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Evolution of epiphytes in Davalliaceae and related ferns

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The evolution of epiphytes in Davalliaceae was investigated by field observations and molecular phylogenetic analyses. Field studies revealed that in Davalliaceae and related ferns, epiphytes in a broad sense are classified into climber, secondary hemi-epiphyte, and obligate epiphyte, based on combinations of the places (ground vs. tree) of inferred spore germination and sporophyte growth. Some species of Davalliaceae have multiple life forms, i.e. secondary hemi-epiphyte and obligate epiphyte, whereas others are obligate epiphytes. Phylogenetic trees obtained from *rbcL* and *accD* gene sequences supported that secondary hemi-epiphytic *Oleandra* is sister to the epiphytic Davalliaceae and polygrammoid ferns. Analyses of life form evolution based on the phylogenetic relationships suggested that obligate epiphytes of the Davalliaceae and polygrammoid ferns evolved from secondary hemi-epiphytes, or less likely from climbers. We hypothesized a scenario for the evolution of life forms in Davalliaceae and related groups that involves successive changes in rhizome habit, root function, and germination place. Rhizome dorsiventrality and scale morphology, shared by climbers, secondary hemi-epiphytes, and obligate epiphytes examined, may be other innovations for the ferns to have evolved into epiphytes. *Botanical Journal of the Linnean Society*, 2006, **151**, 495–510.

ADDITIONAL KEYWORDS: character evolution – climber – *Leucostegia* – life form – molecular phylogeny – secondary hemi-epiphyte.

INTRODUCTION

The epiphyte is one of the major life forms of plants, accounting for 30% of tropical South American vascular plant species and 50% of pteridophytes on Mt Kinabalu (tropical Asia) (Gentry & Dodson, 1987; Parris, Beaman & Beaman, 1992). Because of their life on trees, epiphytes have limited access to above-ground water and nutrient supplies, and are more diverse in the water economy and patterns of metabolism than any other rain forest synusiae (Richards, 1996). Vascular epiphytes in a broad sense are classified into holo-epiphytes (true/obligate epiphytes), facultative epiphytes, and hemi-epiphytes (Benzing, 1989). Among them, hemi-epiphytes are generally primary hemi-epiphytes (e.g. *Ficus*), which grow as epiphytes at the early stage of the life cycle and later become terrestrial by rooting into the soil, whereas secondary hemi-epiphytes are reversely terrestrial at the early stage and become epiphytic at maturity (Putz & Holbrook, 1986).

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In pteridophytes, epiphytes were classified into low epiphytes and high epiphytes (Holttum, 1938). The life form hemi-epiphyte was recognized later for ferns. Recently, Dubuisson *et al*. (2003b) recognized terrestrials, true lianas, hemi-epiphytic climbers, and true epiphytes in *Trichomanes s.l.* of the Hymenophyllaceae, a basal leptosporangiate fern family. Hemi-epiphytic climbers are distinct from true lianas in their roots not necessarily being connected with soils. Regarding the evolution of the life form, Dubuisson *et al*. (2003b) inferred that in *Trichomanes* true epiphytes evolved from terrestrials, whereas hemi-epiphytic climbers were derived from true epiphytes or terrestrials, and true lianas evolved from terrestrials independent of hemi-epiphytic climbers and true epiphytes. A possible evolution of true epiphytes from hemi-epiphytic climbers is also suggested (Dubuisson *et al*., 2003b: fig. 15).

Systematically, epiphytes are distributed in a wide spectrum of pteridophytes, suggesting recurrent origins of the epiphyte. The largest mostly epiphytic family is Polypodiaceae; smaller such families are Davalliaceae and Vittariaceae, and a number of epiphytes are included in two other large families,

Aspleniaceae and Hymenophyllaceae (Kress, 1989). The Psilotaceae are a small epiphytic family, and in the microphyllous Lycopodiaceae nearly half of the species are epiphytes (Kress, 1989).

Davalliaceae comprise four to ten genera and 50–130 species (Copeland, 1947; Kato, 1985; Kramer, 1990a; Nooteboom, 1992, 1994). The Davalliaceae are characterized by the epiphytic life form, long creeping dorsiventral rhizomes, peltate or pseudopeltate scales densely covering the rhizomes, and indusiate sori (Kato, 1985; Kramer, 1990a). Among the genera, *Leucostegia* is distinct in having basifixed scales and a few other characters described below, although it shares those characters with the other genera. Our previous molecular phylogenetic study, with species representing five genera of Davalliaceae, showed that none of the genera is monophyletic and the most basal clade is a group of *Davallodes* and some species of *Araiostegia* (Tsutsumi & Kato, 2005).

In a molecular (*rbcL*) analysis of the interfamilial relationships of ferns, Hasebe *et al*. (1994, 1995) disclosed that Davalliaceae, along with the polygrammoid ferns (Polypodiaceae and Grammitidaceae), form the largest epiphytic group. It was supported by a combined molecular and morphological analysis (Pryer, Smith & Skog, 1995) and a two-gene (*rbcL* and *rps4*) study (Schneider *et al*., 2004b). Available data suggest that epiphytism of the group evolved at or near the base of the clade. Hasebe *et al*. (1994, 1995) also suggested that the davallioid–polygrammoid ferns may be sister to *Arthropteris*, *Oleandra*, and *Tectaria*, but the relationships among them had low bootstrap supports. Schneider *et al*. (2004b) found that the sister group of the davallioid–polygrammoid ferns is *Oleandra*, with high posterior credibility, but did not analyse *Arthropteris* and *Tectaria*. The precise relationships of the davallioid–polygrammoid group with more non-epiphytic relatives are useful to understand the evolution of the epiphytic Davalliaceae. The aim of our study was to clarify the life forms of Davalliaceae and related species from field observations, and to infer the evolution of epiphytism in Davalliaceae, based on the phylogenetic relationships of the family and related ferns using two chloroplast genes, *rbcL* and *accD*.

MATERIAL AND METHODS

Field studies

To identify the life forms of ferns accurately, we carried out field studies in Yakushima Island, Japan; Gunung (= Mt) Gede, G. Salak and nearby places in West Java, Indonesia; Doi (= Mt) Inthanon in northern Thailand; Mt Kinabalu and the Crocker Range in Sabah, Malaysia; and north-eastern Queensland, Australia. Plants were carefully observed with a focus on root conditions (connected to the soil or not), the direction of rhizome elongation (upward or downward), the length of rhizomes, the height of tree trunks where the rhizomes attach (lower or upper), and, when available, the place where young plants grow. Vouchers for the field observations and molecular analysis are deposited in the University of Tokyo Herbarium (TI).

Phylogenetic analyses

In Davalliaceae, 36 species and one variety assigned to five genera that had been sequenced in our previous study (Tsutsumi & Kato, 2005) and two species of *Leucostegia* were examined (Appendix 1). *Paradavallodes*, *Parasorus*, and *Trogostolon* were excluded from the analysis, because material was not available. *Paradavallodes* Ching (1966) is usually referred to *Araiostegia*, and *Davallodes membranulosum*, a second species of *Paradavallodes*, is also placed in *Araiostegia* (Holttum in Sen, Sen & Holttum, 1972). *Parasorus* is a specialized monotypic genus characterized by simple leaves and coenosori (Kato, 1985). *Trogostolon* is also such a genus, characterized by the finely dissected leaves and acicular scales (Copeland, 1927, 1947). Therefore, the present analysis excluding those specialized genera may be able to reveal a general systematic structure of the Davalliaceae, and exclusion of those epiphytic genera does not seem to influence seriously the inferred evolution of the life forms of the Davalliaceae. However, there is no doubt that the phylogenetic relationships of Davalliaceae await analysis with more species representing all recognized genera and other particular groups.

In addition we examined species of *Colysis*, *Crypsinus*, *Gymnogrammitis*, *Loxogramme*, *Microsorum*, *Grammitis*, and *Pyrrosia*, which are members of the polygrammoid group sister to Davalliaceae (Hasebe *et al*., 1995; Schneider *et al*., 2004c), and examined species of *Arthropteris*, *Nephrolepis*, *Oleandra*, and *Tectaria*, which are possible sisters of the davallioid–polygrammoid group (Hasebe *et al*., 1994, 1995) (Appendix 1). We also examined four of the six genera of the Lomariopsidaceae, including the epiphytic *Elaphoglossum,* and some genera of the Dryopteridaceae, which were less closely related species to the davallioid–polygrammoid group. *Athyrium* and *Matteuccia* were used for outgroups (Hasebe *et al*., 1995). The species examined in this study represent all major subclades of a monophyletic clade that diverges from the other sister clade to which the outgroup species are assigned in all-family analyses (Hasebe *et al*., 1995).

Leaves were collected in the field or personally provided by friends and colleagues, and dried with silica gel (Appendix 1). The procedures for extraction, amplification, and sequencing used in this study followed Tsutsumi & Kato (2005). A region of *rbcL*

and *accD* was amplified and sequenced using previously described primers (Tsutsumi & Kato, 2005). The sequences obtained were assembled using AUTOASSEMBLER (Applied Biosystems) and assembled sequences were aligned by CLUSTAL X (Thompson *et al*., 1997). The analysed sequences were limited to the obtained coding regions, because the intergenic spacer between *rbcL* and *accD* included too many indels to construct objective alignment. The comparable sequences (1338 + 596 bp) of partial *rbcL* and partial *accD* were examined. We did not find a start codon in *accD*, but all species examined had an ACG codon, which may play a start codon by RNA editing, as suggested for the Davalliaceae (Tsutsumi & Kato, 2005). Therefore, sequences downward to the ACG codon were used as *accD* sequences. Operational taxonomic units with identical sequences were treated as a single unit in phylogenetic analysis. The base that could not be identified in this study was treated as N. The *rbcL* and *accD* sequences of *Davallia denticulata* (Philippine material) had one unidentifiable base, although all other sequences were the same as those of *Davallia denticulata* (Sumatra material). Hence, both sequences were examined in the phylogenetic analysis.

Phylogenetic analyses were performed for both *rbcL* and *accD* data by maximum parsimony (MP) and for combined *rbcL* and *accD* data by MP and maximum likelihood (ML) with PAUP* 4.0b10 (Swofford, 2002). In the MP method, all characters were equally weighted and heuristic searches were conducted with 1000 random addition replicates involving tree-bisection-reconnection (TBR) branch swapping. Bootstrap values were calculated with 100 replicates with ten random additions for both *rbcL* and *accD* data and with 1000 replicates with 100 random addition replicates for the combined data. In the ML method, MODELTEST version 3.5 (Posada & Crandall, 1998) was used to determine the nucleotide substitution model. The GTR + I + G model and gamma rates, which fitted our data using both hierarchical likelihood ratio tests and Akaike information criteria, were specified. The ML analysis was implemented using PAUP 4.0b10 as heuristic searches involving NNI branch swapping with 100 random addition sequence replicates. Bayesian inference of phylogeny was performed using MRBAYES 3.0 to estimate posteriori supports of clades in the ML tree (Huelsenbeck & Ronquist, 2001). MRMODELTEST 2.0 (Nylander, 2004) was used to determine the nucleotide substitution model for the Bayesian analysis. Bayesian searches were conducted by mcmc with four chains over 1 000 000 generations, sampling every 100 generations. One thousand trees were discarded as burn-in trees and the rest of the trees were used to calculate the majority rule consensus tree.

The evolution of the life form was an estimate based on the molecular trees obtained, using MACCLADE 4.06 (Maddison & Maddison, 2003). All characters were treated as unordered and plotted on to the topologies recovered in the MP and ML analyses. Both character evolution optimization criteria, ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation), were examined.

RESULTS

Field observations

Based on the field observations, we distinguished four life forms, i.e. climber, secondary hemi-epiphyte, obligate epiphyte, and terrestrial, in the Davalliaceae and other ferns (Appendix 2).

In the obligate epiphytic *Elaphoglossum callifolium* (Lomariopsidaceae), *Loxogramme avenia* (Polypodiaceae), and *Grammitis reinwardtii* (Grammitidaceae), the rhizomes were short creeping and attached to tree trunks or branches. Many species of the Davalliaceae with long creeping rhizomes were usually obligate epiphytes. Both young and mature plants of *Davallia trichomanoides* occurred on tree trunks and their roots were always separated from the soil. *Scyphularia pentaphylla* was a high epiphyte occurring on tree branches. Some species, e.g. *Humata vestita*, often occurred on fallen wood, although they sometimes grew on mossy rocks as lithophytes with their roots unconnected to the soil.

Oleandra and *Nephrolepis* were secondary hemi-epiphytes. The long creeping rhizomes of most individuals (relatively young plants) of *Oleandra pistillaris* climbed tree trunks and may have reached a height of about 10 m on tree trunks with the basal roots connected to the soil. In some other plants (mature), the proximal parts of the climbing rhizomes were dried and free from the ground. *Nephrolepis acuminata* and *N. cordifolia* (Nephrolepidaceae) had short erect rhizomes with leaves in fascicles and long creeping stolons spreading radially. Most individuals were terrestrials or climbers with the basal roots connected to the soil, and some individuals were epiphytic with stolons dry at the proximal parts. Young plants usually climbed trees and had roots connected to the soil. Some polygrammoid species were also secondary hemi-epiphytes or hemi-lithophytes. The secondary hemi-epiphytic *Microsorum buergerianum*, *M. nigrescens*, and *M. scolopendria* had long creeping rhizomes with the basal roots connected to the soil at their youth, but they were not examined in the phylogenetic analysis.

Some species of the davallioid–polygrammoid ferns had two life forms, i.e. obligate epiphyte and secondary hemi-epiphyte. In *Araiostegia hymenophylloides*, *Davallia denticulata*, and *D. divaricata* (Daval-

liaceae), both young and mature plants were low epiphytes (sometimes high), and some individuals crept on the ground or climbed tree trunks with the roots connected to the soil. *Crypsinus enervis* and *Goniophlebium persicifolium* (Polypodiaceae) may be obligate epiphytes and secondary hemi-epiphytes, because they were usually low epiphytes and sometimes climbers with rhizomes and roots connected to the soil, although we did not find epiphytic juveniles. Some species that were low epiphytes (e.g. *Davallia embolostegia*) may also be obligate epiphytes and secondary hemi-epiphytes, although we did not observe the life form of young plants.

Arthropteris backleri (Oleandraceae) and *Lomariopsis spectabilis* (Lomariopsidaceae) were climbers with long climbing rhizomes with short adhesive roots on tree trunks. *Arthropteris backleri* had only sparse adhesive roots and may attach with the help of scales. They always anchored to the soil by long, branched underground roots.

Molecular phylogeny

Prior to the analysis with the combined data sets of the two coding regions, the phylogenetic trees based on each of them were constructed by MP analysis. The *accD* sequences had relatively more informative characters (29.9%) than the *rbcL* sequences (24.7%), although the strict *accD* tree was not resolved well, presumably because of the small size of the data set. Trees based on combined *rbcL* and *accD* sequences showed finely resolved relationships (Figs 1, 2), and were in part inconsistent with each MP tree based on *rbcL* or *accD* sequences. A noteworthy difference was that, in the *accD* tree, *Loxogramme avenia* was sister to the Davalliaceae with low support (data not shown). The relationship was, however, not supported by derivative morphological characters such as the simple leaves, reticulate venation, and exindusiate sori.

Both ML and MP trees based on the combined coding regions of *rbcL* and *accD* showed that the Davalliaceae formed a monophyletic clade except for *Leucostegia* and *Gymnogrammitis* (Figs 1, 2). *Leucostegia* was sister to the nondavallioid *Hypodematium crenatum*. *Gymnogrammitis* formed a monophyletic clade with *Crypsinus enervis* of Polypodiaceae, in accordance with Schneider *et al*. (2002). Davalliaceae excluding the two genera and the polygrammoid group formed an ultimate monophyletic clade. This clade was the sister to *Oleandra* (*O. pistillaris* and *O. wallichii*) in accordance with Schneider *et al*. (2004b). The clade of the davallioid–polygrammoid group and *Oleandra* was in turn sister to the *Arthropteris* clade consisting of *Arthropteris backleri*, *Tectaria phaeocaulis*, and *Quercifilix zeylanica*. The clade of these ferns formed a monophyletic clade together with *Nephrolepis acuminata*, *N. cordifolia*, and *Lomariopsis spectabilis*. This clade was in turn sister to another clade comprising two subclades, one of which consisted of some Dryopteridaceae (*Polybotrya caudata*, *Ctenitis eatonii*, *Polystichum fibrilloso-paleaceum*, *Dryopteris erythrosora*, and *Arachniodes aristata*) and the other consisting of *Rumohra adiantiformis*, *Bolbitis repanda*, *Elaphoglossum callifolium*, and *Teratophyllum wilkesianum*. In the latter *Elaphoglossum* clade examined, *Rumohra adiantiformis* was sister to the rest of the species, in which *Bolbitis repanda* was basal. A clade of all species examined was sister to a clade of *Leucostegia immersa*, *L. pallida*, and *Hypodematium crenatum*. These interfamilial phylogenetic relationships had high support (≥ 1.00 in ML, 80% in MP), except for the monophylies of the *Arthropteris* clade, Dryopteridaceae, and the *Elaphoglossum* clade.

Intrafamilial relationships of the Davalliaceae were deduced from combined *rbcL* and *accD* sequences analysed here and generally corresponded with the more finely resolved relationships based on a larger data set of *atpB*, *rbcL*, *accD*, *atpB-rbcL* spacer, and *rbcL-accD* spacer (Tsutsumi & Kato, 2005), particularly in that *Araiostegia* 1 and *Davallodes* were basal. However, there was a considerable difference in the relationships of subbasal clades. The second basal clade *Davallia* 3 *sensu* Tsutsumi & Kato (2005) (Figs 1, 2) in their tree split into *Davallia* 3A and *Davallia* 3B. *Davallia* 3A formed a monophyletic clade with *Araiostegia* 2 in both ML and MP trees, whereas *Davallia* 3B formed the second basal clade in Davalliaceae. *Davallia* 3A and *Araiostegia* 2 formed a monophyletic clade with the *Humata* clade in the present ML tree and four of 14 MP trees. The topologies, based on the smaller data sets, were supported by weak credibility. Although the present intrafamilial relationships of the polygrammoid ferns were in part inconsistent with those of Schneider *et al*. (2004c), who analysed *rbcL*, *rps4*, and *rps4-trnS* spacer region for nearly 100 species, the topology that *Loxogramme* is basal was the same.

The relationships of the Dryopteridaceae clade were inconsistent between the ML and MP trees. *Polybotrya caudata* was basal in the ML tree (Fig. 1), whereas the strict MP tree (Fig. 2) showed that the family examined comprised two clades, in one of which *Polybotrya caudata* was basal. The credibility of both topologies was not enough.

Evolution of life forms

In order to examine the evolution of epiphytism in Davalliaceae, the character phylogeny of the life form was analysed using the ML tree (Fig. 1) and 14 MP trees (the strict consensus of which is shown in

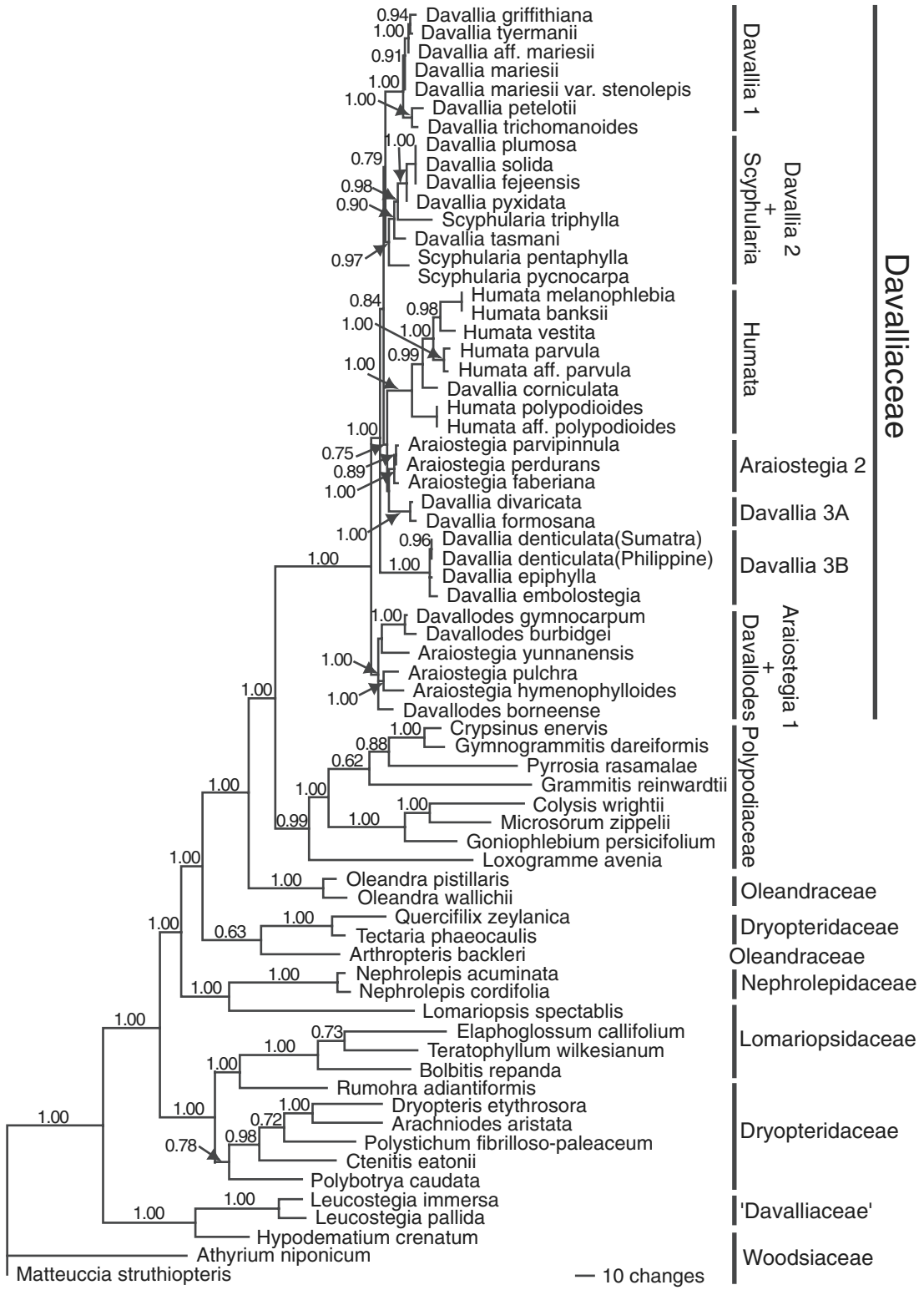

Figure 1. Maximum likelihood tree (ln = –12833.44988) of Davalliaceae and related ferns based on combined *rbcL* and *accD* sequences (1934 bp). The numbers above the branches indicate posterior probability values (> 0.6) calculated by Bayesian analysis. Species data are shown in Appendix 1. The tree is rooted by *Athyrium niponicum* and *Matteuccia struthiopteris* (Hasebe *et al*., 1995). The groups of Davalliaceae on the right follow Tsutsumi & Kato (2005), except for *Davallia* 3A and 3B.

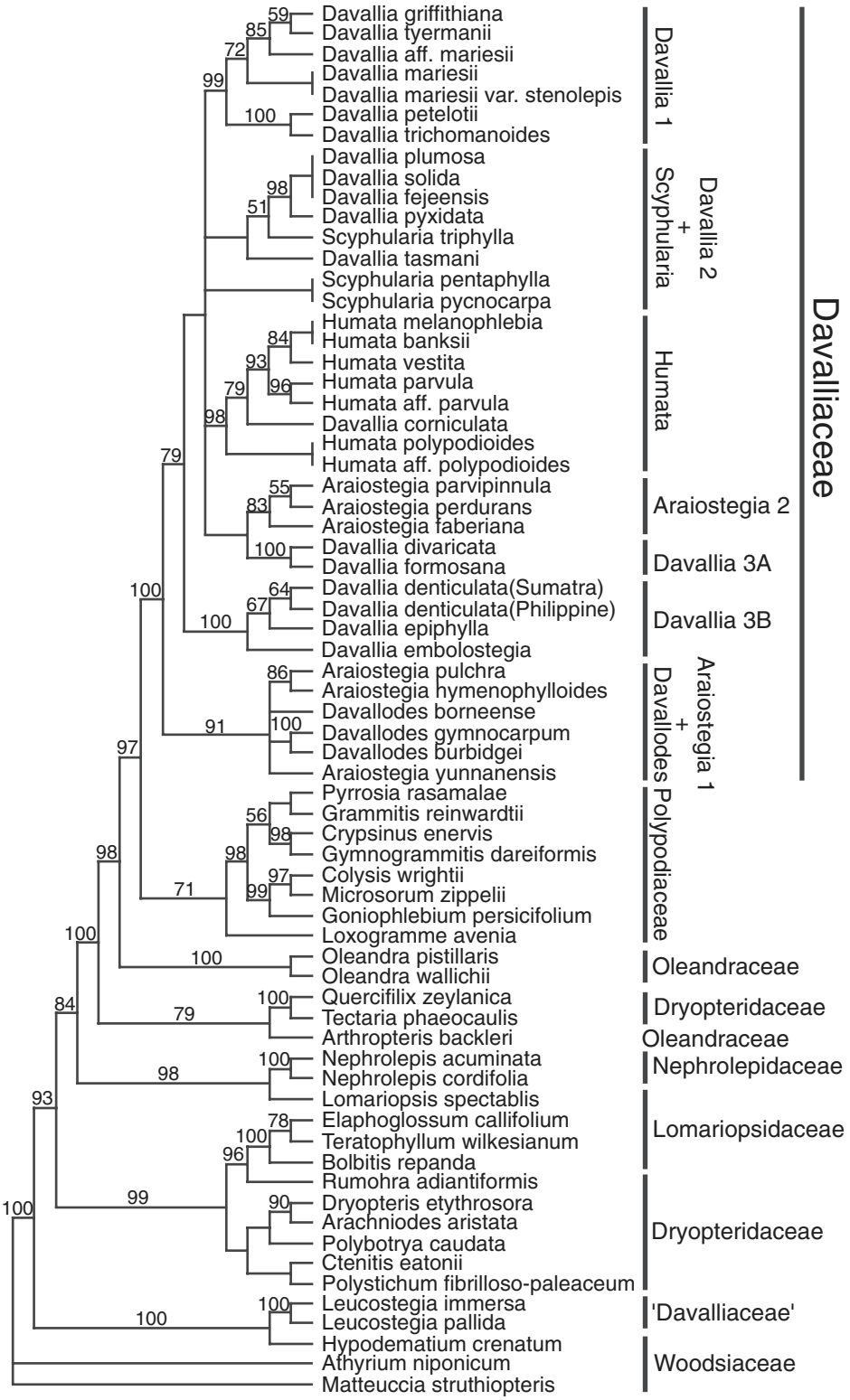

Figure 2. Strict consensus tree of 14 trees obtained by maximum parsimony analysis for Davalliaceae and related ferns based on combined *rbcL* and *accD* sequences (1934 bp) [consistency index (excluding uninformative characters) = 0.3587; homoplasy index (excluding uninformative characters) = 0.6413; retention index = 0.6955]. The numbers above the branches indicate bootstrap values (> 50%). Species data are shown in Appendix 1. The tree is rooted by *Athyrium niponicum* and *Matteuccia struthiopteris* (Hasebe *et al*., 1995). The groups of Davalliaceae on the right follow Tsutsumi & Kato (2005), except for *Davallia* 3A and 3B.

Figure 2). The inferred character evolutionary trees based on the 14 MP trees were the same. Analyses were performed for all the species examined for phylogenetic relationships, and the results are shown using simplified trees with reference to the Davalliaceae groups (Figs 3, 4). Life form data were based on field observations, herbarium specimen data, personal communications, and the literature (Appendix 2). Because obligate epiphytes also occur on rocks, species that live on both trees and rocks were treated as obligate epiphytes, whereas species that are described to grow only or usually on rocks were treated as lithophytes (Appendix 2). Species with multiple life forms were treated as polymorphic (ex *Araiostegia hymenophylloides* as secondary hemi-epiphyte + obligate epiphyte). Because the life forms of the basal Davalliaceae are influential to infer the life form evolution of the family, the life forms of *Araiostegia* were carefully surveyed. Their life forms may also include secondary hemi-epiphytes, as in *Araiostegia hymenophylloides*. Therefore, we analysed the life form evolution for all possible life forms of other *Araiostegia* (secondary hemi-epiphyte, secondary hemi-epiphyte + obligate epiphyte, and obligate epiphyte, except for *Araiostegia*

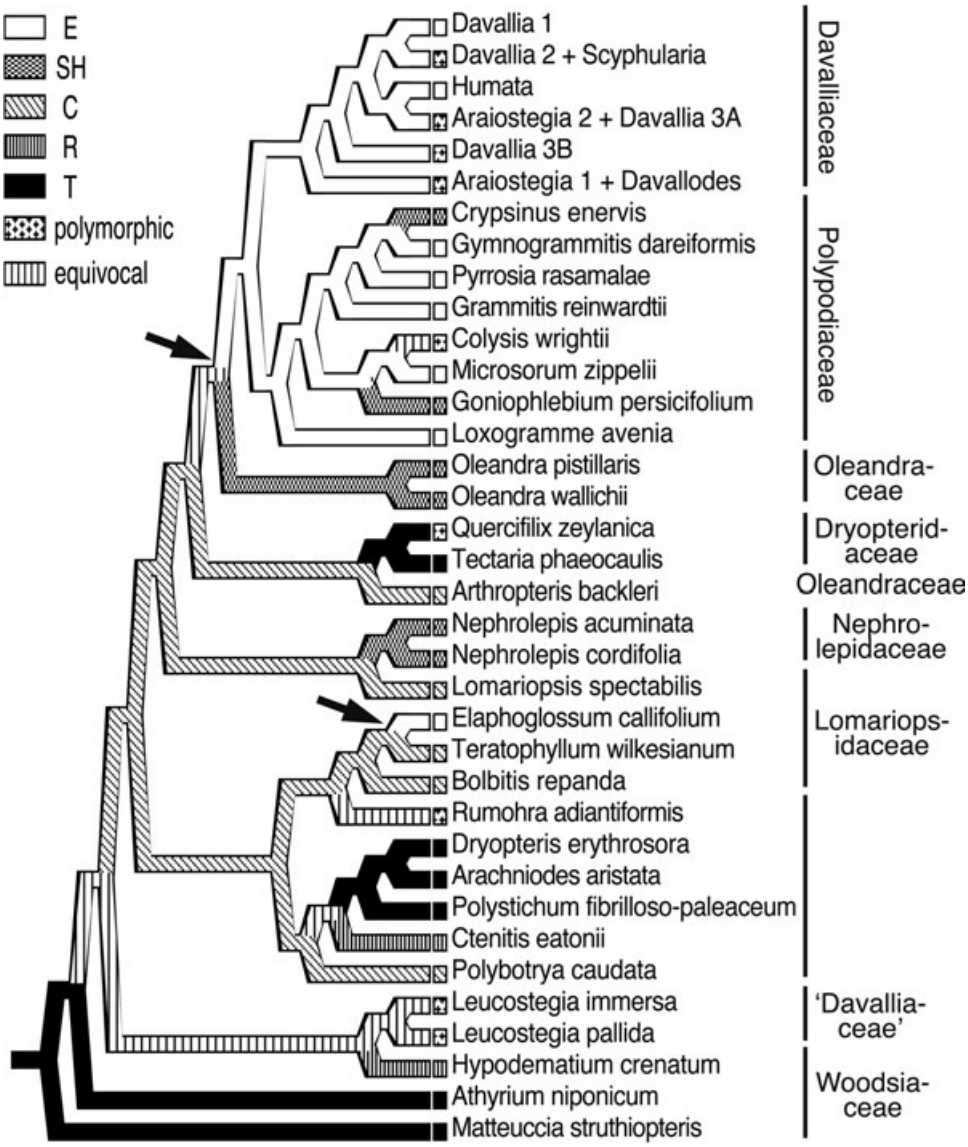

Figure 3. Inferred evolution of the life forms in Davalliaceae and related ferns constructed by MACCLADE 4.06 with ACCTRAN optimization based on the maximum likelihood tree (Fig. 1), which is simplified for groups of Davalliaceae. Life form data are shown in Appendix 2. Species with multiple life forms are treated as polymorphic. Arrows indicate positions where obligate epiphytes arose. C, climber; E, obligate epiphyte; SH, secondary hemi-epiphyte; R, lithophyte; T, terrestrial.

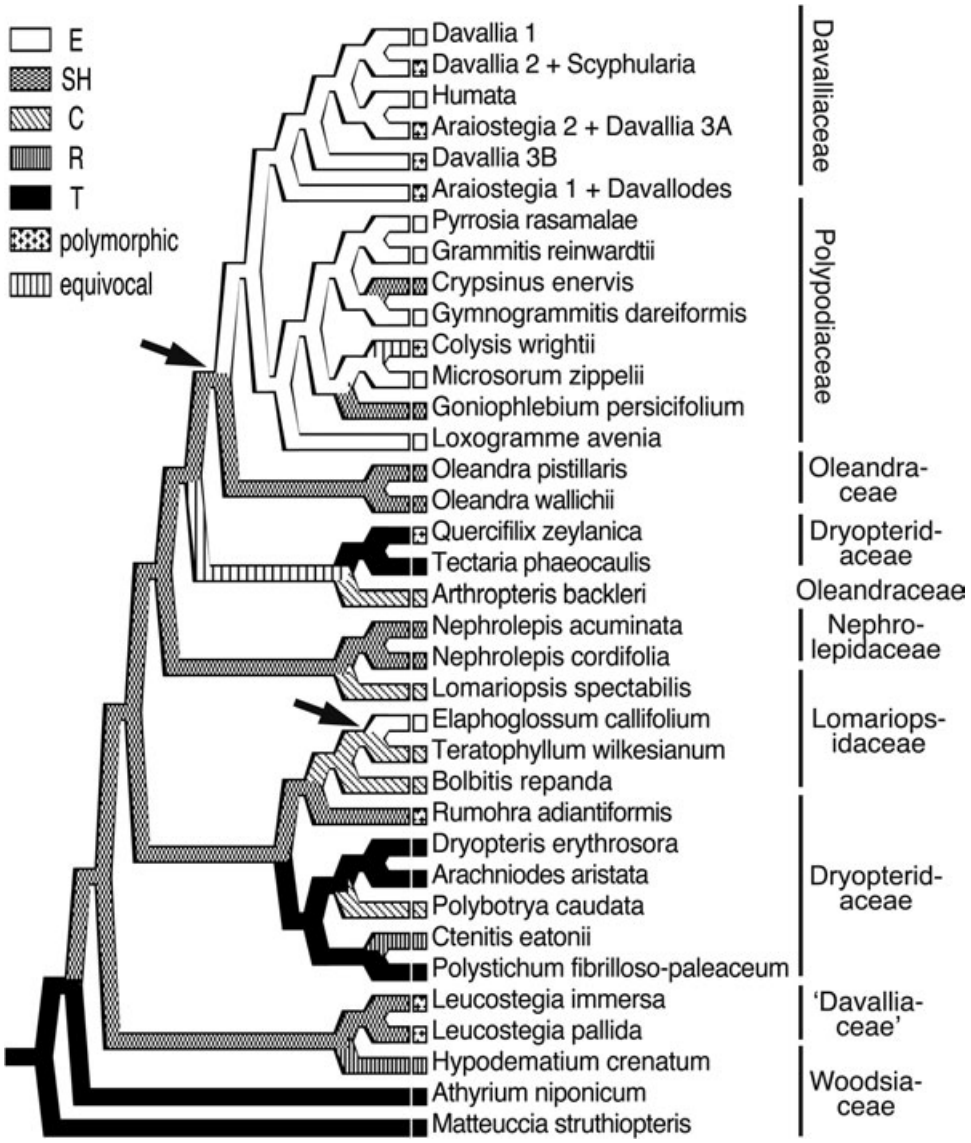

Figure 4. Inferred evolution of the life forms in Davalliaceae and related ferns constructed by MACCLADE 4.06 with ACCTRAN optimization based on one of 14 maximum parsimony trees, which is simplified for groups of Davalliaceae (Fig. 2). Life form data are shown in Appendix 2. Species with multiple life forms are treated as polymorphic. Arrows indicate positions where obligate epiphytes arose. C, climber; E, obligate epiphyte; SH, secondary hemi-epiphyte; R, lithophyte; T, terrestrial.

yunnanensis treated as lithophyte + secondary hemi-epiphyte, lithophyte + secondary hemi-epiphyte + obligate epiphyte, and lithophyte + obligate epiphyte), and the results were congruent with those from analyses with observed and described life forms (shown below).

The character trees by ACCTRAN optimization based on the ML (Fig. 3) and 14 MP trees (one of which is shown in Figure 4), suggested that obligate epiphytes arose in two lineages, i.e. at or near the base of the davallioid–polygrammoid group and at the branching of *Elaphoglossum callifolium*, although the evolutionary pattern of life forms are different between the two. The character evolution in the ML tree inferred that a climber was plesiomorphic in the species examined except for the lithophytic *Leucostegia* and *Hypodematium*, and that either a climber or secondary hemi-epiphyte was ancestral to the obligate epiphyte of the davallioid–polygrammoid group. The pattern at these nodes was equivocal in DELTRAN optimization (data not shown). The tree also showed that the secondary hemi-epiphyte evolved from a climber in the lineage of *Nephrolepis* independently of *Oleandra*. Character

evolution based on the 14 MP trees using ACCTRAN optimization (one of which is shown in Figure 4), as well as using DELTRAN optimization (data not shown), indicated that the secondary hemi-epiphyte appeared below the node where the clade of *Hypodematium* and *Leucostegia* diverged from the rest, and evolved into the obligate epiphyte of the davallioid–polygrammoid group. The obligate epiphytic *Elaphoglossum callifolium* evolved from a climber independently of the davallioid–polygrammoid clade, as shown in the ML character tree.

The present intrafamilial phylogenetic relationships of the Davalliaceae are mostly consistent with those of the previous study with a larger data set (*atpB*, *rbcL*, *accD*, *atpB-rbcL* spacer, and *rbcL-accD* spacer) (Tsutsumi & Kato, 2005), although those are inconsistent for part of the subbasal clade. Because the relationships based on the larger data set seem to be more accurate than those obtained here, we also reconstructed character evolution of the life form based on a tree with a constraint of the topology of the Davalliaceae inferred by the previous study (results not shown), and this resulted in the same patterns as the present ones (Figs 3, 4).

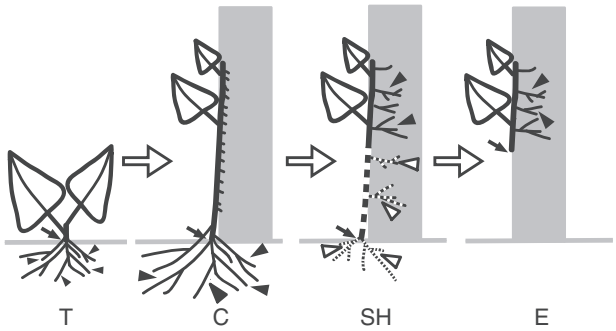

Figure 5. Hypothesized scenario of life form evolution (marked by open arrows) of an obligate epiphyte of davallioid–polygrammoid ferns from a secondary hemi-epiphyte, which was derived from a climber. The horizontal grey line and vertical grey bars indicate the ground surface and tree trunks, respectively. Thick lines indicate living rhizomes; long thin lines, roots absorbing water and nutrients; short thin lines in C, adhesive roots; broken thick lines, dried rhizomes; and broken thin lines, dried roots. Solid arrows indicate the place of spore germination and gametophyte growth. Solid arrowheads indicate the source of water and nutrients absorbed, and open arrowheads indicate that roots no longer absorb water and nutrients. C, climber; E, obligate epiphyte; SH, secondary hemi-epiphyte; T, terrestrial.

DISCUSSION

Life forms

Our results showed that in Davalliaceae and related species there are four life forms, i.e. terrestrial, climber, secondary hemi-epiphyte, and obligate epiphyte, based on the places of germination and growth and the place of water and nutrition absorption (Fig. 5). This characterization differs from the definition of Dubuisson *et al*. (2003b).

Terrestrial ferns germinate, grow to maturity, and reproduce on the ground (Fig. 5). By contrast, obligate epiphytes do so on trees without contact with the soil throughout their life history and so exclusively absorb water and nutrients available on trees (Fig. 5). Climbing ferns are terrestrial at the early stage of their life history, when spores germinate and gametophytes develop into sporophytes on the ground, and then climb tree trunks (Fig. 5). The roots are usually dimorphic, i.e. long branched roots anchoring to the soil and short epiphytic roots borne on climbing rhizomes. If the rhizomes of some climbers are separated at certain heights, a portion distal to the separating point becomes dried. This indicates that those plants cannot live without water absorption from the ground, and the underground roots absorb water and nutrients predominantly from there throughout life, and the short epiphytic roots that adhere to tree trunks may not contribute much to water absorption. Secondary hemi-epiphytic ferns are similar to climbers at the early stage of their life history, but after the rhizomes and roots are interrupted, the ferns can live separate from the soil, like obligate epiphytes (Fig. 5). The roots are usually monomorphic and epiphytic roots not only adhere to tree trunks but also absorb water and nutrients on tree trunk surfaces or from humus on them.

During the field research we had difficulties with the exact characterization of the life forms of ferns. It was partly because ferns that appeared epiphytic were not always obligate epiphytes, but may include hemi-epiphytes, which do not differ from obligate epiphytes if the rhizomes and roots are not connected to the soil. In a similar way, hemi-epiphytes are hardly distinguished from climbers if the rhizomes and roots anchor to the soil. Therefore, precise life form characterization needs detailed and long-term field observations. Our field observations were short term, but paid attention to the life forms of young plants and whether the rhizomes and roots were connected to the soil or not. As a result, they suggested that there are secondary hemi-epiphytes even in Polypodiaceae (e.g. *Microsorum buergerianum*, *M. nigrescens*), which are generally regarded as epiphytes (Kress, 1989). Furthermore, some other species have two life forms, i.e. secondary hemi-epiphyte and obligate epiphyte (e.g. *Araiostegia hymenophylloides*). Therefore, we stress that extensive field observations of wild plants at

various stages of their life history may find that some epiphytic ferns, in particular those of Davalliaceae and Polypodiaceae, are secondary hemi-epiphytes, and the life forms observed in this study and cited from the literature may be revised in a future survey.

Climbers may be ontogenetically transferable to secondary hemi-epiphytes. Some species of *Philodendron* sect. *Philodendron* of the Araceae, which are mostly secondary hemi-epiphytes (Croat, 1997), live as climbers when young and become secondary hemi-epiphytes with an ontogenetic transition of the life form (M. Kato, unpubl. data; H. Okada, pers. comm.). Such a paedoclimber is so far unknown in ferns.

Evolution of epiphytes

The ML character evolution tree (Fig. 3) shows that the epiphytic Davalliaceae evolved from either climbers or secondary hemi-epiphytes, although their immediate ancestral life form is shown to be equivocal. The MP character evolution tree (Fig. 4) indicates that the epiphytic Davalliaceae evolved from secondary hemi-epiphytes. *Oleandra*, sister to the davallioid–polygrammoid ferns, is a secondary hemi-epiphyte. Therefore, it seems more probable that the epiphytes of the Davalliaceae were derived from secondary hemi-epiphytes. Life form multiplicity of early diverging groups of the davallioid ferns (e.g. *Araiostegia*) may possibly represent ancestry. In comparison, the obligate epiphytic (and lithophytic) *Anarthropteris*, *Dictymia*, and *Loxogramme* (Hennipman, Veldhoen & Kramer, 1990) are inferred to be the most basal group of the polygrammoid ferns, a sister group of Davalliaceae (Schneider *et al*., 2004c). It suggests that obligate epiphytes evolved at the base of the davallioid–polygrammoid ferns and secondary hemi-epiphytes of some polygrammoid ferns evolved reversely from obligate epiphytes.

The obligate epiphytic *Elaphoglossum callifolium* is sister to the climbing *Teratophyllum wilkesianum*, and the two species are sister to the terrestrial or climbing *Bolbitis repanda*. *Bolbitis* has multiple life forms, i.e. terrestrial, lithophyte, low climber and high climber (Hennipman, 1977) and probably includes the secondary hemi-epiphyte. The character evolution trees infer that *Elaphoglossum callifolium* was derived from a climber, but the phylogenetic relationships among the three species are not very robust. Hence, it is also not ruled out that the obligate epiphytes evolved via secondary hemi-epiphytes, which has not yet been found or were extinct from this lineage.

The phylogenetic position of *Polybotrya caudata* (Dryopteridaceae) differs between the ML and MP trees, and the difference partly leads to inconsistent patterns in the hypothesized life form evolution (Figs 3, 4). Surprisingly, the present result showed that the terrestrial species of the Dryopteridaceae may be derived from climbers or secondary hemi-epiphytes, a direction opposite to the one generally proposed. The family Dryopteridaceae has many species with diverse life forms, such as mostly terrestrial, lithophytic or sometimes climbing (e.g. *Maxonia*, *Olfersia*) (Kramer, 1990b) and therefore an analysis with many unexamined species of Dryopteridaceae will provide a more accurate pathway of life form evolution.

We propose a possible scenario for the evolution of the characters that define the life forms of the Davalliaceae and related ferns (Fig. 5). The scenario is that the most parsimonious is based on the hypothesized life form evolution and the results of the field observations. The present analyses did not give decisive results for the evolutionary relationship between secondary hemi-epiphytes and climbers. Nonetheless, the polarity from climber to secondary hemi-epiphyte seems to be more probable rather than the opposite way, because secondary hemi-epiphytes go through the stage of climbers early in their life history. The scenario comprises three successive steps that characterize major phases of the life history. The first evolutionary change from terrestrial to climber involved rhizome elongation to allow plants to climb and the development of adhesive roots adhering to upright tree trunks. These roots may absorb water much less efficiently than the long, branched underground roots. The next change from climber to secondary hemi-epiphyte acquired absorptive roots borne on climbing rhizomes and without use of water and nutrients from the soil. The roots can retain water and nutrient balance. The last change from secondary hemi-epiphyte to obligate epiphyte involved a shift of the place of spore germination from the ground to tree trunks.

There are high correlations between the life forms and morphological traits. The rhizomes are long creeping in all climbers, all secondary hemi-epiphytes, and most obligate epiphytes examined (Appendix 2). In an extreme case, *Oleandra pistillaris* has internodes about 2 m long. In another secondary hemi-epiphytic *Nephrolepis*, buds or young erect shoots are scattered between long intervals along the length of the long creeping stolons. In comparison, in the terrestrial species examined and described, the rhizomes range from short and erect to long creeping. The correlationships of the life forms and rhizome habits, along with the phylogenetic relationships, support the hypothesis of Dubuisson *et al*. (2003b) that long creeping stems allow climbers and secondary hemi-epiphytes to colonize vertical supports rapidly. The small obligate epiphytic *Grammitis reinwardtii*, like other grammitids and some polypods, have short rhizomes, which may be secondarily derived in obligate epiphytes.

The dorsiventrality of fern rhizomes is indicated by the arrangement of lateral organs that are produced by the rhizomes; the roots are inserted on the ventral side and the leaves, on the dorsal or dorsolateral side. Dorsiventral rhizomes tightly attached to tree trunks by such roots were seen in the climbers, secondary hemi-epiphytes, and obligate epiphytes examined (Appendix 2).

Scales cover rhizomes, in particular their apices, in most ferns. The scales are dense and remain even on their mature part in most of the davallioid–polygrammoid group and probably play a role in protecting rhizomes from desiccation. Compared with the basifixed scales of terrestrial species, the scales are peltate or pseudopeltate with a stalk on the ventral surface of the shield, which are tightly appressed to the rhizome surface, in all the climbers, secondary hemi-epiphytes, and obligate epiphytes examined, except *Leucostegia* and *Loxogramme avenia* (Appendix 2). It is also probably the case with other epiphytic ferns (Ogura, 1972). The peltate trichomes on the leaves of some Bromeliaceae (subfamily Tillandsioideae) and *Polypodium hirsutissimum* (Polypodiaceae) were inferred to absorb water and nutrients (Benzing *et al*., 1976; Müller, Starnecker & Winker, 1981). Their peltate trichomes closely resemble the peltate scales of the davallioid–polygrammoid ferns in their anatomical structure (C. Tsutsumi & M. Kato, unpubl. data). In the davallioid–polygrammoids, the dense, persistent, peltate or pseudopeltate scales with stalks inserted in depressions of the rhizome surface may play a similar role in the absorption and maintenance of water and nutrients and might allow epiphytic life under the condition of insufficient water supply. The abscission layer of the leaf, common in the davallioid–polygrammoid ferns (except for *Loxogramme*) is another adaptive trait for life under the stress of desiccation in the dry season.

Epiphytes are considered to have evolved in several other pteridophyte lineages. Pathways to those epiphytes are not necessarily the same as those in the davallioid–polygrammoid ferns. *Huperzia* (Lycopodiaceae) includes epiphytic and terrestrial species. In a phylogenetic analysis, Wikström, Kenrick & Chase (1999) argued that epiphytism evolved once from the terrestrial *Huperzia selago* group and there was at least one reversal to a terrestrial form within the epiphytic *Huperzia*. There is no hemi-epiphytic species in *Huperzia*, indicating that those epiphytes may have evolved directly from terrestrials.

Asplenium (Aspleniaceae) includes a number of epiphytic, lithophytic, and terrestrial species, but no or few hemi-epiphytes, and most species have short rhizomes (Iwatsuki, 1995). Therefore, those epiphytes may not have evolved from hemi-epiphytes. A phylogenetic study showed that the most basal clades of asplenioid ferns are epiphytes (Schneider *et al*., 2004a) and epiphytism in asplenioid ferns may have occurred before or at the divergence of the group.

In Vittariaceae, almost all the species are epiphytic and have short or long rhizomes (Kramer, 1990c). The family is closely related to *Adiantum* (Hasebe *et al*., 1994, 1995; Crane, Farrar & Wendel, 1995), which includes terrestrial, lithophytic, and rarely epiphytic species (Tryon, 1990). The epiphytic Vittariaceae possibly evolved directly from terrestrials or lithophytes, not via climbers/secondary hemi-epiphytes. Keller *et al*. (2003) inferred that microhabitats of the surface of horizontal tree branches mimic forest floor habitats and allow the typically lithophytic *Polypodium appalachianum* to grow epiphytically. This situation may be similar to the initial stage of evolution from lithophytes.

In *Trichomanes*, Hymenophyllaceae, epiphytes were inferred to have evolved from terrestrials, and hemi-epiphytes may have been derived from epiphytes or terrestrials (Dubuisson *et al*., 2003a, b). All obligate epiphytes, secondary hemi-epiphytes, and climbers in *Trichomanes*, like the davallioid–polygrammoid group, share long creeping rhizomes (Dubuisson *et al*., 2003b). Therefore, it is also possible that the obligate epiphytes evolved from secondary hemi-epiphytes, pending further analysis based on phylogenetic relationships.

Phylogenetic position of *Leucostegia*

The present molecular phylogenetic data show that *Leucostegia* is sister to *Hypodematium*, a nondavallioid member. In the current classifications, *Leucostegia* is assigned to the family Davalliaceae (e.g. Kato, 1985; Kramer, 1990a; Nooteboom, 1992). The assignment is based on similarities in morphological characters, such as the rhizome being long creeping and densely covered by scales, leaves alternate on the dorsal side of the rhizome, extra-axillary lateral buds arranged alternately in two ranks on the ventral and lateral sides, and marginal sori with indusia attached at the posterior base. In contrast, *Leucostegia* has other characters different from Davalliaceae: the roots are scattered around the rhizome, the stelar anatomy is simple with binary leaf traces, the scales are basifixed, and the sori are terminal and single at vein endings (Nayar & Bajpai, 1976; Kato, 1985).

Hypodematium has been placed in various groups, e.g. Athyriaceae (Woodsiaceae), Dryopteridaceae, and Thelypteridaceae, due to its specialized morphology (Iwatsuki, 1964), but currently is referred to the athyrioid group (e.g. Iwatsuki, 1964; Kramer, 1990b; Hasebe *et al*., 1995). *Hypodematium* and *Leucostegia* share the following characters: the rhizome is creeping, dorsiventral, and densely covered by basifixed

scales and the sori are covered by basifixed indusia. The simple dictyostelic vascular organization of the rhizome with binary leaf traces also accords with that of *Leucostegia* (Iwatsuki, 1964; Kato & Mitsuta, 1980). With the dorsiventral rhizomes and dense persistent scales, *Hypodematium* is a lithophyte occurring in the crevices of limestone rocks. Thus, the results of comparative morphology and the molecular phylogeny show that *Leucostegia* should be excluded from the Davalliaceae and placed near *Hypodematium*.

CONCLUSIONS

In addition to terrestrials, lithophytes, and hydrophytes, the life forms of ferns include obligate epiphytes, secondary hemi-epiphytes, and climbers, defined by the places of spore germination and sporophyte growth. In Davalliaceae and Polypodiaceae there are three life forms: obligate epiphyte, secondary hemi-epiphyte, and lithophyte, among which obligate epiphyte is the most common. Phylogenetically, the davallioid–polygrammoid group is sister to *Oleandra* (secondary hemi-epiphyte), together sister to a clade of *Arthropteris* (climber) and *Tectaria* (lithophyte), and then to a clade of *Nephrolepis* (secondary hemi-epiphyte) and *Lomariopsis* (climber). The obligate epiphyte life form of the Davalliaceae, along with that of the polygrammoid group, probably evolved from the secondary hemi-epiphyte than from climbers. In the hypothesized evolution of life forms, the first step from terrestrial to climber involved the climbing habit, the second step from climber to secondary hemi-epiphyte involved the development of absorbing roots on epiphytic rhizomes, and the last step to obligate epiphyte accompanied a shift in spore germination place from the ground to on trees. Long creeping rhizomes, rhizome dorsiventrality, and peltate or pseudopeltate persistent scales, as well as abscission layers, were usually shared by the climbers, secondary hemi-epiphytes, and obligate epiphytes examined, and so these morphologies may be early innovations for the epiphytic Davalliaceae. *Leucostegia* is excluded from the Davalliaceae and is closely related to *Hypodematium*.

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APPENDIX 1

Species used in the molecular phylogenetic analyses, sources, and GenBank accession numbers. For information of Davalliaceae except for *Leucostegia, Arthropteris backleri*, and *Oleandra wallichii*, see Tsutsumi & Kato (2005)

Family and species	Source and voucher	GenBank accession number of *rbcL* and *accD*
Davalliaceae		
Leucostegia immersa (Wall. ex Hook.) C.Presl	Mt Ali, Taiwan; *CT1056*	AB232388; AB232416
Leucostegia pallida (Mett.) Copel.	Ponape Island; *CT1057*	AB232389; AB232417
Dryopteridaceae		
Arachniodes aristata (G.Forst.) Tindale	Niijima Island, Japan; *CT1002*	AB232390; AB232418
Ctenitis eatonii (Baker) Ching	Cultivated in Koishikawa*(Origin, Taiwan); *CT1064*	AB232391; AB232419
Dryopteris erythrosora (D.C.Eaton) Kuntze	Niijima Island, Japan; *CT1001*	AB232392; AB232420
Polybotrya caudata Kunze	Costa Rica; *Moran 2178*(NY)	AB232393; AB232421
Polystichum fibrilloso-paleaceum (Kodama) Tagawa	Niijima Island, Japan; *CT1003*	AB232394; AB232422
Quercifilix zeylanica (Houtt.) Copel.	Cultivated in Koishikawa; *CT1065*	AB232395; AB232423
Rumohra adiantiformis (G.Forst.) Ching	Locality unknown; *CT1006*	AB232396; AB232424
Tectaria phaeocaulis (Rosenst.) C.Chr.	Cultivated in Koishikawa; *CT1066*	AB232397; AB232425
Grammitidaceae		
Grammitis reinwardtii Blume	Gunung (= Mt) Gede, Indonesia; *IN108*	AB232398; AB232426
Lomariopsidaceae		
Bolbitis repanda (Blume) Schott	Bogor Bot. Gard., Indonesia; *IN125*	AB232399; AB232427
Elaphoglossum callifolium (Blume) T.Moore	Gunung Gede, Indonesia; *IN44*	AB232400; AB232428
Lomariopsis spectabilis (Kunze) Mett.	Cibodas, Indonesia; *IN103*	AB232401; AB232429
Teratophyllum wilkesianum (Brack.) Holttum	Plateau of Dogny, Sarramea, New Caledonia; *CT1062*	AB232402; AB232430
Nephrolepidaceae		
Nephrolepis acuminata (Houtt.) Kuhn	Cibodas, Indonesia; *IN1*	AB232403; AB232431
Nephrolepis cordifolia (L.) C.Presl	Bogor Bot. Gard., Indonesia; *IN126*	AB232404; AB232432
Oleandraceae		
Oleandra pistillaris (Sw.) C.Chr.	Gunung Gede, Indonesia; *IN28*	AB232405; AB232433
Polypodiaceae		
Colysis wrightii (Hook.) Ching	Cultivated in Koishikawa (Origin, Okinawa, Japan); *CT1067*	AB232406; AB232434
Crypsinus enervis (Cav.) Copel.	Gunung Gede, Indonesia; *IN43*	AB232407; AB232435
Goniophlebium persicifolium (Desv.) Bedd.	Cibodas, Indonesia; *IN36*	AB232408; AB232436
Gymnogrammitis dareiformis (Hook.) Ching ex Tardieu & C.Chr.	Sikkim, India; *CT1043*	AB232409; AB232437
Loxogramme avenia (Blume) C.Presl	Cibodas, Indonesia; *IN54*	AB232410; AB232438
Microsorum zippelii (Blume) Ching	Gunung Gede, Indonesia; *IN112*	AB232411; AB232439
Pyrrosia rasamalae (Racib.) K.H.Shing	Bogor Bot. Gard., Indonesia; *IN81*	AB232412; AB232440
Woodsiaceae		
Athyrium niponicum (Mett.) Hance	Tokyo, Japan; *CT1005*	AB232413; AB232441
Hypodematium crenatum (Forssk.) Kuhn ssp. *fauriei* (Kodama) K.Iwats.	Saitama, Japan; *CT1063*	AB232414; AB232442
Matteuccia struthiopteris (L.) Tod.	Tokyo, Japan; *CT1004*	AB232415; AB232443

*Botanical Gardens, University of Tokyo.

APPENDIX 2

Life forms, rhizome habit and dorsiventrality, and scale morphology of species used for inferred character evolution based on field observations, personal communications, and literature

Family and species	Life form	Rhizome habit	Rhizome dorsiventrality	Scale
Davalliaceae				
Araiostegia pulchra	E*	Long creeping	++	Stalked
Araiostegia faberiana	E*	Long creeping	++	Stalked
Araiostegia hymenophylloides	SH & E	Long creeping	++	Stalked
Araiostegia parvipinnula	E*	Long creeping	++	Stalked
Araiostegia perdurans	E*	Long creeping	++	Stalked
Araiostegia yunnanensis	R*	Long creeping	++	Stalked
Davallia corniculata	E	Long creeping	++	Stalked
Davallia denticulata	SH & E	Long creeping	++	Stalked
Davallia divaricata	SH & E	Long creeping	++	Stalked
Davallia embolostegia	*SH & E*	Long creeping	++	Stalked
Davallia epiphylla	E*	Long creeping	++	Stalked
Davallia fejeensis	E*	Long creeping	++	Stalked
Davallia formosana	E*	Long creeping	++	Stalked
Davallia griffithiana	E*	Long creeping	++	Stalked
Davallia mariesii	E	Long creeping	++	Stalked
Davallia mariesii var. *stenolepis*	E*	Long creeping	++	Stalked
Davallia petelotii	E*	Long creeping	++	Stalked
Davallia plumosa	E*	Long creeping	++	Stalked
Davallia pyxidata	*E*	Long creeping	++	Stalked
Davallia solida	*SH & E*	Long creeping	++	Stalked
Davallia tasmani	E*	Long creeping	++	Stalked
Davallia trichomanoides	E	Long creeping	++	Stalked
Davallia tyermanii	E*	Long creeping	++	Stalked
Davallodes borneense	E	Long creeping	++	Stalked
Davallodes burbidgei	E	Long creeping	++	Stalked
Davallodes gymnocarpum	E*	Long creeping	++	Stalked
Humata banksii	E*	Long creeping	++	Stalked
Humata melanophlebia	E*	Long creeping	++	Stalked
Humata parvula	E*	Long creeping	++	Stalked
Humata polypodioides	E*	Long creeping	++	Stalked
Humata vestita	E	Long creeping	++	Stalked
Scyphularia pentaphylla	E	Long creeping	++	Stalked
Scyphularia pycnocarpa	E*	Long creeping	++	Stalked
Scyphularia triphylla	E	Long creeping	++	Stalked
Davalliaceae				
Leucostegia immersa	*SH & E*	Long creeping	+	Stalkless
Leucostegia pallida	*SH & E*	Long creeping	+	Stalkless
Dryopteridaceae				
Arachniodes aristata	T	Long creeping	–	Stalkless
Ctenitis eatonii	R*	Short erect	–	Stalkless
Dryopteris erythrosora	T	Short and suberect	–	Stalkless
Polybotrya caudata	C*	Long creeping, stout†	?	?
Polystichum fibrilloso-paleaceum	T	Short erect or suberect	–	Stalkless
Quercifilix zeylanica	T & R*	Creeping or suberect‡	–‡	Stalkless
Rumohra adiantiformis	*SH & E*	Long creeping	++	Stalked
Tectaria phaeocaulis	T	Short creeping or erect	–	Stalkless
Grammitidaceae				
Grammitis reinwardtii	E	Short creeping	–	Stalked

APPENDIX 2 *Continued*

Family and species	Life form	Rhizome habit	Rhizome dorsiventrality	Scale
Lomariopsidaceae				
Bolbitis repanda	T & C*	Short creeping§	++§	Stalked?
Elaphoglossum callifolium	E	Short creeping	++	Stalked
Lomariopsis spectabilis	C	Long creeping	++	Stalked
Teratophyllum wilkesianum	C*	Long creeping	++	Stalked
Nephrolepidaceae				
Nephrolepis acuminata	SH	Short erect rhizome on long stolon	+/–	Stalked
Nephrolepis cordifolia	SH	Short erect rhizome on long stolon	+/–	Stalked
Oleandraceae				
Arthropteris backleri	C	Long creeping	(+)	Stalked
Oleandra pistillaris	SH	Long creeping and erect	++/–	Stalked
Oleandra wallichii	SH	Long creeping and erect	++/–	Stalked
Polypodiaceae				
Colysis wrightii	R	Long creeping	++	Stalked
Crypsinus enervis	SH (& *E*)	Long creeping	++	Stalked
Goniophlebium persicifolicum	SH (& *E*)	Long creeping	++	Stalked
Gymnogrammitis dareiformis	*E*	Short creeping	++	Stalked
Loxogramme avenia	E	Short creeping	++	Stalkless
Microsorum zippelii	*E*	Long creeping	++	Stalked
Pyrrosia rasamalae	*E*	Long creeping	++	Stalked
Woodsiaceae				
Athyrium niponicum	T	Long creeping	–	Stalkless
Hypodematium crenatum	R	Long creeping	+	Stalkless
Matteuccia struthiopteris	T	Erect rhizome on long stolon	–	Stalkless

C, climber; E, obligate epiphyte; R, lithophyte; SH, secondary hemi-epiphyte; T, terrestrial; E & SH, obligate epiphyte and secondary hemi-epiphyte; SH (& E), secondary hemi-epiphyte and probably obligate epiphyte. Italics indicate that the life form is valid for the adult, and that of juvenile plants was not observed.

++, leaves on dorsal side of rhizome and roots on ventral side; +, leaves on dorsal side and most roots on ventral side and a few roots on dorsal side; (+), leaves and roots on lateral sides of rhizome; –, leaves and roots radial on rhizome; ++/–, leaves on dorsal side and roots on ventral side of creeping rhizome, and radial on upright rhizome; +/–, roots on ventral side of stolon and, leaves and roots radial on erect shoot.

Stalked, peltate or pseudopeltate scale attached by a stalk on the ventral surface of shield; stalkless, scale sessile and attached with a broad base.

*Derived from the literature and personal communication. The life form merely described as an epiphyte in the literature is treated as an obligate epiphyte.

†Kramer (1990b).

‡Holttum (1955).

§Hennipman (1977).

Unmarked data in the columns of rhizome habit and dorsiventrality are based on the present observations.