



The new fern genus *Calciphlopteris* (Pteridaceae)

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Abstract

A new genus of Pteridaceae subfamily Cheilanthroideae is established for what has long been known as *Doryopteris ludens*. The newly erected genus is named *Calciphlopteris* in reference to its substrate specificity to limestone. *Calciphlopteris* can be found throughout Southeast Asia, from Indo-China to New Guinea and Australia. New combinations are established for the four known species (*Calciphlopteris alleniae*, *C. ludens*, *C. papuana* and *C. wallichii*). *Calciphlopteris* is characterized by having a horizontal rhizome, semi-clathrate scales, indumentum on the petiole and lamina usually with fibrils and/or semi- to non-clathrate scales, and sporangia with 32 echinate or cristate spores.

Key words: Asia, *Calciphlopteris*, Cheilanthroideae, *Doryopteris*, ferns, Pteridaceae, taxonomy

Introduction

The application of DNA sequences to reconstruct the relationships among extant ferns has generated an unprecedented improvement in our knowledge of their deeper relationships (Hasebe *et al.* 1994, 1995, Pryer *et al.* 2004, Schneider *et al.* 2004, Smith *et al.* 2006a) and aided in the clarification of taxonomic concepts at the species and genus levels. Several of these studies provided evidence to support the merger of monotypic or small genera into larger genera, e.g. *Ceterach* Lam. & DC., *Diellia* Brack., *Phyllitis* Ludw. and other satellite genera in *Asplenium* L. (Pinter *et al.* 2002, Schneider *et al.* 2004a, 2005); *Hyalothrighopteris* W.H. Wagner in *Campyloneurum* C.Presl (Kreier *et al.* 2007), whereas others found evidence for the reestablishment of previously questionable genera such as *Acanthocorus* Underw. & Maxon (Crane 1997), *Haplopteris* C.Presl (Crane 1997), *Pentarhizidium* Hayata (Gastony & Ungerer 1997), *Polytaenium* Desv. (Crane 1997), *Scoliosorus* T.Moore (Crane 1997) and *Synammia* C.Presl (Schneider *et al.* 2006). The discovery of new genera is less common but relevant examples include *Radiovittaria* (Benedict) E.H.Crane (Crane 1997) and *Serpocaulon* A.R.Sm. (Smith *et al.* 2006b). In summary, all these studies underline the value of identifying flaws in our generic concepts (Smith *et al.* 2006a).

Evidence for inconsistent generic concepts has been reported in all studies on the pteridoid ferns, one of the three most species rich lineages among extant ferns (Pryer *et al.* 2004, Schneider *et al.* 2004b, Smith *et al.* 2006a). The phylogeny of this fern lineage was the subject of several recent studies using either a single genomic marker regions such as *rbcL* (Hasebe *et al.* 1995, Prado *et al.* 2007, Zhang *et al.* 2005) or up to three chloroplast genome markers (Schuettpelz *et al.* 2007, Zhang *et al.* 2007). Except for the exhaustive study on the Neotropical *Eriosorus* Fée/*Jamesonia* Hook. & Grev. complex (Sanchez-Baracaldo 2004) and the vittarioids (Crane 1997) most studies using DNA sequences focused on the cheilanthoid ferns (Gastony & Rollo 1995, 1998, Zhang *et al.* 2007). As might be expected, these studies reinforced major conflicts between the current classification and the observed phylogenetic hypothesis (Gastony & Rollo 1995, 1998, Smith *et al.* 2006b, Zhang *et al.* 2007).

One especially important conflict is the position of *Doryopteris ludens* (Wall. ex Hook.) J.Sm. as it appears in all phylogenetic studies including this taxon (Prado *et al.* 2007, Schuettpelz *et al.* 2007, Zhang *et al.* 2007). This taxon has always been treated as a member of the predominantly Neotropical genus *Doryopteris* even in the revision presented by Tryon (1942). Rolla Tryon placed *Doryopteris ludens* in a distinct category called ‘miscellaneous’ within *Doryopteris*. Yesilyurt (2004) first reported the oddity of the relationships of *D. ludens* in her PhD thesis presented at the University of Reading. Yesilyurt’s study (A systematic revision of the genus *Doryopteris*) was an attempt to unravel and evaluate the generic circumscription—aiming to clarify the taxonomic concepts at species and genus levels. The study included all the problematic species related to *Doryopteris* such as *Doryopteris concolor* (Langsd. & Fisch.) Kuhn, *Heteropteris doryopteris* Fée and *Doryopteris ludens*.

In studies employing DNA sequences, *D. ludens* was not only found outside of the *Doryopteris* clade, but also as sister to all other cheilanthoid ferns—with the exception of some analyses indicating closer relationships to adiantoids (Prado *et al.* 2007, Schuettpelz *et al.* 2007, Zhang *et al.* 2007, Yesilyurt 2004). Subsequent closer study of morphological variation supported the segregation of *D. ludens* and relatives (Yesilyurt 2004). To resolve the phylogenetic conflict within the genus *Doryopteris*, we describe here a new genus for *D. ludens* and its relatives.

Taxonomy

Calciphlopteris Yesilyurt & H.Schneider, *gen. nov.*—Figs. 1A–C

Calciphlopteris gen. nov. *Doryopteridis affinis sed rhizomate breviter vel longe repenti, paleis rhizomatum lanceolatis vel anguste lanceolatis clathratis vel semiclathratis, petiolo tereti fasciculum vascularem unum tantum continenti, petiolo laminaque fibrillas (pilos squamiformes) atque squamas non clathratis vel semiclathratis ferentibus, sporangio plerumque longipedicellato 32 sporas continenti, plantis plerumque rupicola locus calcareos incolentibus differt.*

Type species:— *Calciphlopteris ludens* (Wall. ex Hook.) Yesilyurt & H.Schneid. = *Pteris ludens* Wallich ex. Hooker (1858: 210). Holotype: INDIA: Wallich 88 (K).

Plants terrestrial or rupicolous; essentially growing on limestone. *Rhizome* slender, short- to long-creeping, scales up to 3 mm, linear to ovate-lanceolate, acuminate to caudate, predominantly bicoloured, with clathrate to semi-clathrate centre, and paler, narrow to broad border, margin entire to dentate towards the apex. *Petiole* terete to slightly sulcate (towards) at the base of the lamina; one vascular bundle; dark brown, atropurpureous to black, base with scales as those of the rhizome, higher up the petiole with indumentum (generally dense towards the base of the lamina) usually scaly, scales semi- to non-clathrate, with fibrils, rarely with white hairs or glabrous. *Sterile* and *fertile fronds* dimorphic (architecture of fertile lamina more complex), sub-coriaceous to coriaceous; glabrescent to glabrous, indumentum on the abaxial side with glandular hairs and/or fibrils and non-clathrate scales at the base of the lamina; veins anastomosing, without included free veinlets. *Sterile fronds* up to 45 cm; lamina up to 17 cm, ranging from simple, entire or 3-lobed to pedate; oblong-oval, cordate, sagittate, hastate, lobed to pentagonal in outline; pinnae/segments 1–2(–4) pairs; the margins usually with a whitish or brown cartilaginous border, entire; hydathodes generally present on the upper surface; veins ending free near the margin (occasionally confluent in *C. allenae*); basal pinnae lobed basiscopically or not. *Fertile fronds* up to 65 cm; lamina up to 20(–25) cm; sagittate, hastate, pentagonal to broad-cordate or suborbicular in outline, 3-lobed to pedate, pedate-pinnatifid (pedate-2-pinnatifid); pinnae/segments 2–5(–6) pairs; ascending to patent, deltoid to long-lanceolate, acute or acuminate, predominantly with entire margins; basal pinna/segment with acroscopic and/or with basiscopic segments/lobes; first segment/lobe divided or not, falcate to lanceolate. *Sori* marginal, usually on a continuous vascular commissure (connecting the vein-tips), rarely interrupted at sinuses, covered by a continuous modified marginal indusium, without paraphyses; receptacle and indusium continuous, including in the sinuses; indusium with margin entire to slightly eroded.

Sporangium with pedicel 1–2(–2.5) times the capsule length; capsule without basal cell; annulus with 17–34 indurate cells; with 32 spores per sporangium. *Spores* trilete, tetrahedral to globose, echinate or cristate, without equatorial flange. Chromosome number $n = 29, 30$ or multiples thereof.

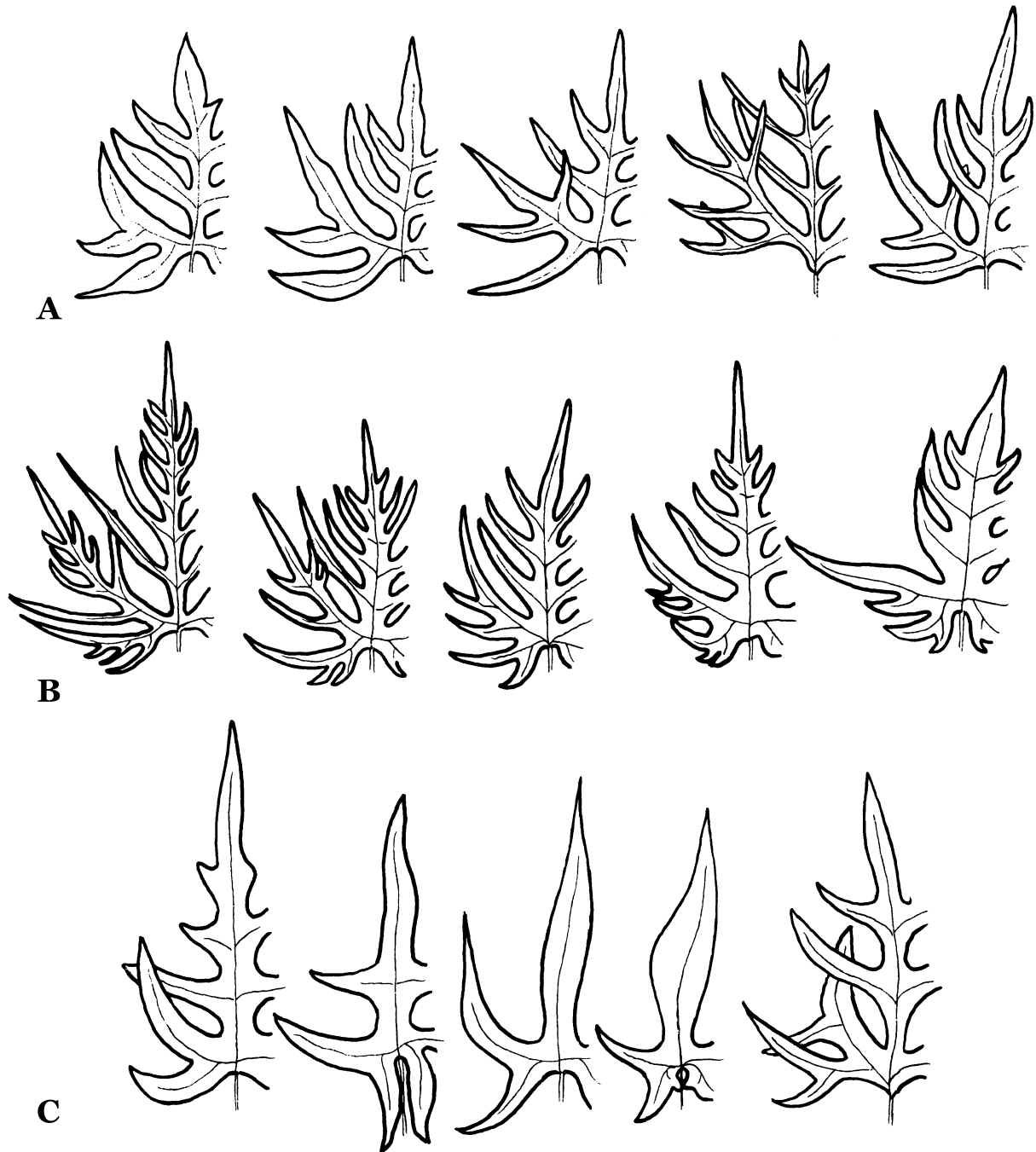


FIGURE 1. Sketches of fertile leaves showing their general attributes and morphological variation: **A.** *Calciophilopteris ludens*. **B.** *Calciophilopteris papuana*. **C.** *Calciophilopteris wallichii*.

Distribution:—Southeast Asia, from Indo-China to New Guinea (and Australia).

Habitat & Ecology:—exclusively on limestone outcrops.

Etymology:—the genus name is a composite from the Greek *calx* (limestone), *philus* (loving) and *pterus* (fern) and emphasizes the exclusivity of limestone outcrops as the natural habitat for this fern.

Diagnostic key to the species of *Calciphlopteris*

1. Basal pinna/segment with 2–4 basiscopic segments, all ascendant; first basiscopic segment with 1–3 lobes (Fig. 1B), conspicuous or not, ascendant; sinus (between pinnae/segments) usually narrow, acute or round (seldom slightly rectangular); fertile lamina pedate-pinnatifid to pedate-2(–3)-pinnatifid, broadly ovate to cordate-ovate, pinnae/segments 3–7 (Fig 1A), all equally ascendant, long lanceolate to linear lanceolate (except basal pinna)..... *C. papuana*
 - Basal pinnae/segment with 1–3 basiscopic segments, ascendant or not; first segment very rarely lobed; sinus (between pinnae/segments) rounded to slightly rectangular; fertile lamina pedate to pedate-pinnatifid, hastate to trilobed, ovate-lanceolate, slightly pentagonal or obovate, pinnae/segments 1–4, all equally ascendant or not, usually lanceolate (except basal one) 2
2. Scales of rhizome and base of petiole long lanceolate to linear lanceolate, caudate, margin (half way towards apex) dentate; fertile lamina generally sagittate to trilobed (rarely pedate), hydathodes absent; marginal veins regularly anastomosing along the leaf margin *C. alleniae*
 - Scales of rhizome and base of petiole lanceolate to long lanceolate, not caudate, margin (half way towards apex) remotely dentate to entire; fertile lamina hastate, pedate to pedate-bipinnatifid, hydathodes present (sometimes obscure); marginal veins ending free along the leaf margin 3
3. Basal pinnae with acroscopic and basiscopic segments; scales margin (half way towards apex) entire; fertile lamina commonly pedate-pinnatifid to pedate-2-pinnatifid, pentagonal, pinnae/segments 2–4, all equally ascendant; basal pinna/segment with 1(–2) acroscopic segment and 2–3 basiscopic segments/lobes (Fig. 1A), all ascendant; first basiscopic segment/lobe generally unlobed *C. ludens*
 - Basal pinnae with acroscopic pinnae only; scales margin (half way towards apex) dentate to occasionally dentate; fertile lamina commonly hastate to pedate (pedate-pinnatifid), ovate-lanceolate, slightly pentagonal, pinnae/segments 1–2(–3), basal pinna/segment ascendant, other segments/lobes patent to slightly ascendant; basal pinna/segment with 1(–2) basiscopic segment/lobe, which is usually unlobed and generally parallel to the petiole (Fig. 1C) ...
..... *C. wallichii*

1. *Calciphlopteris alleniae* (R.M.Tryon) Yesilyurt & H.Schneider, *comb. nov.*

Basionym:—*Doryopteris alleniae* Tryon (1962: 91, fig 1–4), as ‘*allenae*’. Holotype: MALAYSIA: Perak: Gunong Idong, near Perak, 24 May 1962, *B.M. Allen 4763* (GH). Paratypes: 12 January 1959, *B.M. Allen 4103* (GH, US), 13 August 1959, *B.M. Allen 4343* (GH).

Rhizome predominantly short-creeping, scales 3 mm, ferruginous, lanceolate to linear-lanceolate, caudate, margin dentate. *Petiole* terete, black, indument of fibrils, particularly dense towards the base of the lamina. *Sterile* and *fertile fronds* coriaceous; glabrescent, indument on the abaxial side with glandular hairs and/or fibrils, veins usually joined at the vein-ends (at the margin of the lamina). *Sterile fronds* up to 20 cm long; lamina up to 10 cm, simple, entire to 3-lobed, ovate to oblong-ovate, hydathodes absent. *Fertile fronds* up to 35 cm; lamina up to 15 cm; suborbicular, obovate to 3-lobed (rarely pedate); pinnae/segments conspicuously ascendant, long linear-lanceolate. *Indusium* with margin entire to more or less irregular. *Sporangium* with pedicel 1–1½ × the capsule length; annulus with up to 34 indurated cells. *Spores* light castaneous to dark castaneous, echinate.

Distribution:—known only from a few localities on the Malay Peninsula (Perak: Gunong Idong, Gunong Temurong and Selangor: Gua Batu).

Note:—there is an orthographic error in *Doryopteris allenae* which is regulated in the ICBN by Article 60.11, recommendation 60C.1 and it is here therefore, corrected (it should be *Calciphlopteris alleniae* instead of *C. allenae*).

Selected specimens:—MALAYSIA: *Ding Hou 709* (L); *Molesworth-Allen 4103* (GH), *4393* (GH), *4763* (GH, US).

2. *Calciophilopteris ludens* (Wall. ex Hook.) Yesilyurt & H.Schneider, *comb. nov.*—Fig. 1A.

Basionym:—*Pteris ludens* Wallich (1828: 88), *nomen nudum*, *Pteris ludens* Wall. ex. Hooker (1858: 210), *Lithobrochia ludens* (Wall. ex Hook.) Beddome (1865: t. 27), *Pellaea ludens* (Wall. ex Hook.) Prantl (1882: 419), *Doryopteris ludens* (Wall. ex Hook.) Smith (1875: 289). Holotype: INDIA: Wallich 88 (K).

Rhizome predominantly long-creeping, scales up to 3 mm, dark brown, lanceolate, margin entire. *Petiole* terete to sulcate adaxially towards the base of the lamina, dark brown to atropurpureous, indumentum usually with hairs (whitish), non-clathrate scales and fibrils. *Sterile* and *fertile fronds* glabrescent to glabrous, indumentum on the abaxial side with fibrils and non-clathrate microscales. *Sterile fronds* up to 35 cm; lamina up to 20 cm, sagittate to pedate; ovate to pentagonal; pinnae/segments 1–2(–3) pairs; hydathodes generally present (sometimes obscure). *Fertile fronds* up to 45 cm; lamina up to 25 cm, pentagonal to broad-cordate, pedate, pedate-pinnatifid (to pedate-2-pinnatifid); pinnae/segments in 2–4(–5) pairs; basal pinna/segment falcate, with 1(–2) acroscopic lobes and 2–3 basispic segments/lobes, which are ascendant, falcate to lanceolate, rarely the first basispic segment/lobe is divided; other pinnae/segments all equally ascendant, lanceolate to long-lanceolate. *Indusium* with margin entire to slightly eroded. *Sporangium* with pedicel 1–2(–2½) × the capsule length; capsule with annulus with 17–34 indurated cells. *Spores* dark castaneous, cristate.

Distribution:—India, Indochina, southern China, western parts of Malesia (Flores, Java, Malay Peninsula, Simbawa, Sumatra), Thailand, and Australia (where it was once recorded from north-eastern Queensland by *D.L. Jones s.n.* (BRI), see: Bostock 1998).

Note:—some specimens (*Congdon 617, Molesworth-Allen 2785, E. Smith 250A, Kerr 250, 11365*) show unique leaf and spore characters that are similar but not identical with characters observed in other species of *Calciophilopteris*. It was decided to assign these specimens here to *C. ludens*, because available collections are insufficient to make unequivocal taxonomic assignments. These specimens may represent either a unique form of *C. ludens* or an undiscovered species.

Selected specimens:—MALAYSIA: Perlis: *Molesworth-Allen 2816* (US, S). Kedah: *Alphonso & Samsuri 123* (BM); *Henderson 29066* (BM); *Littke 260* (L). INDONESIA: Java: *Horsfield s.n. 110* (BM); *Mosset 188* (C, GH, L, PE). THAILAND: *Geesink et al. 5949* (BM, L); *Hennipman 3029* (BM, L, NY, U, US); *Kerr 5476* (BM); *Kostermans 762* (L); *Larsen 5790* (BM, GH); *Rock 503* (US); *Shimizu et al. 13325* (C, L); *Tagawa et al. 1903* (L, US); . MYANMAR: *Dickason 7762* (GH); *Kress et al. 97-6017* (US); *J. F. Smith 89* (GH). VIETNAM (Cochinchina): *Larsen 8964* (GH); *Pierre s.n.* (GH). SINGAPORE: *Corner & Henderson 22815* (C). CHINA: *Yunan: Henry 13325* (MO, NY). INDIA: Assam: *Mann s.n.* (UC).

3. *Calciophilopteris papuana* (Copel.) Yesilyurt & H.Schneider, *comb. nov.*—Fig. 1B.

Basionym:—*Doryopteris papuana* Copeland (1911: 86). Holotype: PAPUA NEW GUINEA: Goodenough Bay, *King 208*, (MICH, isotype BO).

Rhizome slender, short- to long-creeping, scales up to 2.5(–3) mm, dark brown, lanceolate, to ovate-lanceolate, margin entire. *Petiole* terete, dark brown to atropurpureous, with fibrils and usually scaly, scales semi- to non-clathrate. *Sterile* and *fertile fronds* glabrescent to glabrous, indumentum on the adaxial side with fibrils on the main veins only, abaxial side with fibrils throughout (smaller on the lamina, bigger on the main veins) and non-clathrate to semi-clathrate microscales on the main veins. *Sterile fronds* up to 28 cm; lamina up to 15 cm, pedate; ovate to pentagonal; pinnae/segments 1–3 pairs; hydathodes present (sometimes obscure). *Fertile fronds* up to 42(–45) cm; lamina up to 27 cm; pentagonal to broadly-cordate or suborbicular, pedate-pinnatifid to pedate-bipinnatifid; pinnae/segments in 2–6(–7) pairs; basal pinnae/segment falcate, with 1–2 acroscopic lobes and 2–4 basispic segments/lobes, which are ascendant, falcate to lanceolate, first segment/lobe divided into 1–3 lobes, lobes ascendant, lanceolate; other pinnae/segments conspicuously ascendant, lanceolate to linear-lanceolate. *Indusium* with margin entire to slightly eroded. *Sporangium* with pedicel 1(–

1½) × the capsule length; capsule with annulus with 17–25 indurated cells. *Spores* castaneous to light castaneous, cristate.

Distribution:—endemic to New Guinea, mainly in the eastern part.

Selected specimens:—PAPUA NEW GUINEA: *Brass* 21853 (BM, GH, L, US); 21623 (GH, L); *Carr* 12372 (BM, L, NY); *Kairo* 629 (BM, L); *King s.n.* (BM, UC, PE); *Hartley* 10656 (GH, L).

4. *Calciphlopteris wallichii* (J.Sm.) Yesilyurt & H.Schneider, *comb. nov.*— Fig. 1C.

Basionym:—*Doryopteris wallichii* Smith (1841: 404), *Lithobrochia smithii* T.Moore (1862: 342), *nomen nudum*, based on *D. wallichii* J.Sm. Holotype: PHILIPPINES: Luzon, *Cuming* 238 (K, isotypes BM, C, G, L).

Rhizome usually short-creeping, scales 2.5(–3) mm, light brown, lanceolate to long-lanceolate, margin entire to rarely dentate. *Petiole* terete to slightly sulcate towards the base of the lamina; dark brown, atropurpureous, with fibrils. *Sterile* and *fertile fronds* sub-coriaceous; glabrescent, indumentum on the abaxial side with glandular hairs and fibrils on the main veins. *Sterile fronds* up to 30 cm; lamina up to 17 cm, ranging from simple, entire to sagittate, hastate, or basally lobed; hydathodes generally present on the upper surface only (sometimes obscure). *Fertile fronds* up to 40 cm; lamina up to 19 cm; sagittate, hastate, sub-pedate to rarely pedate, with 2(–3) pairs of pinnae/segments; basal pinna/segment falcate to lanceolate, conspicuously ascendant, with 1–2 basiscopic segment/lobes, which are ascendant to usually parallel with the petiole; other pinnae/segment broadly lanceolate to lanceolate, usually patente. *Indusium* usually with entire margin. *Sporangium* with pedicel 1–1½ × the capsule length; capsule with annulus with 20 (24) indurated cells. *Spores* usually castaneous to light castaneous, cristate.

Distribution:—Philippines (mainly Luzon).

Selected specimens:—PHILIPPINES: *Copeland* 95 (BM, C, S); *Curran* 15608 (BM, C). *Elmer* 6349 (C, NY); *Price* 2007 (BM, L, US); *Ramos* 33245 (BM, L); *Topping* 857 (C, GH, MO, NY, S); 1014 (GH, NY); 1247 (GH, US); 1219 (GH, NY); *Williams* 1501 (PE, UC).

Discussion

Evidence from both the distinctness of the chloroplast genome sequence which is presented in Yesilyurt (2004) and several recently published studies (Prado *et al.* 2007, Schuettpelz *et al.* 2007, Zhang *et al.* 2007), and from morphological features, supports recognition of this new genus. *Calciphlopteris* differs from *Doryopteris* and its relatives in having a short- to long-creeping rhizome; lanceolate to linear lanceolate, semi-clathrate (occasionally clathrate) scales; indumentum on lamina and petiole usually with fibrils and non-clathrate scales; a simple, entire, 3-lobed, pedate to pedate-bipinnatifid lamina; sori in a narrow, inconspicuous continuous vascular commissure (receptacle); the sporangium with pedicel up to twice the capsule length and containing 32 spores; the spores echinate or cristate. *Calciphlopteris* is restricted to limestone habitats and geographically distributed from Indo-China to New Guinea.

Members of the new genus were formerly treated as part of the cheilanthoid genus *Doryopteris* (*Doryopteris ludens sensu* Tryon (1942) and its allies, essentially on the basis of shared similarities in leaf morphology. Tryon (1942), however, pointed out that the rhizome scales were different from the majority of the *Doryopteris* species. Similarities of the lamina architecture between these two genera are likely the result of convergent evolution (Yesilyurt 2004). This argument found further support in the fact that similar leaves have evolved independently in several lineages of cheilanthoid ferns such as the *Aleuritopteris argentea* (S.G.Gmel.) Fée group and species of *Notholaena* R.Br.. Independent evolution of similar characters appeared to be commonly misleading in attempts to discover the generic classification of these ferns, as can be demonstrated by previous studies (Gastony & Rollo 1995, 1998, Zhang *et al.* 2007).

We here include three species as further members of the new genus *Calciphlopteris*: *C. alleniae*, *C. papuana*, and *C. wallichii* although we lack chloroplast genome sequence data for these additional species. This conclusion is based on morphological similarities of these three species with *C. ludens*, e.g. creeping rhizomes with semi- to non-clathrate scales, frond indumentum of fibrils (scale-like hairs) and scales (semi- to non-clathrate), usually the pedicel (sporangium stalk) up to twice as long as the capsule, 32 spores per sporangium and preference of limestone rocks as substrate. In short, all four species of *Calciphlopteris* share the same differences to the genus *Doryopteris*. This classification is also consistent with the distribution of these four species in Southeast Asia and Malesia, whereas true *Doryopteris* is restricted to the Neotropics except for seven species occurring in Afro-Madagascar and Hawaii, as well as the pantropically distributed *Doryopteris concolor*. We present this revision of the genus based on morphological evidence alone.

The recovery of a separate new genus occurring in the Southeast Asian-Australasian region provides further evidence for the importance of this region as a refuge for fern diversity during Caenozoic climatic fluctuations. This hypothesis is supported by the remarkable isolation in phylogenetic reconstructions and observed genetic differences to its sister clade (Schuettpelz *et al.* 2007), indicating a long separation of this genus from all other cheilanthoid ferns. The most iconic examples for Malesian relicts are likely the Dipteridaceae and Matoniaceae, which are members of a lineage that had its greatest diversity in the mid-Mesozoic (Tidwell & Ash 1994). The newly described genus differs from these two lineages by being part of the derived fern lineage that began to diversify in the Upper Cretaceous (Schneider *et al.* 2004). The recovery of this isolated genus with a distinct position in the phylogeny of the Pteridaceae holds the promise of further similarly intriguing discoveries by closely studying the fern diversity of Southeast Asia and other parts of the world.

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