Lygodium hians E.Fournier (Pteridophyta, Schizaeales) – an endemic unusual ground-clothing member of a modern climbing fern genus in New Caledonia

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ABSTRACT
A colony of a fern, *Lygodium hians* E.Fournier (Schizaeales), studied on the southwest Pacific Island of New Caledonia, displays a growth form unusual for any member of this genus. Other living species of the genus *Lygodium* Sw. are characterized by twining fronds, with indefinite growth, which climb extensively on the support provided by other nearby vegetation. These fronds can arise from as early as the sporeling stage and fulfil both vegetative and reproductive functions, with spores produced in lateral sorophores in the upper parts of the fronds. By contrast, in *L. hians*, climbing fronds are only rarely produced and these carry terminal to subterminal sorophores. The main vegetative growth is of a low-growing (here termed 'ground-clothing') frond-type, of definite, rather than indefinite, growth and of unusual dichotomous blade structure. This life form has survived, in this rare and little known remote species, under conditions of considerable ecological, as well as geographic, isolation in the mountains of New Caledonia. Blade/pinnule abscission occurs in *L. hians* in both ground-clothing and climbing fronds, therefore shed foliar units in the

fossil record do not imply that ancient *Lygodium* were climbers. The features of *L. hians*, uniquely within *Lygodium*, provide morphological links with *Schizaea* Sm. and *Actinostachys* Wall. The morphology considerably expands our concept of variation in the genus *Lygodium* and suggests that this life form today may represent an evolutionary phase near to the early stages of diversification of the genus. For these reasons *L. hians* is worthy of inclusion in future molecular and morphological phylogenetic analyses and should be incorporated in comparative studies by palaeobotanists studying fossil ferns.

KEY WORDS
Schizaeales,
Lygodiaceae,
ground-clothing fern,
New Caledonia,
morphology,
Lygodium evolution.

RÉSUMÉ

Lygodium hians *E.Fournier (Pteridophyta, Schizaeales) – une espèce endémique de Nouvelle Calédonie à port inhabituellement tapissant appartenant à un genre moderne de fougères grimpantes.*

Une colonie de la fougère *Lygodium hians* E.Fournier (Lygodiaceae), dans le milieu naturel sur l'île de Nouvelle-Calédonie, montre une forme de croissance qui est inhabituelle pour le genre. Les espèces du genre *Lygodium* Sw. sont généralement caractérisées par des feuilles volubiles, à croissance indéfinie, grimpant sur la végétation voisine. Ces feuilles peuvent se développer précocement et assurer les fonctions aussi bien végétatives que reproductives, avec des spores produites dans des sorophores latéraux dans la partie supérieure de la fronde. Au-contraire, chez *L. hians*, les feuilles grimpantes sont exceptionnelles et elles portent des sorophores terminaux à sub-terminaux. Le développement végétatif produit principalement un type de feuille à croissance réduite et définie (ici nommé 'forme tapissante'), présentant un limbe inhabituellement dichotome. Cette forme de croissance se maintient chez cette espèce rare et mal connue, dans des milieux écologiques et géographiques très isolés des montagnes de Nouvelle-Calédonie. Chez *L. hians*, aussi bien les feuilles 'tapissantes' que les feuilles grimpantes présentent une abscission au niveau du limbe et des pinnules; ainsi, l'observation d'unités foliaires caduques dans le registre fossile n'implique pas forcément que les *Lygodium* du passé étaient des plantes grimpantes. Les caractéristiques de *L. hians*, uniques chez *Lygodium*, illustrent une proximité morphologique avec *Schizaea* Sm. et *Actinostachys* Wall. L'observation de cette morphologie particulière a des implications importantes sur le concept de variation au sein du genre *Lygodium* et suggère que cette forme de croissance actuelle pourrait refléter une étape évolutive proche des premiers stades de diversification du genre. Pour ces raisons, *L. hians* devra être inclus dans de futures analyses phylogénétiques moléculaires et morphologiques et être intégré dans les études comparatives des paléobotanistes étudiant les fougères fossiles.

MOTS CLÉS
Schizaeales,
Lygodiaceae,
fougère couvre-sol,
Nouvelle-Calédonie,
morphologie,
évolution de *Lygodium.*

INTRODUCTION

The fern genus *Lygodium* Sw. (Schizaeales, Lygodiaceae *sensu* Smith *et al.* 2006, Christenhusz *et al.* 2011) consists of some 30-40 living species (Copeland 1947; Tryon & Tryon 1982). These collectively have a pantropic range, with a few more temperate members and are often familiar elements in mainly lowland tropical vegetation (e.g., Copeland 1907; Holttum 1938; Page 1979; Jaffré & Veillon 1990). *Lygodium* is known from fossils (macrofossils and spores) since at least the Cretaceous (Collinson 1996, 2001, 2002; van Konijnenburg-van Cittert 1991, 1992, 2002). Wikström *et al.* (2002) suggest that the genus appears to have passed through a diversity bottleneck and that the modern species array originated in the Neogene.

Today the genus *Lygodium* is characterized by a life-form, which is unusual for any pteridophyte (living or fossil). They typically bear profuse growths of fronds, with indeterminate growth, centred around a rachis, which twines. These fronds extensively climb on other surrounding woody vegetation eventually forming veritable curtains of leafy growth suspended amongst other tropical lowland vegetation. The lower parts of these fronds typically fulfil much of the vegetative functions of each plant, and the upper parts bear the spore-producing growth. Such climbing fronds can arise from as early as the sporeling stage in individual plants of most species, and thus characterize much of the life of each individual plant. By contrast, a colony of the fern *Lygodium hians* studied and collected on Plateau de Dogny (*c.* 21°37'S, 166°51'E) (*fide Page 23 221 & 23 222*, 18.XI.1984, E), a schistose (i.e. non-ultramafic) mountain on the south-west Pacific Island of New Caledonia, displays a sporophyte life-form that is very different from the typical condition. This colony is an exclusively low-growing, ground-clothing, frond-type, which had become locally extensive across the rainforest floor (Fig. 1A, B). Here, each frond is of definite growth, with slender erect stipes arising from creeping underground rhizomes. The stipes each bear simple, elongate, spreading bifurcating blades (Fig. 2A, B). The population has been studied for over 20 years, since a colleague (Dr A. Newton) was able to be directed to the site two decades later, and was able to re-locate the site and confirm that there was a lack of change in general status over this time, hence affirming the continuation and hence semi-permanent occurrence of exclusively this frond form at this site across this time. The existence of this unusual ground-clothing life form in *Lygodium* is as unexpected as the very remarkable creeping life form of the genus *Cyathea* Sm. (Arens & Smith 1998).

Therefore, the aims of this study are: 1) to fully describe the habitat, the life form and frond morphology of this distinctive Plateau de Dogny New Caledonian population; 2) to combine these field data with information from herbarium collections, especially for sorophores and spores, of *Lygodium hians* from other sites in New Caledonia (including from Noumea herbarium and the lectotype in the Paris Herbarium), hence raising awareness of this little known species; and 3) to establish if the *L. hians* 'morphotype' is known in the fossil record of the Schizaeales. The new information, derived from a combination of observations of the living plant in the field and morphological investigations of herbarium and fossil material, has implications for the current concept of variation within the genus *Lygodium* as well as for interpretation of the fossil record and future phylogenetic studies of the Schizaeales.

BIOLOGY AND ECOLOGY OF 'TYPICAL' *LYGODIUM*

Phytogeography

Lygodium shares with *Schizaea* a modern range of occurrence virtually throughout the tropics. Of some 40 living species of *Lygodium*, more than half occur in the Old World. The great majority of these are confined to the wider Indo-Pacific region, within which many of their main species-groupings tend to be more local either in Malaysia, Australasia or the western fringes of the Pacific. *Lygodium* tends to be a predominantly lowland genus. Within the Americas, *Lygodium* is most characteristic of vegetation below 350 m, with a few species ascending to 1 000 m (Tryon & Tryon 1982). In the Old World, the highly mountainous island of New Guinea reflects a similar pattern. Here *Lygodium* occurs from near sea-level to 1 800 m, but is most frequent at lower altitudes (Johns 1985). In the much smaller island mass of New Caledonia, *Lygodium* (excluding *L. hians*, discussed here) is also mostly at altitudes below 500 m (Brownlie 1969, personal field observations [CNP] and herbarium data [NOU, P, K, BM & E]).

Ecology

Existing ecological information on *Lygodium* across the Indo-Pacific region is somewhat sparse and fragmentary. Personal observations (CNP) show that *Lygodium* tends to occur in conditions of generally

Fig. 1. — Forest habitat (**A**) and forest floor (**B**) of the *Lygodium hians* E.Fournier colony on Plateau de Dogny, *c.* 710 m, New Caledonia.; **A**, natural vegetation showing temperate character of relatively open, mature forest community (lacking, for example, in such tropical fern families as Cyatheaceae and Gleicheniaceae, which are abundant at lower, more tropical altitudes). The surrounding nearby forest-floor vegetation also contains abundant *Blechnum* L. ferns; **B**, fronds of part of the colony, showing predominance of typically dichotomous-bladed vegetative frond growth, with some variation in blade form. The conifer seedling is *Austrotaxus spicata* Compton.

high year-round moisture availability, and its more detailed range especially reflects the overall extensive occurrence of tropical lowland rainforests developed within habitats of such high-rainfall environments. Within these settings, most *Lygodium* nevertheless tends to be relatively forest-marginal, where its species mostly favour better-illuminated sites such as along damper forest edges and along banks of lower courses of riversides through forest (see e.g., Westgate & Gee 1990). Some species extend also to habitats around and into sandy margins of lowland swamp forests. Across such sites plants occur especially on clays or in sandy and gravely soils, and its species often tend to be somewhat opportunistic invaders of sites where recent edaphic disturbance occurs in the vicinity of available adjacent tree-support structures. In the longer-term, therefore, its sites may well re-locate with considerable frequency, as denser vegetation closes, following patterns of local disturbance episodes after storm-damage and storm-torrent events, where *Lygodium* species colonise onto both recent erosional and depositional surfaces, and especially the latter. Here they benefit from temporarily low-competition levels for such sites, and gain advantage by the generally high mobility of its species to occupy these (e.g., Cousens 1980; Cousens *et al.* 1985; pers. comm. 1985; Madeira *et al.* 2008; Lynch *et al.* 2009).

SPOROPHYTE STRUCTURE AND HABIT

In a majority of *Lygodium* species the characteristic frond life-form shows an indefinite growth and characteristically climbing habit. Frond morphology in some *Lygodium* species has been relatively intensely studied, including its morphogenetic processes, largely as a result of its curious (for ferns) climbing frond habit (e.g., Müller 1982a, b; 1983). Further, as a consequence of the ecological behaviour of a few species of *Lygodium* (mainly *L. microphyllum* (Cav.) R.Br. and *L. japonicum* (Thunb.) Sw.), in achieving an invasive potential in disturbed ground (mainly in tropical wet forest-marginal habitats), the field potential of a fern with a climbing frond-habit has become especially practically appreciated (e.g., Nauman & Austin 1978; Cousens 1980; Lott *et al.* 2003; Violin *et al.* 2004; Madeira *et al.* 2008; Lynch *et al.* 2009). Evolution of the *Lygodium* frond

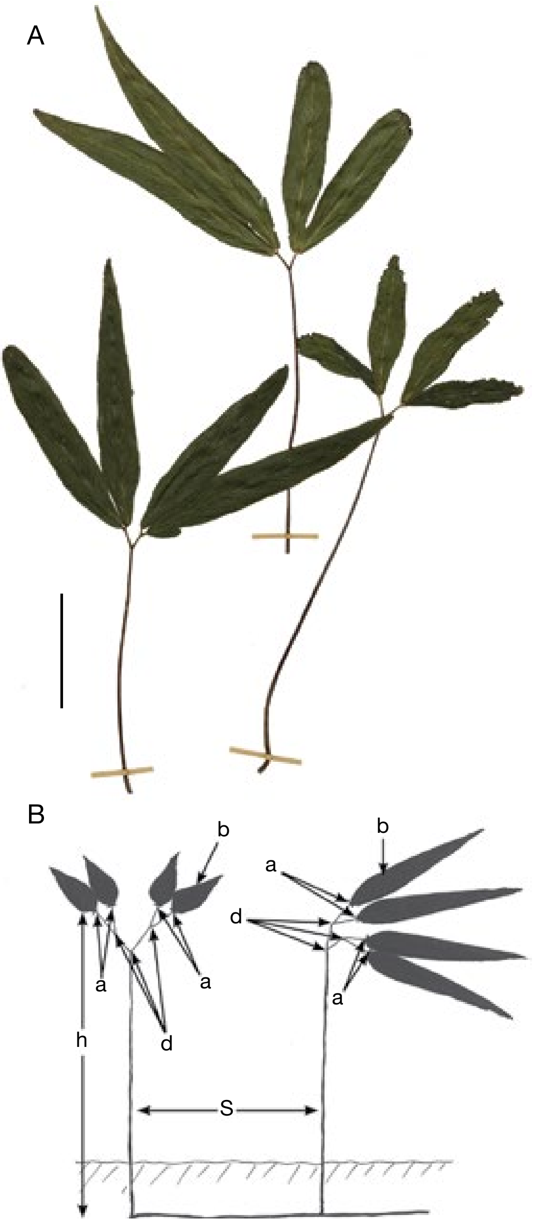

Fig. 2. — Dichotomous form of ground-clothing fronds of *Lygodium hians* E.Fournier: **A**, herbarium sheet of specimens from Plateau de Dogny showing blade form. The reduced length of some blades (right frond and right blade pair of centre frond) is due to extensive insect feeding damage (detail in Fig. 5C). *Page 23222*, Herb. E; **B**, stylised diagram of end and side view showing characteristic structure. Abbreviations: **a**, abscission zones; **b**, blades; **d**, double true-dichotomies at top of main stipe; **h**, height 15 (9-20) cm; **S**, stipe, distance between stipes 8-15 cm. Scale bar: A, 4 cm.

type has also been compared with the much more widespread evolution of epiphytism which occurs in many fern families, including especially Polypodiaceae, Grammitidaceae, Davalliaceae, Oleandraceae, Vittariaceae and Hymenophyllaceae (e.g., Copeland 1907, 1929, 1932, 1947; Holttum 1938; Jones & Clemisha 1976; Page 1979, 2002; Johns 1985; Parris *et al.* 1992; Dubuisson *et al.* 2003; Tsutsumi & Kato 2006). These studies, however, even where focussed on *Lygodium*, have concentrated upon relatively few species of the genus.

The climbing in *Lygodium* fronds has been achieved by a twining ('vining') rachis with indefinitely extending fronds winding upwards through and around other surrounding woody vegetation and can even climb a vertical artificial string (see illustration in Page 1979: 34). These climbing fronds can eventually reach 8-10 metres or more in climbing height from the ground. In great contrast to rhizome-climbers, they are also remarkably fast-growing, light-demanding, and have a rachis that rapidly becomes remarkably tough, and, once twisted, setting in a quite wiry and rigid manner. Chiefly in the upper parts of fronds, and sometimes almost throughout a frond's entire length, these laminar areas also bear distinctive sori, which are placed on specialised, usually peg-like, narrow marginal laminar outgrowths ('sorophores'). These distinctive sorophores in the genus *Lygodium* (except *L. hians*) are arrayed numerously and regimentally along almost the whole lateral margins of the lamina, leaving laminar tips usually tapering to bluntly rounded and characteristically free of any fertile growth, although in some species (e.g., *L. microphyllum*) sorophores typically surround the whole of the margin. Often a weak to relatively strong dimorphy occurs between vegetative and fertile laminar areas, with the lamina of fertile portions sometimes much reduced in size and often with abbreviated overall structure. Within the laminar areas, veins are free in most species, but are anastomosing in a very few (e.g., *L. reticulatum* Schkuhr.). Once spores have been produced and shed, the sorophore-bearing laminae eventually become shed as well at their basal abscission zones. The whole of the twining-and-vining frond is then represented only by the persistent wiry stipes, which remain indefinitely in-situ, up which future successions of later fronds additionally climb (typically until the support itself eventually collapses with the weight!). However, observations suggest that the laminas are remarkably thin in texture, and this may well be a weight-reducing adaptation. Successive nearby-seasons of such growth typically build up veritable curtains of these twining fronds, reaching high into tall surrounding woody angiosperm vegetation. The climbing and light-demanding fronds achieve not only better access to forest and forest-margin illumination by so-climbing, but also produce their entire component of spore-output high on these, thus effectively enabling spore-release to occur at relatively high air-layers within the forest structure. In the life of the plant, such specialised climbing fronds of indefinite growth can begin to arise from a very early stage in the succession in the frond morphology of sporeling plants (Fig. 3), and thereafter, individual plants of most *Lygodium* species produce a multi-year succession exclusively of such twining fronds. Occasionally, however, as pointed out by Holttum (1968), production of such climbing fronds can be preceded in young plants by a few, more briefly-lived, individual fronds which have a more regularly dichotomous structure, before the plant gives rise to its first climbing fronds (Fig. 3). It appears to be fronds of this relatively juvenile type, which are the predominant form seen in the sporophyte of *Lygodium hians* in the material examined here.

OTHER CLIMBING FERNS

The few other modern ferns attributed to having a 'climbing' habit include *Stenochlaena* J.Sm. (Blechnaceae), *Microsorium* Link (Polypodiaceae), *Arthropteris* J.Sm. (Oleandraceae) and *Teratophyllum* Mett. ex Kuln (Lomariopsidaceae) across the Indo-Pacific region (Page 1979; Collinson 2002), as well as some *Lomagramma* J.Sm. and *Lomariopsis* Fée (Lomariopsidaceae), and *Lindsaea macraeana* Copel. (Lindsaeaceae) of the south-east Asian tropics, *Blechnum filiforme* (A.Cunn.) Ettingsh. (Blechnaceae) of New Zealand and *Maxonia* C.Chr. (Dryopteridaceae) in the New World. The climbing habit is also widespread within the relatively smaller-structured Hymenopyllaceae, especially in the genera *Vandenboschia* Copel. and in *Trichomanes* subg. *Lacostea* Bosh (Domin) (Ebihara *et al.* 2006; Nitta & Aps 2009). None of these fronds, however, twine and vine around in the sense of *Lygodium*. *Stenochlaena* is a 'rhizome-sprawler', the rhizome of which grows very rapidly and partly sprawls and partly climbs with a loosely twining action reaching some 3-4 m from the ground. *Microsorium*, *Arthropteris*, *Lomagramma*, *Lomariopsis*, *Teratophyllum*, *Blechnum filiforme*, *Maxonia* and the Hymenophyllaceae are rhizome climbers, adhering to tree-bark. Most ascend at least *c.* 10-15 m, *Maxonia* and the Hymenophyllaceae usually less, but *Teratophyllum* has been observed to reach around 50 m in Malaya and Fiji. All but *Maxonia,* which is usually in open scrub, are found only within interiors of well-developed rainforest, where they typically climb large and well-established rainforest trees (Holttum 1932, 1938, 1954; Page 1979; Tryon & Tryon 1982).

DESCRIPTION OF *LYGODIUM HIANS*

HABIT AND HABITAT

In the site (discovered by CNP November 1984 and revisited by Dr. Adrian Newton in 2006), Plateau de Dogny in the central mountain backbone of New Caledonia (*c.* 21° 37'S, 165°50'E, at *c.* 710 m elevation), the *Lygodium* colony is present in mid-montane rainforest off the ultramafic rocks, on a schistose rock site. The site is in a relatively remote forest-floor habitat (Fig. 1), with a deep, moist, fine silty forest loam, on a south to south-easterly (hence shaded) aspect, beneath a continuous canopy of tall mid-montane rainforest, and near-to and beneath the canopy of a tree of *Austrotaxus spicata* Compton. Here, the fronds of this fern were numerous (more than 100), together forming a relatively contiguous frond-colony structure, *c.* 4-5 m in overall width, of exclusively ground-clothing fronds, across a single patch of forest floor. This montane *Lygodium* was found on this mountain only in this single location, and no comparable colony was found on several other mountains climbed. At this site, the life-form of this colony, across the period for which it has been known, has been exclusively that of a colony-forming network of ground-clothing fronds. The extent of the colony when first found indicates that it has likely developed slowly but steadily for a considerable period before this, probably decades. Subsequently gathered evidence from

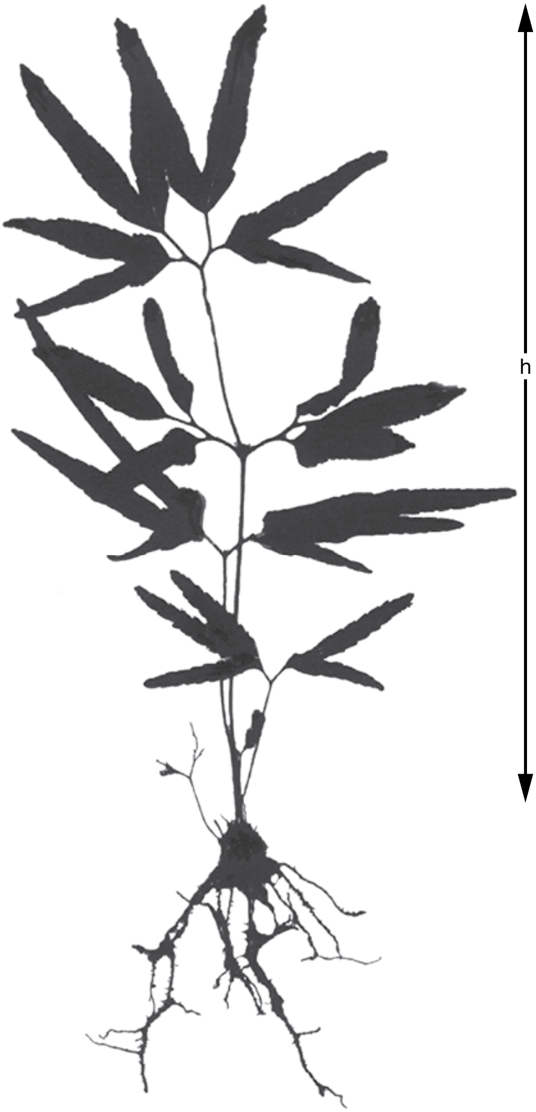

FIG. 3. — Sporeling plant of typical *Lygodium* Sw. (*L. reticulatum* Schkuhr.) showing typical progression of juvenile dichotomous growth more or less immediately into climbing-frond form, collected at lower altitude (*c.* 25 m) in New Caledonia. *Hadfield 76*, Herb E. Height (h): 10 cm.

previously existing herbarium collections enabled identification of this colony to *Lygodium hians* E.Fournier. Herbarium specimens typically include either entirely fertile (Fig. 4B), or fertile plus vegetative fronds (Fig. 4A) – the latter serving to firmly make the material-connection with fronds of the type of vegetative structure shown by the Plateau de Dogny colony studied here. The total known range of this species shows its presence on several other New Caledonian high mountains [Mt. Humboldt (type locality, *Balansa 1564* 'in sylvis, 1000 m'; Fournier 1873), Mt. Panié, Mt. Mou, Mt. Arembo, Mt. Colnett, Mt. Dzumac, Nekando, massif de Ton, Massif du Tchingou, Koghis, Puébo, Haute Tchamba, all at altitudes 700-1350 m and especially around 950+ m], with the records most often from single collections (Brownlie 1969 plus subsequent herbarium data). The majority of the 19th century herbarium specimens of *L. hians* add little further ecological information, typically beyond that of location and altitude, although several bear the annotation: "très rare". Perhaps significantly, we have found no previous record of the species for Plateau de Dogny. Indeed, all of the herbarium sheets seen (including those in major European herbaria and those in Noumea Herbarium, and thus representing probably virtually the total that exists), all except two are exclusively of the climbing phase of the plant only, and thus do not recognise the existence of the long-lived vegetative life-phase of the species as described here. Thus with respect to the known herbarium material, had others encountered such purely vegetative material in such mid-montane forest interior locations, it is likely that absence of fertile parts and difficultly in taxonomic attribution of such curious vegetative material, would have discouraged collection of such fronds, and/or their subsequent incorporation into herbaria, through entirely unknown taxonomic affinity. This may explain the apparent lack of any previous description of such morphologically unusual vegetative pteridophyte material. Further, a great majority of the few herbarium specimens located (NOU, P, K, BM, L, E) are from higher-altitude sites (see above), around upper forest limits (Fig. 4B). It is thus to such sites that the occurrence of fertile material would appear to be restricted. Despite the limited herbarium annotations, it is clear that all represent the occurrence of *L. hians* at such higher altitudes, which would probably be in upper tree-line vegetation, and in cooler and probably lower-growing, more open vegetation, subjected to frequent passing cloud and light precipitation. Indeed, the vegetation type here is of a relatively open forest structure of distinctly temperate character, as indicated especially by the absence at this altitude of lianas, most epiphytes, tree-ferns and palms, all abundant in new Caledonian forests at lower (tropical) altitudes (Fig. 1A). Such high-altitude and temperate forest sites are themselves totally uncharacteristic of most other *Lygodium* species both in New Caledonia and elsewhere. The location of the patch of *L. hians* under study on Plateau de Dogny is not only within the overall forest floor community, but is also a relatively mesic, deep forest soil habitat. This is on a sloping mountainside site which is also immediately around and exclusively in close vicinity and over the root-circle of an equally unusual conifer, *Austrotaxus spicata*. The tree of *Austrotaxus spicata* was itself the only specimen of its species encountered within the vicinity, and several seedlings of *Austrotaxus* occurred amongst the fronds of this *Lygodium* colony (Fig. 1B). Perhaps significantly, this genus is monotypic and endemic to New Caledonia, and the only member of its family (Taxaceae) in the southern hemisphere (and is unknown anywhere as a fossil; Page 1990, 2003; Farjon 2008).

SPOROPHYTE MORPHOLOGY AND SOROPHORE POSITION

Including both herbarium data and those from the site studied in the field, the sporophyte of *L. hians* differs in structure from that of more typical members of the genus *Lygodium* in four principal ways:

a) Its vegetative fronds are largely or exclusively composed of ones of a definite, rather than indefinite, growth habit, and in the Plateau de Dogny colony of *Lygodium hians*, the plant shows a predominance, through its life, of a remarkably distinctive frond type (Figs 1B; 2A, B). The colony consists of long-creeping slender underground rhizomes, which are *c.* 2-3 mm in diameter, and occur at a soil depth of c.10-15 cm and deeper, and which give rise to erect stipes spaced at intervals of *c.* 5-12 cm or

FIG. 4. — Herbarium sheets from other collections of *Lygodium hians* E.Fournier including lectotype: **A**, herbarium sheet of *Lygodium hians* from Mt. Arembo (New Caledonia) showing both a dichotomous determinate ground-clothing frond and a climbing fertile frond, the latter with terminal and sub-terminal sorophores (MNHN, P00630569, Herb. P); **B**, lectotype of *Lygodium hians* from Mt. Humboldt (New Caledonia), showing a climbing frond with terminal and subterminal sorophores (MNHN, P00523232, Herb. P). Sheet height: 42 cm.

more (Figs 1B; 2B). Each stipe, at its top, bears directly a single or usually repeated pair of Y-shaped bifurcations (Figs 2A; 5A). These bifurcations, and the blades they bear, terminate the growth. There are no arrested false bifurcations involved, and the form of each frond is, thus, of definite, rather than indefinite growth habit, throughout the vegetative colony (Figs 1B; 2).

b) These dominant ground-clothing fronds have an entirely dichotomising blade structure (Figs 1B; 2). Each stipe ascends for 8-20 cm, before forming the two closely successive Y-shaped dichotomies. The first branch is regularly of a wide angle of *c.* 60 degrees spread, the second the narrower at *c.* 45 degrees spread (Figs 2; 5A). Each half of the second branch is sometimes shortly-stalked or, more often, sessile (Fig. 5A). Each of the second dichotomies usually carries only a single blade, which is obtuse at its base, widening rapidly to about 2.2-2.5 cm, thence tapering gradually over a length of up to 9-18 cm (fide *Page 23221*, E). The reduced length of some blades (Fig. 2A right frond and right blade pair of centre frond) is due to extensive insect feeding damage (Fig. 5C). Because of the narrower second angle, most fronds appear to be structured as two separated sets of closely-paired long-tapering 'pinna'-like leafy-segments (Fig. 2). Across the region of the dichotomies, the frond orientates each of these 'pinnae' to an ascending-spreading angle of *c.* 30-50° from horizontal. Significantly, the very base of each blade carries a well-formed abscission zone, itself a rare feature in Pteridophyta as a whole. The blades have open dichotomous venation with one or two dichotomies between mid-vein and margin (Fig. 5B). Blade margins are finely denticulate, tooth positions not related to vein endings (Fig. 5B). The overall appearance of the vegetative fronds is so distinctive and unusual that close examination was needed on first encounter to initially establish that this was indeed a fern. Superficially, the fronds have an overall similarity to a dwarf bamboo (such as *Sasa).* Fronds with such dichotomising blades thus not only predominate the life-cycle, but also can persist relatively indefinitely through time in this form building substantial colonies as on Plateau de Dogny.

c) These ground-clothing fronds are of a quite dark-blue-green colouration, and have a tough-leathery, fairly thick and semi-rigid texture, totally unlike the pale yellow-green colour and thin blade texture more characteristic of the vegetative parts more widely known on climbing fronds of other species of *Lygodium*.

d) Herbarium data indicate that climbing fronds can be eventually produced, at least by some higher-altitude colonies in New Caledonia. Indeed, two Paris herbarium specimens (Fig. 4) from Mt. Arembo & Mt. Panié) show both a sterile and fertile frond on the same sheet, the latter specimen with a note (translated): "fern climbing through the bushes or ground-covering, very common but almost always sterile". (We think the reference to "common" may refer to a local frequency of fronds, as members of a single large clone, similar to the one on Plateau de Dogny). These demonstrate that fertile fronds when formed can climb to 1-4 m high, but such a climbing frond-state may be produced relatively briefly (both in stature and likely duration). Each fertile blade is usually appreciably shorter than the vegetative ones in the ground-clothing fronds studied here, usually 5.0-7.5(-11.5) cm in overall length. Sporangia are produced within specialised sorophores, themselves borne from peg-like protrusions, with the sorophores each placed singly or in pairs at the end of a vein. Laminar protrusions bearing the sorophore clusters are very occasionally few, imperfectly-formed and lateral, but on most specimens are abundant, regularly formed and grouped into continuous close-spaced terminal and immediately sub-terminal positions, thus forming regularly regimented arrays around the apex of each fertile blade (Fig. 4, including Lectotype P00523232, but demonstrated especially clearly and extensively also on Noumea herbarium sheets *Buisson 1425* and *Veillon 5660*). Thus the distribution of sorophores around the blades differs in *L. hians* from those of other species of *Lygodium*, in being mostly *terminal on each blade* (rather than arrayed in mainly lateral positions along both longer margins as in most other species of *Lygodium*).

Sorophore and Sporangia morphology

Sorophores and sporangia of *L hians* are typical for all *Lygodium*, characterized by having the sporangia borne in so-called sorophores, in two rows at the end of veins; each row bearing 5-6 sporangia (Fig. 6A, B). Sporangia are borne on marginal lobes covered by a laminar outgrowth (indusium) (Fig. 6A, B). Sporangia in *L. hians* are ca. 600 µm long (Fig. 6A, B), with a clear apical annulus (Fig. 6C). Longitudinal dehiscence of the sporangia reveals a number of irregularly reticulate to verrucate spores (Fig. 6D).

Spores of *Lygodium* are in general 50-130 µm in diameter, always trilete, often with a margo along the laesurae and have a thick perispore that is usually scabrate, granulate or verrucate; sculptural elements sometimes fused to form a reticulum; the exospore is slightly thinner and more finely sculptured (van Konijnenburg-van Cittert 1991, 1992). The spores of *L. hians* are no exception, except that they are the largest of all known *Lygodium* spores: with the perispore they measure between 120 and 150 µm (Fig. 7A); when the perispore is lost (Fig. 7B) they are between 100 and 140 µm. The laesurae are *c.* ⅔rd of the spore radius, and are accompanied by a clear margo (Fig. 7B). The exospore (up to 5 µm thick) is granulate, granules often forming an irregular, fine reticulum (Fig. 7A, B). Perispore thick (up to 8 µm), coarsely and irregularly verrucate to even rugulate (Fig. 7C); verrucae often fused, forming a coarse, very irregular reticulum (Fig. 8A, B). The spore morphology is character-

FIG. 5. — Blade details in *Lygodium hians* E.Fournier from Plateau de Dogny, New Caledonia: **A**, long blades from Figure 2A showing morphology and basal dichotomies; **B**, blade from Figure 2A showing various arrangements of lateral vein departure from mid-vein, open dichotomous venation with up to two dichotomies, and denticulate margin with vein endings not related to position of marginal teeth; **C**, tip of short blade from right frond in Figure 2A showing insect damage and wound reaction tissue. *Page 23222*, Herb E. Scale bars: A, 1cm; B, 2 mm; C, 1 mm.

istic of the *Lygodium* subgenus *Odontopteris* (van Konijnenburg-van Cittert 1991, 1992). However, its large spore size might be a derived feature, as a spore size between 50-70 µm is considered as being original in Schizaeales and much larger spore sizes (e.g., in *Lygodium* and some *Schizaea* species) may be derived (see e.g., Van Konijnenburg-van Cittert 1991, 1999).

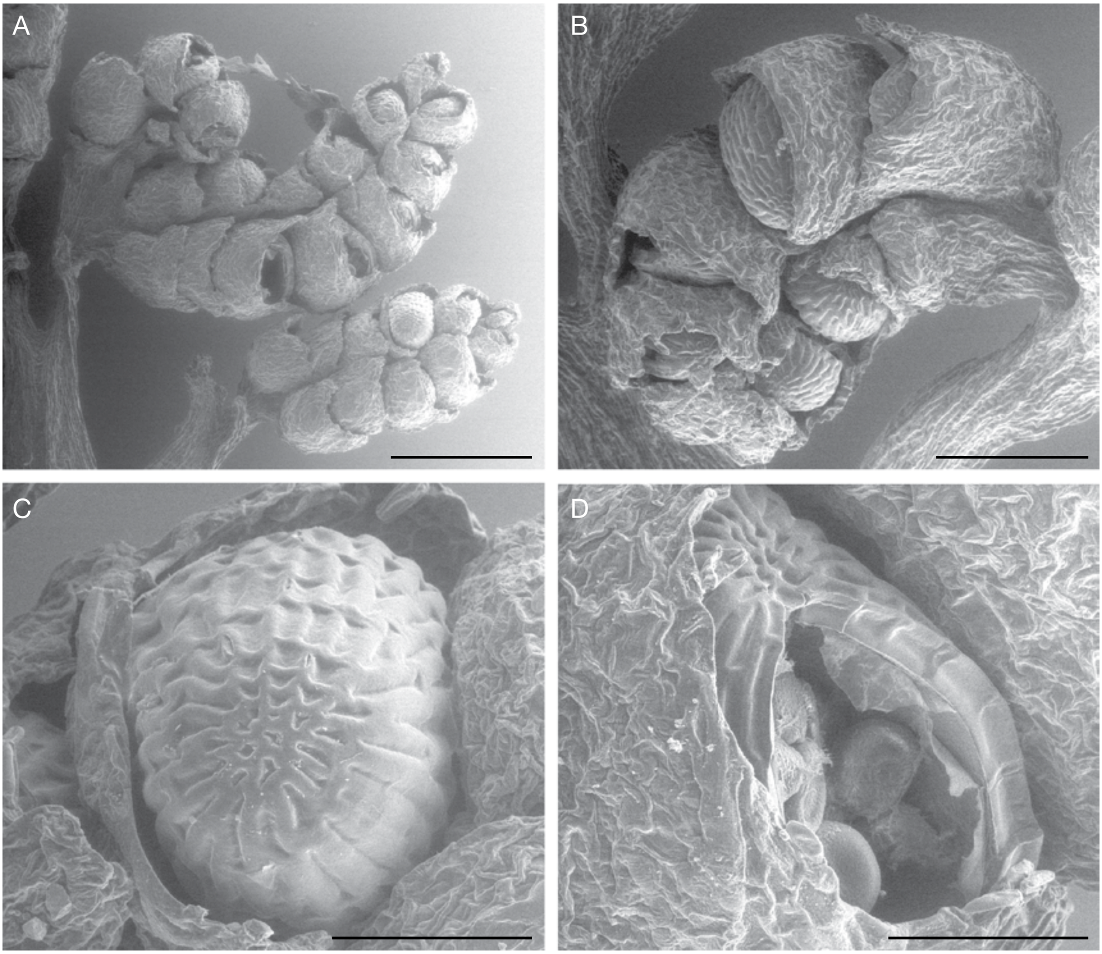

Fig. 6. — Sorophores and sporangia *from Lygodium hians* E.Fournier, scanning electron microscope images, uncoated FEGSEM. Preparation from specimen from Mt. Panié, New Caledonia (Nr. 00.nov.00 01836, Herb. Leiden). SEM stubs now deposited in Leiden. **A**, sorophores situated on laminar protrusions and bearing 5-6 single indusiate sporangia in two rows; **B**, detail of part of sorophore showing indusiate sporangia; **C**, detail from **A** showing apical annulus of sporangium; **D**, detail from **A** showing longitudinal dehiscence of sporangium revealing verrucate to irregularly reticulate spores. Scale bars: A, 1 mm; B, 500 μm; C, D, 200 μm.

COMPARISON WITH *LYGODIUM RETICULATUM* AND *LYGODIUM MICROPHYLLUM*

On the basis of morphological comparison of herbarium materials held at RBG Kew, UK, the most similar other species in the genus *Lygodium* to *L. hians* seems to be *L. reticulatum*. *L. reticulatum* bears its sorophores mainly laterally and to a degree around the tips of its fertile lamina, thus appearing somewhat intermediate between *L. hians* and most other *Lygodium*. *L. reticulatum* is, however, a much more typical *Lygodium*, with the sporophyte life-cycle concentrated upon much more extensive development of climbing fronds into which vegetative and fertile functions of the plant are mainly focussed, and ecologically specialised to forest-margin habitats at mostly mid- to low altitudinal range. The reticulate venation pattern of the sterile fronds differs from the non-reticulate, dichotomous venation in *L. hians*

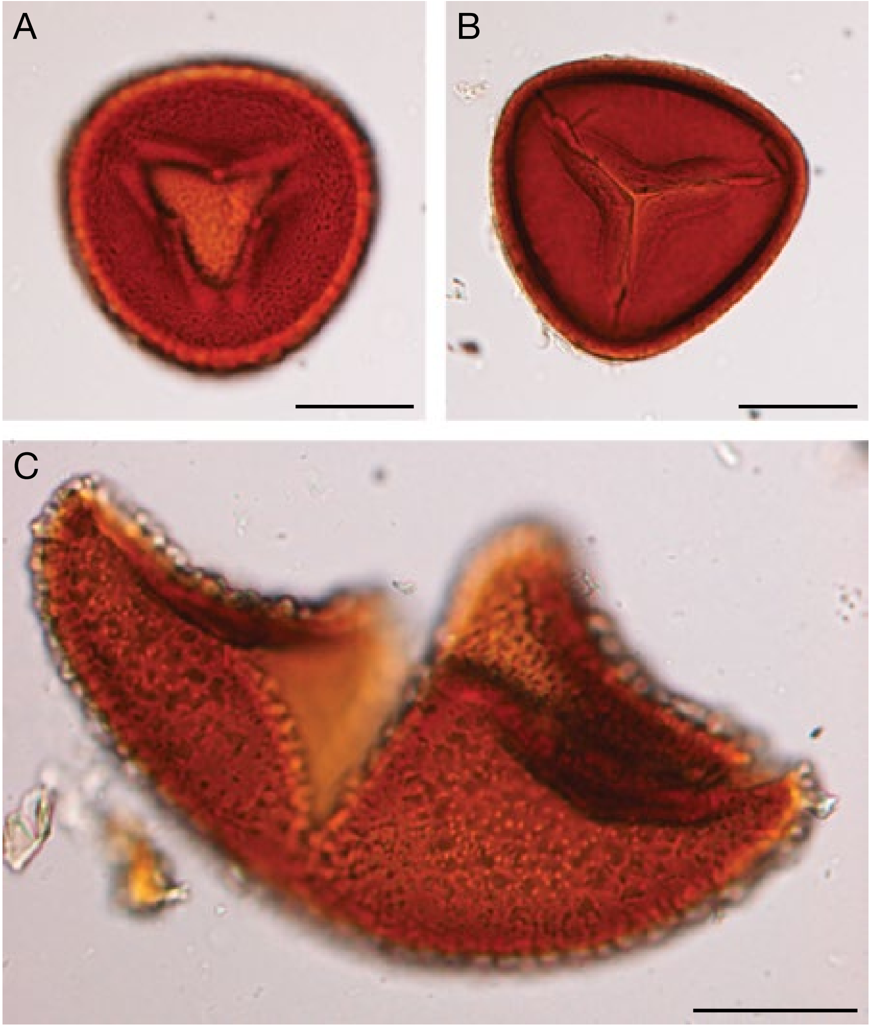

Fig. 7. — Isolated spores of *Lygodium hians* E.Fournier, light microscope images; preparation from specimen from Mt. Panié, New Caledonia (Nr. 00.nov.00 01836, Herb. Leiden). Slides now deposited in Leiden: **A**, spore with perispore showing verrucate to irregularly reticulate ornament; **B**, spore lacking perispore, showing clear margo adjacent to trilete laesurae; **C**, perispore isolated from spore showing thick and robust structure and verrucate to irregularly reticulate ornament. Scale bars: 50 µm.

fronds (Fig. 4A; 5B). *L. reticulatum* spores are reticulate, with a slightly more pronounced sculptural pattern on the distal than on the proximal surface (van Konijnenburg-van Cittert 1991, 1992). Their reticulum is quite regular, and thus different from the very irregular, verrucate-reticulate sculpture of *L. hians*. They measure between 80 and 120 µm in diameter and are thus slightly smaller than *L. hians* spores. *L. reticulatum* also occurs in New Caledonia, and is additionally present more widely, ranging to the New Hebrides, northern Queensland and the Polynesian islands (e.g., Copeland 1929, 1932, Brownlie 1969, and herbarium data).

Another species *L. hians* should be compared with, is *L. microphyllum*, also in the subgenus *Odontopteris*. Although dissimilar to *L. hians* in general morphology with its typical climbing fronds, it is one of the very few *Lygodium* species that bears its sorophores all around the margin, from the base of the fertile lamina to the tips (e.g., Copeland 1929, 1932, and herbarium data). Its spores are smaller than those of *L. hians* and *L. reticulatum*, *c.* 85 µm in diameter, with a slightly more rugulate than reticulate morphology (van Konijnenburg-van Cittert 1981).

Synthesis of *Lygodium hians* characteristics

Hence the combination of examination of this colony of *L. hians*, plus that of known herbarium material from all other known localities, clearly demonstrates:
- the existence of an exceptional life-form in *Lygodium*;
- the ability of this determinate-fronded life-form to achieve extensive 'ground-clothing' local development;
- the nature of this ability to persist (semi-permanently) as a member of a rainforest floor vegetation community;
- the unusual position of sorophores grouped terminally and sub-terminally on fertile fronds;
- that spores are irregularly verrucate to rugulate to irregularly reticulate characteristic of those of *Lygodium* subgenus *Odontopteris*;
- that the most closely comparable modern species is *L. reticulatum*, which differs in having reticulate frond venation, regularly reticulate spores and a more typical climbing frond growth form.

DISCUSSION

Similarities with modern *Schizaea* and *Actinostachys*

Schizaea and *Actinostachys* form ground-spreading colonies, with fronds arising individually from deep-seated rhizomes, and such colonies grow only slowly but probably persist for long periods in suitable sites. The fronds generally have a small laminar area, thick structure, and terminal sorophores (or sporangiophores as these are sometimes called). In addition *Schizaea* extends to montane altitudes. In all these characteristics these two genera are very similar to *Lygodium hians* but quite different from typical climbing *Lygodium*. Therefore, the distinctive morphology of *L. hians* provides an important link between *Lygodium* and these other two members of the schizaealean clade.

L. hians as a relictual survivor of an ancient genus

A substantial proportion of both the Pteridophyta and the conifers of New Caledonia are known to be insular relictual survivors of relatively ancient genera which have, through time, become isolated on this particular dispersing tectonic raft, and upon which a subsequent complex mixture of processes of either stasis or local diversification have acted to produce the modern generic arrays (e.g. Jaffré *et al.* 1987; Jaffré 1995; Page 1999, 2003). The ground-clothing habit and blade-form of the *Lygodium hians* fronds represent a morphological stage seen only briefly (Fig. 3), if at all, very early in the lifetime of other members of this genus. Using the concept that ontogeny may recapitulate phylogeny, one interpretation is, therefore, that the ground-clothing determinate frond morphology is a relictual survivor for *Lygodium*.

The conditions that seem to have enabled the survival of *L. hians*, with ground-clothing determinate fronds, are a forest interior habitat (Fig. 1), with low light levels at a stable site with high site longevity and reduced competition in a temperate climate on a low nutrient substrate. In the Plateau de Dogny *L. hians* colony these conditions are provided by the mid-montane altitude and schistose rocks, together with the root mass, tree longevity and shade cast by the evergreen conifer *Austrotaxus* (which might also offer as yet unknown mycotrophic potential). In addition, the deep soils the mesic, non-ultramafic habitat, and conditions of year-round adequacy of moisture, drainage, shelter and shade, suggest that the location has long been a relatively stable forest-interior slope (Page 1988, 1997). One factor promoting occurrence of ferns generally within such forest-interior floor environments, is normally the possession of low light-level tolerance abilities, in which photosynthetic systems become effectively saturated at low levels of ambient illumination (Page 1979, 2002) as suggested in *L. hians* by the deep blue-green colouration. Such sites, within a locally gymnosperm-dominated forest, may have

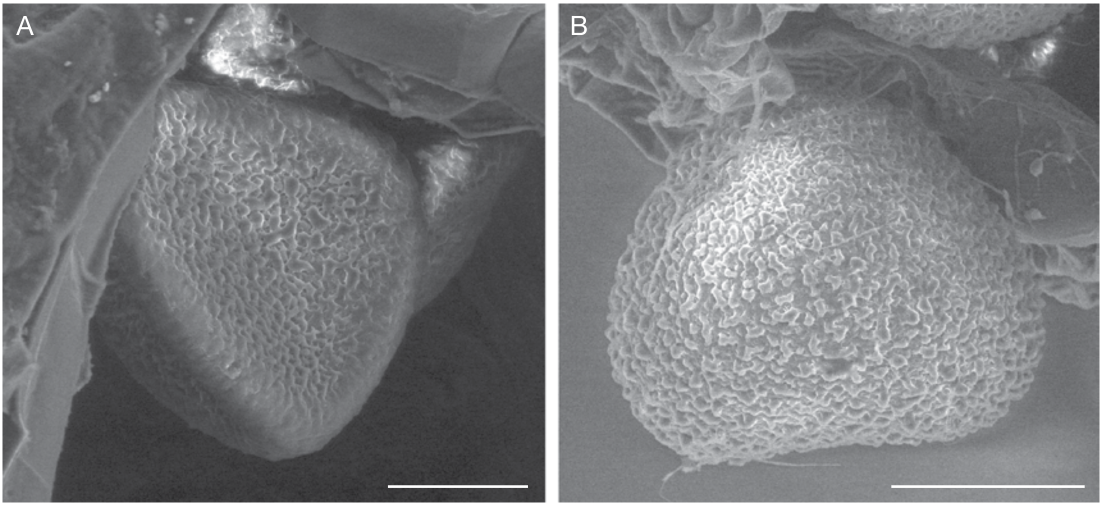

Fig. 8. — In situ spores of *Lygodium hians* E.Fournier, scanning electron microscope images, uncoated FEGSEM: **A**, spore showing verrucate to irregularly reticulate ornament (preparation from specimen Nr. 00.nov.00 01836, Herb. Leiden), SEM stub now deposited in Leiden; **B**, spore showing verrucate to irregularly reticulate ornament (preparation from specimen MNHN P00630569, Herb. P., SEM stub now deposited in Paris. Scale bars: A, 30 µm; B, 50 µm.

enabled survival of such an archaic morphology in the genus *Lygodium* in the mountains of New Caledonia today in spite of the spread elsewhere of angiosperm competition.

RELEVANCE FOR FUTURE PHYLOGENETIC ANALYSES

In recent years considerable advances have been achieved in the Pteridophyta utilising molecular data in elucidating phylogenetic interrelationships between families, and to an extent between genera or major elements within genera (e.g. Hasebe *et al.* 1993, 1994, 1995; Pryer *et al.* 1995, 2001, 2004; Schneider *et al.* 2004; Korall *et al.* 2006; Schuettpelz *et al.* 2006; Smith *et al.* 2006; Nagalingum *et al.* 1997; Schuettpelz & Pryer 2007). Smith *et al.* (2006) presented family delimitations in which Schizaeaceae are separated from a proposed Anemiaceae, the two as sister families, and collectively placed in a clade with a proposed family Lygodiaceae, the whole forming a distinct order Schizaeales. A defining character of the Lygodiaceae is that they are climbing ferns, and that the family is monophyletic (Skog *et al.* 2002; Wikström *et al.* 2002).

Schuettpelz and Pryer (2007) and Lethonen (2011) have subsequently shown that Lygodiaceae are sister to a clade containing Schizaeaceae and Anemiaceae, implying that *Schizaea* and *Actinostachys* may be closely related to *Anemia* rather than to *Lygodium*. *Lygodium* appears thus as a distinct lineage of Schizaeales exhibiting a particular and unusual climbing growth-form. *L. hians* however is an exception, which appears to show through its early life-cycle phases a recapitulation of development from non-climbing to climbing growth. It also differs in its dichotomous frond structure, and the predominance of this frond form in all of the initial purely-vegetative fronds of the colony, appears to further strengthen its apparent links to the frond-structure so characteristic of *Schizaea*.

In a phylogenetic analysis based on rbcl sequences (Wikström *et al.* 2002; including 11 of 40+ known species of *Lygodium*) *L. palmatum* (Bernh.) Sw. is presented as the most basal. In a separate phylogenetic analysis using *trn*L and *trn*L-F spacer (chloroplast) sequence data on 14 species of the genus *Lygodium*, Madeira *et al.* (2008) also concluded that (of the species used), *L. palmatum* plus *L. articulatum* A.Rich. formed a basal clade, with *L. microphyllum* and *L. reticulatum* (both with reticulate spores) as the next, apparently ancient, long branch. The authors consider these four species a paraphyletic group of ancient derivation.

However, material of *L. hians* has not been included in any of these molecular analyses. From the morphological evidence, *L. hians* is most similar to *L. reticulatum* and *L. microphyllum* thus might be part of this ancient group. Madeira *et al.* (2008) note that *L. palmatum*-like fossils are widespread in the fossil record during the Paleogene; that fossil record was reviewed by Collinson (2001) and is considered below. Morphogically, however, *L. palmatum* is a characteristic species of the 'modern' *Lygodium* dominantly climbing-fronded type, and is very considerably more typical of the genus today than is *L. hians* (as, indeed, are all other species included in the analyses mentioned above).

Questions arising are thus whether, as we suggest, *Lygodium hians* represents a basal group in *Lygodium*, whose growth-form could represent the ancestral state for the genus and maybe for the order (Schizaeales), or whether all aspects of structure of *L. hians* are derived. The former implies that *L. hians* has retained this ancestral growth form in relatively unmodified condition, and the latter would imply that that the studied population is the result of local selection. The former is supported by the coincidence of multiple features, which include its ground-spreading habit, the simple dichotomy of the frond-structure, terminal sorophore position, and the similarity of its dominant stages (we suggest recapitulatively), to those passed-through briefly in juvenile stages of other members of *Lygodium*. By comparison, we are aware of no evidence linking any of its features to processes of more modern, local derivation.

Considering the rarity of *Lygodium hians*, it is not surprising that it has not been included (or, indeed, mentioned to exist!) within any of the above molecular phylogenetic analyses. It is thus recommended that *L. hians* should be included in future molecular phylogenetic analyses of the Schizaeales in order to test the above hypotheses.

COMPARISON WITH, AND IMPLICATIONS FOR, THE FOSSIL RECORD

The earliest fossils attributed with certainty to the Schizaeales (Jurassic *Stachypteris spicans* (Harris 1961) and *Phialopteris tenera* [Weber 1968; JHAVKVC pers. obs.]) have spores (*Odontopteris* type) and terminal sorophores very similar to *Lygodium hians*. However they have pinnate fronds unlike *L. hians* (Van Konijnenburg-van Cittert 1991, 1992). Early Cretaceous members of the family may also have terminal sorophores but they have fan-like fronds and totally different spores. *Schizaeopsis* E.W.Berry is known from complete fronds, which are clearly not climbing but are dichotomous in morphology and venation, bear terminal sorophores on their frond segments and resemble extant *Schizaea* Sm. or *Actinostachys* Wall. However, the spores (60-80µm) are trilete instead of monolete (unlike *Schizaea* and *Actinostachys*, and show a typical striate pattern that is completely different from any known spore in the genus *Lygodium* (Van Konijnenburg-Van Cittert 1991, 1992; Kvacek *et al.* 2006).

Foliage and sorophores attributed to the genus *Lygodium* have been recorded from the Late Cretaceous onwards (Debey & Ettingshausen 1859; Brown 1943; Gandolfo *et al.* 2000). Turonian *L. bierhorstiana* Gandolfo, Nixon, Crepet & Ratcliffe is the oldest known Cretaceous *Lygodium* species; it has the typical sorophores of the genus with two rows of indusiate sporangia. The *in situ* spores are psilate to scabrate and no sterile foliage is known (Gandolfo *et al.* 2000); thus we cannot compare this species with *L. hians* with its irregularly reticulate to verrucate spores (*Odontopteris* type). Santonian *L. cretaceum* Debey & Ettingshausen is represented by small sterile and fertile fragments (Fig. 9A; Debey & Ettingshausen 1859: pl. II, figs 19, 21), clearly resembling *Lygodium* dichotomous foliage, and sorophores with two rows of sporangia partially enclosed by an indusium (Fig. 9B), just as in *L. hians* (Debey & Ettingshausen 1859; Wikström *et al.* 2002). Therefore, it would be important to discover if this species possessed spores of the *Odontopteris* type such as are present in *L. hians.* Unfortunately new observations on this material (MEC and JHAVKVC pers. obs.) failed to recover *in situ* spores (or indeed any organic preservation) and no further details could be observed by SEM study of several specimens (e.g., Fig. 9B) so that comparison with *L. hians* is not possible.

Lygodium macrofossils with dimorphic fronds are very common and widespread in the Paleogene (Paleocene, Eocene and Oligocene) and Miocene (Collinson 2001, 2002). This fossil material, (reviewed by Collinson 2001) has highly dissected non-laminar fertile pinnae and smooth to scabrate spores (both quite unlike *L. hians*). The dimorphic fronds are similar to those of modern *Lygodium palmatum* a typical climbing *Lygodium* but in the absence of any known fossil record of pinnules attached to a rachis, or of twining rachis fossils, it is possible that Paleogene to Miocene *Lygodium* with dimorphic fronds had not developed the indeterminate climbing rachis, and there are no known examples of possible climbing fern macrofossils in the Cainozoic (Collinson 2002).

The fossil record contains no examples of climbing *Lygodium* frond fossils so the ground-clothing determinate frond form of modern *L. hians* may be the closest modern morphology to the fossils in this respect. *L. hians* shows that abscission zones developed at the base of individual blades of both vegetative and fertile fronds. Therefore, abscission zones are present in non-climbing fronds so shed laminar units, such as are found in fossil *Lygodium*, cannot be taken as an indication of a climbing habit for their parent fronds. Spores like those of *L. hians* are present in the earliest fossils of Schizaeales suggesting that this spore morphology is likely to represent a primitive state. The dichotomous blade form seen in *L. hians* today appears to characterize all members of the overall *Lygodium-Schizaea-Actinostachys* alliance and is present in the oldest fossils attributed to the genus *Lygodium* from the Late Cretaceous.

The Plateau de Dogny colony studied here demonstrates a marked ability for the development of a highly alternative life-form in *Lygodium* compared with that characteristic of a majority of living members of the genus. The details of the sporophyte structure of *L. hians* studied here thus widens the concept of variation within the genus *Lygodium* that occurs today, and hence that which can be accommodated within the limits of this genus also in the past. Palaeobotanists should therefore incorporate *L. hians* into their comparative studies of modern ferns. For *L. hians* itself, ironically perhaps, it is the ground-clothing forest-interior habitats that are least likely to have contributed foliage to sites of extensive fossilization, thus leaving no fossil record, except potentially of spores.

A SCENARIO FOR THE PREDOMINANCE OF CLIMBING FRONDS IN *LYGODIUM*

The habitats of *L. hians*, within humid, stable forest interiors, favour persistence of larger, vegetative laminar areas and a slow growing, ground-clothing frond structure that remains vegetative for long periods. Fertile-frond production may be stimulated by exposure to occasional forest-interior light gaps (e.g., after tree-fall), where locally greater air-turbulence would provide a degree of enhanced natural spore-dissemination potential. Growth in settings with such short-lived light gaps for spore-production (including forest margins and canopy breaks along rivers) may have been the driver initiating the evolution of a rapidly climbing habit with indefinite growth for fertile fronds, maximising the benefit from the period for which the gap persisted. Typical *Lygodium* climbing fronds represent the majority of sporophyte growth, having both vegetative and reproductive functions rendering obsolete an initially long-lived, slow-growing, ground-clothing vegetative phase, such as in *L. hians*. The dichotomous structure of the blades, as seen in *L. hians* vegetative fronds, can form the basis of a scenario for achievement of the climbing habit within *Lygodium* fronds. A climbing habit would seem unlikely to evolve from a purely pinnately-structured frond (although this is what the climbing frond of *Lygodium* is usually, incorrectly, regarded as being). In this scenario it is proposed that climbing could be achieved from a dichotomously structured blade, in which the number and position of dichotomies becomes indefinitely re-iterated as follows: 1) left and right halves of the blade become unequal; 2) one half develops a further dichotomy and consequently overtops the other; and 3) this is repeated indefinitely in alternate mirror-image fashion (Fig. 10).

If each dichotomy continued an indefinite growth, the resulting frond would be unsupportable. Alternate left- and right-held branches of these dichotomies might have ceased development through the innate formation of an arrested, non-developing terminal bud

Fig. 9. — Cretacous *Lygodium cretaceum* Debey & Ettingshausen: **A**, pinnule fragment with sterile basal portion (left of image) and fertile terminal sorophore (Natural History Museum, Vienna, Department of Geology and Palaeontology, specimen 1857/0008/0004). **B**, scanning electron microscope image, FEGSEM uncoated directly of specimen on rock, showing part of sorophore from **A**, with three 'bulges' likely representing original positions of single sporangia, each associated with an elongate marginal protrusion interpreted as an indusium; no details of sporangia and no spores were visible on any specimens examined. Scale bars: A, 2 mm; B, 1 mm.

(Fig. 10B). Either side of this bud, pinnate leafy sub-structures may have developed (hence the formation of a lateral pseudo-dichotomy), with all subsequent sub-divisions on each of these foliar units of definite, (rather than indefinite), pinnate-habit (Fig. 10B). Pinnate structures precede the occurrence of dichotomous structure in the Schizaeales fossil record (see above), so the non-continuing pinnate foliar units in *Lygodium* climbing fronds may be a relatively simple evolutionary recall of earlier structure. In this scenario the climbing frond of *Lygodium* is thus of indefinitely re-iterated forking structures in fractal-relationship to one another, with one branch each-time decorated with pinnate appendages (Fig. 10C). Therefore, the traditional terms 'rachis' and 'pinna', though characteristically used for the main axis and lateral leafy-units of *Lygodium* fronds, are non-homologous with those of truly pinnate fronds. These terms are thus used here only in inverted commas. As indefinitely repeated successive frond-portion fractals, *Lygodium* climbing-fronds in this scenario demonstrate fractal relationships that are inherently innate within ferns generally, though seldom developed to the degree shown by *Lygodium*.

On the climbing fronds, developed in this scenario, 'pinnae' would be essentially held perpendicularly (i.e. in spreading orientations) in the most efficient light-intercepting plane. This orientation would also have enabled fronds to 'elbow' their way forward and upward amongst existing woody branches (in contrast to many modern flowering plant climbers, no tendril-like structures are present in *Lygodium*). Subsequent modifications of a weakly-twisting habit, and permanent hardening of the twining-structure, resulted in an efficient twining-vining upward scrambler around potentially supporting existing objects. Such developments may have been a response to the occurrence of slender woody-perennial supports resulting from angiosperm evolution. Conifers, for example, are more likely to have unsympathetically-shed such attempting climbers, and tree-fern trunks, by offering only hanging trunk-ensheathing skirts of dead frond masses, provide only insubstantial support to twining vines (Page & Brownsey 1986). Angiosperm forest also provides more rapid tree life-cycle turnover and hence abundant sapling growth.

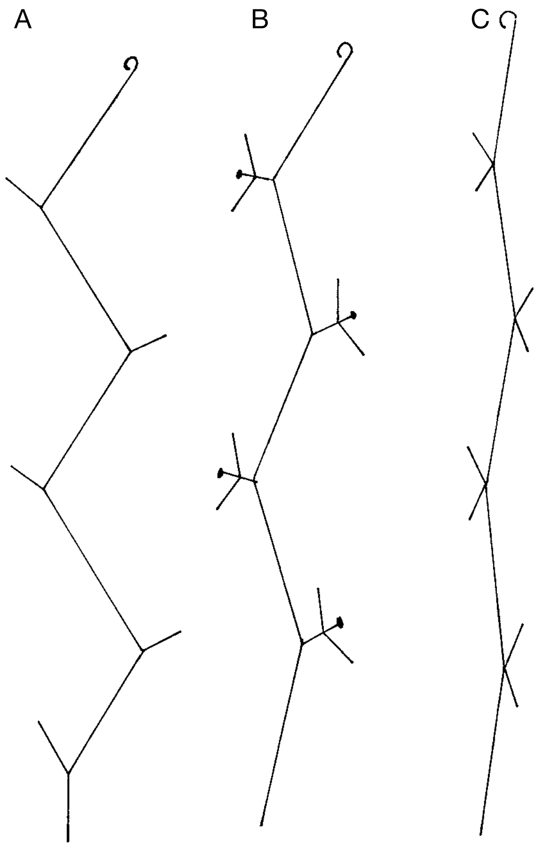

Fig. 10. — Scenario for the predominance of the climbing frond-form of *Lygodium* Sw., developing from a basic dichotomous structure. **A**, a theoretical initial stage in which a series of simple sequenced dichotomies form a successive set in which left and right branches become alternatively indefinitely developed; **B**, the shorter branches of each non-continuing dichotomy are each soon 'stopped' from further indefinite development by establishment of a non-continuing terminal bud, but with a lateral 'pinna' pair of definite growth forming a pseudo-dichotomy; **C**, the typical frond-form in most modern *Lygodium* species in which each non-continuing dichotomous branch and its arresting bud are eventually reduced to nothing. Paired 'pinnae' only remain, and these may bear further sets of foliage in successive complex 'pinna' arrangement developments in individual species.

Model for lateralisation of sorophore position

In contrast to low growing fronds with vertically held blades, foliar-segments bearing terminal sorophores on lateral pinnate units of climbing fronds would potentially droop slightly in rain (partly because of their horizontal orientation, partly because of their overall lightweight lamina structure but heavier sorophores). Water droplets would tend to flow towards, and probably accumulate amongst, the sorophores. Lateralisation of the sorophore position largely avoids this problem and might have been selected for at an early stage of climbing-frond evolution, because terminal sorophores would be highly vulnerable to lingering water accumulation and decay. Sorophore repositioning may enable the tips of the fertile laminar areas to function as drip-tips, drawing surface-water away from the lateral sorophores, achieving greater and drier spore-output as a benefit. Thus it is proposed here that lateralisation of the position of sorophores may be intimately associated with the evolution of climbing fronds in *Lygodium*. Lateral (rather than terminal) sorophore location on separate shed laminar units could be taken as evidence of their having been borne on climbing rather than ground-clothing fronds and might be a proxy for the climbing *Lygodium* habit in the fossil record. The converse is not the case because terminal sorophores do occur on climbing fronds in *L. hians* and also partly on *L. reticulatum*; in *L. microphyllum* the sorophores are positioned all around the margin, but here the fertile laminar areas are relatively small.

CONCLUSIONS

A population of a fern with unusual frond morphology, growing on Plateau de Dogny has been identified as a species of *Lygodium*, *L. hians*, a previously very poorly known New Caledonian endemic. The population is the first of this species to be documented in detail in the field.

Field and herbarium material shows that *L. hians* is a typical member of *Lygodium* in having ultimately a climbing fertile frond with laminar portions bearing sorophores with indusiate single sporangia each with a terminal annulus. The spores are comparable to those of members of subgenus *Odontopteris*. However, *L. hians* is distinctive (unique to our knowledge based on wider herbarium survey) within the genus *Lygodium.* It is distinctive in its: 1) mid-high altitude occurrence and, therefore, temperate climate; 2) forest interior habitat in conifer shade; 3) vegetative fronds with determinate growth and a dichotomous blade structure; 4) vegetative phase which can remain exclusively terrestrial (rather than climbing), building a large, long-lived, ground-covering colony; and 5) terminal and sub-terminal (rather than lateral) sorophore positions on climbing fronds. This combined field and herbarium information on *L. hians* thus considerably widens the concept of variation within the modern genus *Lygodium*.

Other extant *Lygodium* species pass through a very short-lived juvenile phase with determinate dichotomous fronds like those which are long-lived and ground clothing in *L. hians*. If, in this case, ontogeny recapitulates phylogeny, *L. hians* may be a relictual survivor of an early evolutionary phase in the genus. In contrast to *L. hians* (in a shaded forest interior), other living *Lygodium* occupy open forest margin habitats where climbing fronds of indeterminate growth can utilize generally sustained higher illumination levels.

L. hians shows that abscission of blades/pinnules occurs in non-climbing fronds as well as climbing fronds. Therefore isolated laminar units of *Lygodium* in the fossil record cannot be taken to indicate a climbing habit.

Scenarios are presented for drivers of predominance of climbing fronds in *Lygodium* and for lateralisation of the sorophore position. The latter may be intimately associated with the climbing frond habit in *Lygodium* (sorophores shifted away from the water accumulating blade tip, the latter then acting as a 'drip tip'). Exclusively lateral sorophore position on isolated laminar units of *Lygodium* in the fossil record could potentially be used as an indication of their having been shed from climbing fronds.

The ground-spreading colony form, frond structure and terminal sorophore position in *L. hians* differs from other modern *Lygodium* but is similar to *Schizaea* and *Actinostachys*. Thus, uniquely in *Lygodium, L. hians* provides evidence of morphological similarity with the other members of the Schizaeales. The survey of the living *Lygodium hians* presented here adds an array of both micro- and macro-neobotanical data of value in: 1) widening the concept of living structural sporophyte form which occurs in the ancient fern genus *Lygodium*; 2) providing characters which may link *Lygodium* and other genera of Schizaeales (e.g., *Schizaea* and *Actinostachys*); 3) providing data which may help establish likely steps towards the evolution of the unusual climbing-frond habit of *Lygodium*, unique in this family to this genus; and 4) providing guidance for recognition of climbing *Lygodium* species in the fossil record. It is recommended that *Lygodium hians* should be included in future phylogenetic analyses of *Lygodium* and the Schizaeales in general.

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