from *Doryopteris* and *Pellaea*, and placed the latter two in the Cheilanthinae (Fée ex Prantl 1872: 704) but *Cassebeera* in the Pteridinae Diels (1899: 288). Tryon (1942) separated *Doryopteris triphylla*, which he recognized as a member of *Doryopteris* sect. *Lytoneuron*, from the other species he placed in *Pellaea*. The segregation of *D. triphylla* and the *Ormopteris* group was accepted by Copeland (1974) who, however, recognized the latter as separate from *Pellaea*. A rather different interpretation was held by Pichi-Sermolli (1977) who regarded *D. triphylla* and the *Ormopteris* species as a single generic unit and assumed to be allied to *Doryopteris*. According to the recovered phylogeny, *D. triphylla* is, however, not closely related to the species of the *Ormopteris* group. Thus, the oldest available name for this clade is *Ormopteris*, and not *Cassebeera* that is based on *D. triphylla*. Evidence for the monophyly of the *Ormopteris* lineage was reported previously (Barbará 2003, Prado *et al.* 2007). Here, we report further support and have confirmed the sister relationship of *O. pinnata* to the clade comprising all other species (Fig. 2). In addition, we found *O. crenata* to be distinct, whereas the other three species show nearly identical plastid DNA sequences. The results confirm the results reported previously by Barbará (2003). Actually, some differences were found in an ambiguously aligned part of the *trnL-trnF* intergenic spacer that was excluded from the phylogenetic analyses (see Barbará 2003).

Relationships of Doryopteris concolor and relatives

A slightly similar confusion existed about the relationships of *Doryopteris concolor* and its relatives including *D. decora* Brackenridge (1854: 103). Most authors considered this species as part of *Doryopteris* (e.g., Diels 1899) but these mostly free veined species were considered to be *incertae sedis* (Tryon 1942) or to be part of *Cheilanthes* (Tryon & Tryon 1982, Tryon *et al.* 1990). Our results are consistent with other reports (Gastony & Rollo 1998, Yesilyurt 2004, Prado *et al.* 2007, Schuettpelz *et al.* 2007, Eiserhardt *et al.* 2011) in confirming a close or sister relationship of this group and the sect. *Doryopteris*.

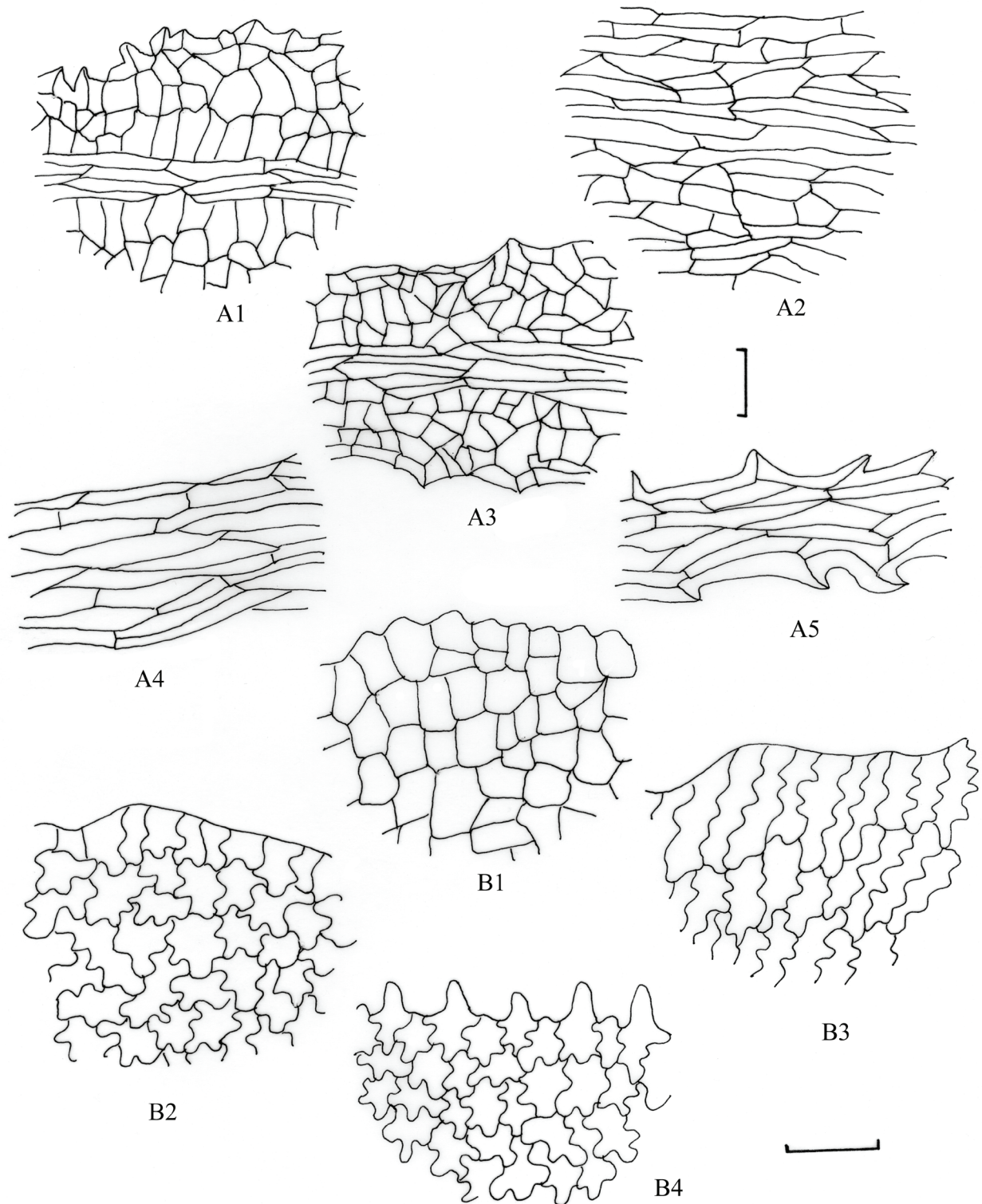


FIGURE 3. A. Types of the margin and cells of the rhizome scales: A1–A3. Lanceolate scales; A4–A5. Linear scales. B. Types of margin and indusium cells. Scale bars= 100µm. (based on: A1: *J. C. Yesilyurt, 732 & J. Prado (BM)*; A2 & B4: *J.C. Yesilyurt 519 & R.N. Cislinski, R.E. Cislinski (BM)*; A3: *J.C. Yesilyurt, 547 & J. Prado, P.H. Labiak (BM)*; A4: Herbarium specimen-GUA 01071; A5: *J. C. Yesilyurt, 738 & J. Prado (BM)*; B1: *J.C. Yesilyurt 726 & J. Prado (BM)*; B2: Herbarium specimen L0066049; B3: *J.C. Yesilyurt 739 & J. Prado (BM)*). (Drawn by J.C. Yesilyurt).

Tryon (1942) pointed out that they share similar scale types (at the base of the petiole) but differ in venation and on the condition of the sori. Species of the sect. *Doryopteris* clade possess anastomosed veins, with the exception of

Doryopteris triphylla, whereas the species of the *D. concolor* group possess either free veins, partially anastomosed or even fully anastomosed (as in *D. decora*). The soral condition in this group varies from moderately developed, with a marginal vascular commissure, which may be discontinuous (Figs 4 A3, A7), to well developed sori found on each vein-end with an indusium-like flap (Fig. 3 A1).

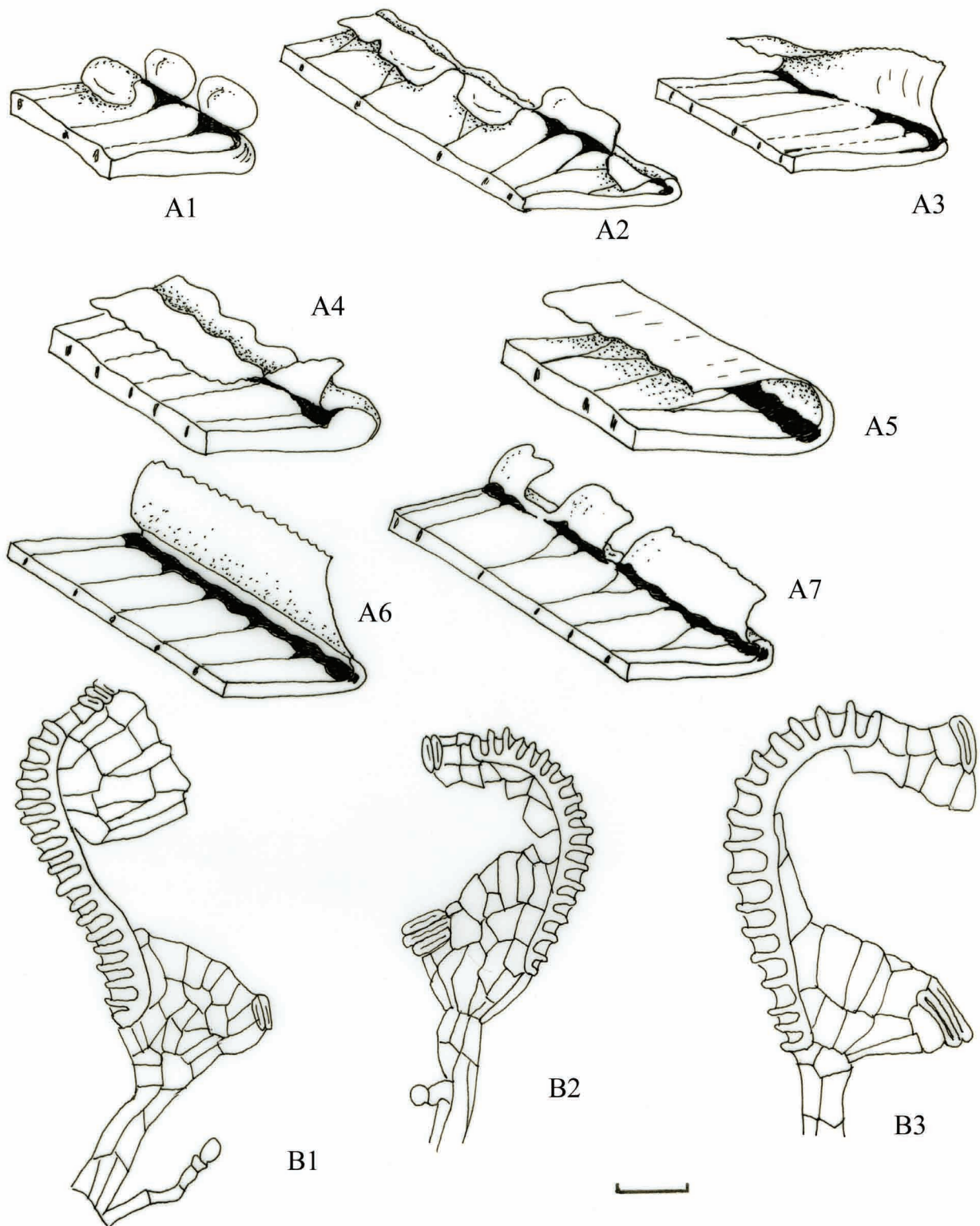


FIGURE 4. A. Types of receptacle and indusium (sketches only which were not based on any particular specimen); B. Types of sporangia and paraphyses. Scale bar= 100µm. (based on B1: Herbarium specimen US 2626408; B2: *J.C. Yesilyurt 529 & R.N. Cislinski, R. E. Cislinski* (BM); B3: *J.C. Yesilyurt 563 & J. Prado, P.H. Labiak* (SP). (Drawn by J. C. Yesilyurt).

In turn, the phylogeny did not provide support for the alternative proposal to include *Doryopteris concolor* and its relatives in the same section as *D. lomariacea* (Diels 1899). We confirm Tryon's hypothesis that *D. decora* and *D. concolor* are closely related to each other and to some extent to the section *Doryopteris*. We also recognize that this group requires further study to understand the separation of species. Although not represented in the present phylogeny, *D. nicklesii* (Tardieu 1948: 166) was nested within this group as well as with the rest of the Hawaiian species (Yesilyurt 2004, 2005) in the *trnL-F* based phylogeny.

Separation of Doryopteris and Lytoneuron

Early studies divided the genus *Doryopteris* into two lineages based on the venation pattern. Anastomosed species were placed in section *Eudoryopteris* (= *Doryopteris*) whereas the free veined species were placed in section *Lytoneuron* (Klotzsch 1847).

Diels (1899) followed Klotzsch (1847) in adopting a broad definition for *Doryopteris*, which was adhered to and upheld by Tryon (1942). However, Tryon (1942) treated *Doryopteris concolor* and relatives as *incertae sedis* and excluded them in later treatments (Tryon & Tryon 1982). The concept of the two sections is supported by the phylogeny because the “*Doryopteris*” clade comprises species recognized as section *Doryopteris* and the “*Lytoneuron*” clade has species recognized as section *Lytoneuron*. As mentioned above (and further comments below), *D. triphylla* is the only exception. Tryon (1942) placed this species within the sect. *Lytoneuron*. The *Lytoneuron* clade is mainly distinguished from sect. *Doryopteris* by the occurrence of two vascular bundles at the base of the petiole and the long-linear scales. Actually, the placement of *Ormopteris* has increased the separation of the two sections and rejects the definition of the genus that was accepted until now.

Placement of Doryopteris triphylla

Since its discovery, this species has been placed in different genera (e.g. *Pteris*, *Pellaea*, *Ormopteris*, *Doryopteris*) and played a major role in the definition of both *Ormopteris* and *Doryopteris*. Most recently, it has been argued that it represents a monotypic genus (de la Sota & Guidice 2004). The species is of special interest because it is the type of the oldest generic name *Cassebeera* (Kaulfuss 1824) applicable to *Doryopteris* and related genera (see Pichi-Sermolli 1977). The placement of this species in *Doryopteris* made it therefore necessary to conserve *Doryopteris* against *Cassebeera* (Tryon 1979). The reported nested position in sect. *Doryopteris* underlines the importance of this name conservation and reject proposals of a segregate genus name. However, the reported results are remarkable.

Doryopteris triphylla (Fig. 2) is the only free-veined species nested in the *Doryopteris* clade. Most remarkably, the species shares plastid DNA sequence with *D. lorentzii* (Hieronymus 1896: 392) Diels (1899: 270), a species with partially anastomosed venation. The same plastid DNA sequences were also found in a species (*Doryopteris* sp.1) of unclear identity, which has anastomosed venation. These results may be explained by contamination during processing the material in the laboratory, although careful checking of the laboratory protocols did not unearth evidence supporting this hypothesis. Thus, we need to consider alternative hypotheses to explain why two morphological distinct species appear to share the same plastid DNA. The most likely hypothesis is based on the assumption that at least one of these species originated from hybridization. Indeed, some evidence was found suggesting *D. lorentzii* to be a hybrid offspring with *D. triphylla* as one putative parent. The hypothesis of hybrid origin of *D. lorentzii* is supported by the abortion of 20–30% of the spores per specimen and karyological evidence for irregular meiosis with ca. 34–35 bivalents and ca. 21 univalents (a probable triploid) (reported by Yesilyurt, 2004). In contrast, *D. triphylla* showed ca. 29–30 bivalents (diploid). As mentioned above, the same plastid DNA was also found in *Doryopteris* sp.1. This specimen of unclear identity carried morphological features indicating that the specimen is a putative hybrid. Further evidence of species originated from hybridization was identified elsewhere in the *Doryopteris* clade. Karyological preparations of *Doryopteris majestosa* (Yesilyurt 2007: 212) found c. 28 bivalents and ca. 18 univalents (ca. triploid), while its sister species, *D. nobilis* (Moore 1862: 932) Christensen (1905: 204) has 29 or 30 bivalents (diploid) (Yesilyurt 2004).

Classification of Doryopteris and relatives

The results presented here show strong evidence that the current classification of these ferns does not reflect adequately their phylogenetic relationships. A new generic concept is required to reflect this. However, it is also important to take into account the uncertainties of the current results. The existing molecular phylogenetic results recovered several clades with Bayesian posterior values $p \geq 0.95$, such as the *Doryopteris concolor* group, sect. *Doryopteris*, sect. *Lytoneuron*, and *Ormopteris*. It also provided posterior confidence in the sister relationship of the *D. concolor* group and sect. *Doryopteris* and the sister relationship of sect. *Lytoneuron* and *Ormopteris*. However, the node showing sister relationships between these two pairs of sister clades (OD in Figs 1, 2) lacked support. Similarly, the nodes of

the next relatives lacked support and this group is here summarized as the *Choristosoria* grade. The name is based on *Choristosoria* Kuhn (1879: 13) with the type *Pellaea (Choristosoria) pteroides* (Linnaeus 1767: 130) Prantl (1882: 420) (Fig. 2). In fact, the next node with considerable support includes all clades of the stem of the *Doryopteris* clade (SD clade in Fig. 1, 2) as well as *Trachypteris* (TD in Figs 1, 2). Thus, the current results do not provide support to re-define *Doryopteris* by including *Ormopteris* because we cannot exclude the possibility that species now found to be part of the *Choristosoria* grade will turn out to be nested within the *Doryopteris*+*Ormopteris* clade with additional DNA sequence data.

Therefore, it may be best to recognize three genera until more comprehensive analyses become available. The proposed classification minimizes the required taxonomic changes and maximizes the possibility to recognize these genera based on diagnostic features. Specifically, we recommend restricting the definition of the genus *Doryopteris* to the sister clade of the *D. concolor* group and sect. *Doryopteris*. We also recommend acceptance of *Ormopteris* as a segregated genus and introduce *Lytoneuron* as a separate genus. Of course, this proposal has the disadvantage of increasing the number of small genera and does not provide a treatment for the species recognized here as part of the *Choristosoria* grade.

The *Choristosoria* grade comprises species previously placed in the polyphyletic genera *Cheilanthes* and *Pellaea*. There are quite distinct morphological differences between them and no obvious morphological similarity exists that allows identification of this group, or its relationships to *Adiantopsis* and *Doryopteris-Lytoneuron-Ormopteris*. However, the group shows some interesting biogeographic patterns. Species of this group occur either in eastern South America or in Afro-Madagascar. Only some more widespread species also have occurrences in Asia. It is also worthy of note that some of these species were previously placed in now widely forgotten genera such as *Choristosoria* Mett ex Kuhn (1879) with *Pellaea pteroides* as the type, and *Pteridellastrum* Prantl (1882: 419) that included *Cheilanthes viridis* Forsskal (1775: 186) (Swartz 1806: 127), *Cheilanthes quadripinnata* Kuhn (1868: 74), and *Pellaea pteroides*, with several species found nested in this grade. Here, we selected the oldest available generic name nested in the grade but future studies may need to consider also the option of multiple clades replacing this grade. The separation of this grade from the genus *Pteridella* Kuhn (Kuhn 1879: 1879) requires further attention. *Pteridella* was already mentioned above in the context of *Doryopteris pedatoides* and *D. pilosa*. This genus is based on the type *Pteridella doniana* (J. Smith ex Hooker 1858: 137) Mettenius ex Kuhn (1879: 13) and includes species of rather similar leaf morphology such as *Pellaea angulosa* (Bory ex Willdenow 1810: 377) Baker (1874: 153), *Pellaea boivinii* Hooker (1858: 147), and *Pellaea dura* (Willdenow 1810: 376) Hooker (1858: 139) (see Eiserhardt *et al.* 2011). However, several species found to be placed in the *Choristosoria* grade were mentioned in older classification under sect. *Pteridella* (Prantl 1882; Diels 1899), such as *Pellaea calomelanos* (Swartz 1801: 70) Link (1841: 61).

In summary, the results highlight the problems of morphology-based delimitation of genera in the cheilanthoid ferns. In this, this study is consistent with other studies on the generic classification of these ferns published since the application of molecular phylogenetics (Gastony & Rollo 1995, 1998). The results are also in agreement with the assumption that these problems are caused partly by convergent evolution (e.g. Ranker, 1990, Gastony & Rollo 1995, Kirkpatrick 2007, Rothfels *et al.* 2008, Sigel *et al.* 2011). In addition, this study highlights new evidence that biogeographic ranges may provide crucial information about the classification of cheilanthoid ferns, because the majority of species in the *Doryopteris-Lytoneuron-Ormopteris* clade occur in Eastern South America. With the exception of *D. concolor* group, all Paleotropical species were removed from *Doryopteris* and placed either in *Calciphlopteris* (Yesilyurt & Schneider 2010) or proposed here to be excluded, such as *D. pedatoides* and *D. pilosa*. The other Paleotropical species recognized under *Doryopteris* (sensu Tryon 1942) have not yet been sampled and thus are considered as *incertae sedis*, also based on their morphological characters.

Taxonomic Treatment

The taxonomy of *Doryopteris* has remained stable for the majority of the species since Tryon's (1942) revision. However, the taxonomy has had some complexities due to hybridization events (Sehnm 1961, 1972), and with the presence of polyploid species, which have been confirmed during the revision of the genus *Doryopteris* (Yesilyurt 2004; 2005).

Characters such as size, shape, and (to some degree) the dissection of the fronds and colour of the petiole have been used in the past to delineate the species; these characters are highly plastic. During the revision of the genus (Yesilyurt, 2004) a thorough study of the characters for morphological phylogenetic analyses has enabled a more satisfactory circumscription, at both generic and species level. As a result, a few species that were considered synonyms by Tryon

(1942) have been re-established, and with the present phylogeny most, if not all, these difficulties have been further clarified.

The genus *Doryopteris* as currently delimited by Tryon *et al.* (1990) has 25 species, the systematic studies of the genus (*sensu lato*) are still ongoing and, according to Yesilyurt (unpublished data), the number of species will certainly increase (with the exception of those taxa that have been here sampled, the species concept of the remaining taxa will be based on macro- and micro-morphology (including spores) and cytological data, which was possible for a few taxa).

Key to the genera of species traditionally placed in the genus *Doryopteris*

1. Two vascular bundles at the base of the petiole (best seen close to the insertion with the rhizome); scales of rhizome and petiole bases linear to linear-lanceolate; lamina varying from simple, entire to 3-lobed, pedate to pedate-pinnatifid to 2-pinnatifid; venation pattern predominantly free (except *L. ornithopus*) *Lytoneuron*
- One vascular bundle at the base of the petiole; scales of rhizome and petiole bases varying from ovate-lanceolate to long-lanceolate; lamina dissection diverse, from sagittate, pedate to pinnate; venation pattern commonly anastomosed, few species with veins free and/or partially anastomosed 2
2. Rhizome erect to sub-erect, short to long and/or slightly decumbent; scales of rhizome and petiole bases clathrate, varying from lanceolate to more or less ovate-lanceolate; lamina sagittate to pedate, pedate-pinnatifid to 3-pinnatifid *Doryopteris*
- Rhizome short to short-creeping; scales of rhizome and petiole bases variable, clathrate to non-clathrate and varying from lanceolate to long-lanceolate (rarely lanceolate-ovate); lamina 1-pinnate to 3-pinnate *Ormopteris*

Doryopteris J.Sm., J. Bot. (Hooker) 3: 404. 1841; emend. J.C. Yesilyurt, *nom. cons.*

Type species:—*Doryopteris palmata* (Willd.) J. Sm., J. Bot. [Hooker] 4: 163. 1841. = *Pteris palmata* Willd., Sp. Pl., ed. 4 [Willdenow] 5: 357. 1810. Type:—VENEZUELA. Distrito Federal: Caracas, *Bredemeyer s.n.* (B–image seen).

Homotypic synonyms:—

Cassebeera Kaulfuss (1824: 216). Type species:—*Cassebeera triphylla* (Lam.) Kaulf. = *Adiantum triphyllum* Lam., Encycl. [J. Lamarck & al.] 1(1): 41. 1783.

Bakeriopteris Kuntze (1891: 807), C. Chr., Index Filicum: 148. 1905. *nom. superfl.* for *Cassebeera* Kaulf.

Heteropteris Fée, Crypt. Vasc. Bresl 1: 123. 1869. Type species:—*Heteropteris doryopteris* Fée.

Tryonella Pic.Serm., Webbia 29: 14. 1974. *nom. nov.* for *Heteropteris* Fée.

Plants terrestrial or rupestral, to 30(–60) cm tall. Rhizomes erect to sub-erect or slightly decumbent; scales of rhizome and petiole bases clathrate, lanceolate to more or less ovate-lanceolate (Fig. 3 A1–A3). Petiole black to brown or dark-brown; cross section terete, sub-terete, sulcate to ridged; indumentum of short hairs, fibrils (scale-like) or acicular trichomes; with one vascular bundle at base, usually U- or V-shaped. Fronds monomorphic to dimorphic. Lamina dissection diverse, varying from sagittate to pedate, pedate-pinnatifid to 3-pinnatifid (sometimes becoming almost pinnate at the base of the lamina) and palmate to palmate-digitate; glabrous or with trichomes, 1–3-celled, sometimes acicular and/or fibrils. Veins free, partially or totally anastomosing, without included veinlets; vein-ends usually free and may end in hydathodes. Sori predominantly marginal, only rarely submarginal, receptacle forming a continuous line (vascular commissure) (Fig. 4 A6) or sori separate on each vein end (no commissure/connection) (Fig. 4 A1); sporangia maybe very densely packed giving a false impression of a continuous vascular commissure. Pseudo-indusium comprises the reflexed lamina margin, which may or may not be continuous around the lamina; pseudo-indusium margin smooth to somewhat irregular (Figs. 3 B1, B2, B4). Paraphyses absent (except for *D. kirkii* and *D. palmata* which have very small, bicellular paraphyses). Sporangia stalks more or less same length as sporangium or shorter to medium-stalked; basal cell of sporangium sometimes conspicuous. Spores predominantly rugulose and cristate.

Distribution:—Central to South America, South Africa, Hawaiian Islands (one species widely distributed).

Notes:—The characters that distinguish the genus *Doryopteris* from *Lytoneuron* and *Ormopteris* are based on the number of vascular bundles at the base of the petiole, petiole shape and indumentum, lamina dissection, venation type, soral condition, spore (ornamentation type rather than size).

The concept includes *Doryopteris triphylla*, which Tryon (1942) included in *Lytoneuron* due to its free venation pattern, and *Doryopteris lonchophora* (Mettenius 1859: 4) Smith (1875: 289), which was excluded by Tryon (1942) on the basis of the anatomy of the receptacle. It also includes the members from the sub-clade (Fig. 2) that diverged from *Doryopteris sensu stricto* clade and comprised *Doryopteris concolor*, *D. kirkii* (Hooker 1861: 81) Alston (1956: 14), as well as *D. decora* and its allies from Hawaiian Islands. With the exception of *Doryopteris triphylla*, *D. concolor*

and *D. tryonii* that have free venation, and *D. lorentzii* and all the rest of Hawaiian species (except *D. angelica* K. Wood & W.H. Wagner in Wagner *et al.* (1999: 147)) that have partially (rarely to) anastomosed veins, all the remaining taxa have anastomosed venation pattern (Yesilyurt, 2005). An exception is *D. lonchophora*, which has a discontinuous soral line (Figs. 4A2, A3, A7) and even has some parts of the sori naked (without any kind of indusium or reflexed margin).

The list of species presented here has been based on Tryon *et al.* (1990) concept for *Doryopteris*, which comprised 25 species. It excludes the taxa that have been referred to the sect. *Lytoneuron* (which is here being proposed as a new genus), except *D. triphylla*, and includes the recently described species. Full systematic account and other nomenclatural questions are being on their final revision and will be presented elsewhere, which will include the status of *Doryopteris majestosa*, as it has been flagged as putative *nom. superfl.* because one of the cited specimen on the examined material being an isotype of a published species.

List of species:

- Doryopteris adornata* J. C. Yesilyurt, Bot. J. Linn. Soc. 158: 73–77. 2008.
Doryopteris collina (Raddi) J. Sm., J. Bot. (Hooker) 4: 163. 1841.
Doryopteris concolor (Langsd. & Fisch.) Kuhn, Reisen Ost Afr. [Decken] 3 [3]. Bot.: 19. 1879.
Doryopteris crenulans (Fée) H. Christ in Schwacke, Pl. Nov. Mineiras 2: 26. 1900.
Doryopteris decora Brack., U.S. Expl. Exped., Filic. 16: 103, t. 13, f. 1. 1854.
Doryopteris decipiens J. Sm., Hist. Fil. 289. 1875.
Doryopteris kirkii (Hook.) Alston, Bot. Soc. Brot. sér. 2, 30: 14. 1956.
Doryopteris leitei (R.M. Tryon, Amer. Fern J. 36: 48. 1946) J. C. Yesilyurt, *stat. nov.*
Doryopteris lonchophora (Mett.) J. Sm., Hist. Fil. 289. 1875.
Doryopteris lorentzii (Hieron.) Diels, Nat. Pfl. 1 [4]. 270. 1899.
Doryopteris nobilis (T. Moore) C. Chr., Ind. Fil. 244. 1905.
Doryopteris majestosa J. C. Yesilyurt, Amer. Fern J. 97(4): 212. 2008. *nom. superfl.?*
Doryopteris palmata (Willd.) J. Sm., J. Bot. (Hooker) 4: 163. 1841.
Doryopteris pedata (L.) Fée, Mém. Foug., 5. Gen. Filic. 133. 1850–1852.
Doryopteris pentagona Pic. Serm., Webbia 60(1): 231. 2005.
Doryopteris rediviva Fée, Crypt. Vasc. Bresil 2: 30, t. 89, f. 1. 1872.
Doryopteris sagittifolia J. Sm., J. Bot. (Hooker) 4: 163. 1841.
Doryopteris stieri Rosenst., Hedwigia 46: 86. 1906.
Doryopteris surinamensis J. C. Yesilyurt, Brittonia 60(1): 63. 2008.
Doryopteris triphylla (Lam.) H. Christ, Bull. Herb. Boissier II, 2: 546. 1902.
Doryopteris varians (Raddi) J. Sm., J. Bot. (Hooker) 4: 163. 1841.

Lytoneuron (Klotzsch) J. C. Yesilyurt, *comb. & stat. nov.*

Basionym:—*Doryopteris* sect. *Lytoneuron*

Type species:—*Doryopteris lomariacea* Klotzsch, Linnaea 20: 343. 1847 = *Lytoneuron lomariaceum* (Klotzsch) J. C. Yesilyurt, *comb. nov.*

Type:—BRITISH GUIANA: Without locality, without date, *Schomburgk 1197* (holotype BM!, isotype K!).

Synonyms:—*Pellaea* sect. *Doryopteridastrum* Fée ex Prantl (1882: 418), *nom. nud.* Type species:—*Pellaea quinquelobata* Fée, Crypt. Vasc. Bresil 1: 42, t. 10, f. 1. 1869.

Plants terrestrial or rupestral, to 30(–50) cm tall. Rhizome decumbent to horizontal; scales of the rhizome and petiole bases clathrate to non-clathrate; linear to linear-lanceolate (Fig. 3 A4–A5), with or without toothed margin (Fig. 3 A5). Petiole terete, sub-terete, rarely sulcate, sometimes with conspicuous roughened to verrucose texture; indumentum of short and/or lanose hairs, fibrils (scale-like), these sometimes with glandular tips or adpressed scales; with two vascular bundle at the base, which unite towards the base of the lamina. Fronds monomorphic to dimorphic. Lamina dissection diverse, varying from simple, entire to 1–3-lobed, pedate, to pedate-pinnatifid to 2-pinnatifid; glabrous or with minute trichomes or fibrils (scale-like). Veins predominantly free (except *Lytoneuron ornithopus* (Mettenius 1867: 166) J. C. Yesilyurt) which has anastomosed venation; vein-ends usually free and forming hydathodes. Sori marginal to predominantly submarginal. Receptacle forms a discontinuous line (vascular commissure) (Fig. 4 A2–A3, A7), usually

forming a narrow or broad line (Fig. 4 A4), giving an aspect of a true indusium. Pseudo-indusium margin usually irregular or crenulated (Fig. 3 B2–B3). Paraphyses often present (Fig. 4 B1), usually tri-quadrangular. Sporangia stalks usually long-stalked (more or less 1 ½ longer than sporangium length); basal cell of sporangium absent or inconspicuous. Spores predominantly smooth to rugulate.

Distribution:—South America, with the majority of the species endemic to Brazil

Notes:—Klotzsch (1847) established section *Lytoneuron* including *Doryopteris geraniifolia* (Raddi 1819: 293) (Klotzsch 1847: 343) (= *D. concolor*) and species from *Cassebeera*. The concept was adopted and followed by Tryon (1942). The concept excludes *Doryopteris triphylla*, which Tryon (1942) included in *Lytoneuron* due to its free venation pattern alongside with *D. concolor*.

The main characters that distinguish the genus *Lytoneuron* from *Doryopteris* and *Ormopteris* are based on the number of vascular bundles at the base of the petiole, petiole shape and indumentum (including scales at the base), lamina dissection, venation type, soral condition and spores (type rather than size).

As stated above, full systematic account and nomenclatural questions including lectotypifications, are undergoing revision and will be presented elsewhere. Type information is limited to citation of type material as further type specimens remain to be investigated to determine their status.

List of species:

Lytoneuron acutilobum (Prantl) J.C.Yesilyurt, *comb. nov.*

Basionym:—*Pellaea acutiloba* Prantl in Bot. Jahrb. Syst. 3: 425. 1882.

Type material:—*Glaziou 2471, 7262* (Brazil, RJ).

Lytoneuron crenulans (Fée) J.C.Yesilyurt, *comb. nov.*

Basionym:—*Pellaea crenulans* Fée, Crypt. Vasc. Brésil 2: 27, t. 87, fig. 3. 1872.

Type material:—*Glaziou 5345, 5343* (Brazil, RJ)

Lytoneuron itatiaense (Fée) J.C.Yesilyurt, *comb. nov.*

Basionym:—*Pellaea itatiaensis* Fée, Crypt. Vasc. Brésil 2: 26, t. 88, fig. 1. 1872.

Type material:—*Glaziou 5348* (Brazil, RJ)

Lytoneuron feei (Brade) J.C.Yesilyurt, *comb. nov.*

Basionym:—*Doryopteris feei* Brade, Arch. Inst. Biol. Veg. Rio de Janeiro 1: 226, fig. 4 & t. 5. 1935.

Type material:—*Toledo & Brade 6496; Kuhlman s.n.* (Brazil, RJ)

Lytoneuron lomariaceum (Klotzsch) J.C.Yesilyurt, *comb. nov.*

Basionym:—*Doryopteris lomariacea* Klotzsch in Linnaea 20: 343. 1847.

Type material:—*R. Schomburgk 1197* (British Guiana)

Lytoneuron ornithopus (Hook. & Baker) J.C.Yesilyurt, *comb. nov.*

Basionym:—*Pellaea ornithopus* Mett. ex Hook. & Baker, Syn. Fil. 166.1867. (*Pellaea lomariacea* (Klotzsch) Hook. var. *digitatopalmata* Hook., Sp. Fil. 2: 133. 1858)

Type material:—*Gardner 5298* (Brazil, MG)

Lytoneuron paradoxum (Fée) J.C.Yesilyurt *comb. nov.*

Basionym:—*Cassebeera paradoxa* Fée, Mém. Fam. Foug. 7: 30, t. 20, fig. 2. 1857, as *Cassebeera*.

Type material:—*Gardner 5930* (Brazil, RJ)

Lytoneuron quinquelobatum (Fée) J.C.Yesilyurt *comb. nov.*

Basionym:—*Pellaea quinquelobata* Fée, Crypt. Vasc. Brésil 1: 42, t. 10, fig. 1. 1869.

Type material:—*Glaziou 2055* (Brazil, RJ)

Lytoneuron rosenstockii (Brade) J.C.Yesilyurt *comb. nov.*

Basionym:—*Doryopteris rosenstockii* Brade, Bol. Mus. Nac. Rio de Janeiro 7: 143, t. 8. 1931.

Type material:—*Brade 9257* (Brazil, RJ)

Lytoneuron rufum (Brade) J.C.Yesilyurt *comb. nov.*

Basionym:—*Doryopteris rufa* Brade, Bol. Mus. Nac. Rio de Janeiro 5: 94, t. 2, fig. 2. 1929.

Type material:—*Bruno de Godoy 28* (Brazil, MG)

Lytoneuron subsimplex (Fée) J.C.Yesilyurt *comb. nov.*

Basionym:—*Pellaea subsimplex* Fée, Crypt. Vasc. Brésil 1: 44, t. 4, fig. 3. 1869.

Type material:—*Glaziou 3160* (Brazil, RJ)

Lytoneuron tijucanum (Brade & Rosenst.) J.C.Yesilyurt, *comb. nov.*

Basionym:—*Doryopteris tijucana* Brade & Ros., Bol. Mus. Nac. Rio de Janeiro 7: 144, t. 9. 1931.

Type material:—*Brade 8598* (Brazil, RJ)

Ormopteris J.Sm. ex J. Sm., Hist. Fil.: 281. 1875.

Type species:—*Cassebeera gleichenioides* Gardner, Icon. Pl. 6: t. 507. 1843.

= *Ormopteris gleichenioides* (Gardner) J.Sm., Hist. Fil. 281. 1875. Type:—BRAZIL. Minas Gerais: Diamantina, Gardner 5295 (K).

Homotypic synonyms:—*Pellaea* sect. *Ormopteris* (J.Sm. ex J.Sm.) R.M.Tryon & A.F.Tryon, Rhodora 83: 135. 1981.

Pellaea subgenus *Ormopteris* (J.Sm.) C.Chr., Index Fil. (1906: XL).

Plants terrestrial or rupestral, to 30 (–60) cm tall. Rhizomes short, ascending (creeping) or horizontal; scales of rhizome and petiole bases clathrate to non-clathrate, lanceolate, long-lanceolate, lanceolate-ovate. Petioles with one vascular bundle at the base, terete to sulcate or strongly grooved, glabrous or with trichomes or scale-like fibrils. Fronds monomorphic to slightly dimorphic. Lamina dissection diverse, varying from 1-pinnate to 3-pinnate; glabrous or occasionally with hairs on the main veins; rachis terete or sulcate adaxially; glabrous. Veins free, and may form hydathodes. Sori marginal to predominantly submarginal. Receptacles discontinuous to rarely forming a continuous line (vascular commissure). Pseudo-indusium abruptly and strongly differentiated from the margin, smooth to somewhat irregular. Paraphyses absent. Sporangia sessile or stalks shorter than the sporangium capsule, length to up to twice its length (long-stalked); basal cell of sporangium sometimes conspicuous. Spores cristate to densely rugose.

Distribution:—South America, with most of the species endemic to Brazil.

Notes:—The concept clearly excludes *Doryopteris triphylla* as Diels (1899) recognized the genus *Cassebeera* with the following taxa: *D. triphylla*, *Ormopteris gleichenioides* and *O. pinnata*, and separates it from *Pellaea*. Although they have on various occasions been put together under the name *Cassebeera* (Kaulfuss 1824, Hooker & Baker 1868, Christ 1897, Diels 1899), the present recovered phylogeny shows that *D. triphylla* is not closely related to the species of the *Ormopteris* group. Therefore, as already stated above elsewhere, the oldest available name for this clade is *Ormopteris*, and not *Cassebeera*, which is based on *D. triphylla*.

The main characters that define this genus are based on the rhizome habit (creeping), scales (mix of clathrate and non-clathrate, lanceolate to long-lanceolate) and the lamina (varying from 1-pinnate to 3-pinnate).

List of species:

Ormopteris gleichenioides (Gardner) J.Sm., Hist. Fil.: 281. 1875.

Ormopteris pinnata (Kaulf.) Lellinger, Mem. New York Bot. Gard. 23: 6. 1972.

Ormopteris crenata (R.M.Tryon) Barbará, *comb. nov.*

Basionym:—*Pellaea crenata* R.M.Tryon, Contr. Gray Herb. 143: 68. 1942.

Type material:—Serra do Cipó, Minas Gerais, Brazil, July 12,13, 1940, Foster & Foster 624 (US)

Ormopteris cymbiformis (J.Prado) Barbará, *comb. nov.*

Basionym:—*Pellaea cymbiformis* J.Prado, Amer. Fern J. 83: 129, fig. 1. 1993

Type material:—Brazil: Goveia, Minas Gerais, April 9, 1982, Furlan *et al. s. n.* (SPF)

Ormopteris flavescens (Fée) Barbará, *comb. nov.*

Basionym:—*Pellaea flavescens* Fée, Crypt. Vasc. Bresil 1: 44. 1869.

Type material:—Brazil: Petrópolis, Rio de Janeiro, Glaziou 2473 (K)

Ormopteris riedelii (Baker) Barbará, *comb. nov.*

Basionym:—*Pellaea riedelii* Baker, Ann. Bot. (Oxford) 5: 213. 1891.

Type material:—Brazil: Riedel *s. n.* (K)

Incertae sedis

According to the present phylogeny and previous observations (Yesilyurt, 2004), a few taxa should be excluded from original concept of *Doryopteris*. These taxa also do not have the morphological characters that would fit the genera defined here and therefore these are placed as *incertae sedis* until further work is done to revise their morphological characters and compare with other cheilanthoid genera and also try to identify their affinities through DNA sequence data:

Doryopteris cordifolia (Baker) Diels, Nat. Pfl. 1 [4]. 270. 1899., not *Doryopteris cordifolia* J.Sm., J. Bot. (Hooker) 4: 163. 1841, *nom. nudum*. *Pteris cordifolia* Baker, J. Bot. 29: 4. 1891.

Distribution:—Madagascar.

- Doryopteris cyclophylla* A.R.Sm., Ann. Missouri Bot. Gard. 77(2): 262. 1990.
Distribution:—Venezuela (Neblina Massif).
- Doryopteris davidsei* A.R.Sm. Ann. Missouri Bot. Gard. 77: 262. 1990.
Distribution:—Venezuela (Guiana Shield).
- Doryopteris harrisoniae* (Jenman) C.Chr., Index Filic.: 244. 1905. *Pteris harrisoniae* Jenman, Gard. Chron. ser. 3, 24: 414. 1898.
Distribution:—British Guiana (Kaieteur falls).
- Doryopteris humbertii* Tardieu, Fl. Madagasc. Fam. 5. 1: 144. 1958.
Distribution:—Madagascar.
- Doryopteris kitchingii* (Baker) Bonap., Index Filic., Suppl. 16. 1913. *Pellaea kitchingii* Baker, J. Bot. 18: 327. 1880.
Distribution:—Madagascar.
- Doryopteris latiloba* C.Chr., Arch. Bot., Caen 2. Bull. Mens. 213. 1928.
Distribution:—Madagascar.
- Doryopteris madagascariensis* Tardieu, Fl. Madagasc. Fam. 5. 1: 148. 1958. Distribution:—Madagascar.
- Doryopteris pedatooides* (Desv.) Kuhn, Reisen Ost Afr. [Decken] 3 [3]. Bot.: 63. 1879. *Pteris pedatooides* Desv., Mém. Soc. Linn. Paris 6(3): 293. 1827.
Distribution:—Mascarene Islands (Mauritius, Réunion, Rodriguez).
- Doryopteris pilosa* (Poir.) Kuhn, Reisen Ost Afr. [Decken] 3 [3]. Bot.: 63. 1879. *Pteris pilosa* Poir., Encycl. [J. Lamarck & al.] 5: 717. 1804.
Distribution:—Madagascar.

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