THE ROYAL SOCIETY

Epiphytism and pollinator specialization: drivers for orchid diversity?

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Epiphytes are a characteristic component of tropical rainforests. Out of the 25 000 orchid species currently known to science, more than 70% live in tree canopies. Understanding when and how these orchids diversified is vital to understanding the history of epiphytic biomes. We investigated whether orchids managed to radiate so explosively owing to their predominantly epiphytic habit and/or their specialized pollinator systems by testing these hypotheses from a statistical and phylogenetic standpoint. For the first approach, species numbers of 100 randomly chosen epiphytic and terrestrial genera were compared. Furthermore, the mean number of pollinators per orchid species within the five subfamilies was calculated and correlated with their time of diversification and species richness. In the second approach, molecular epiphytic orchid phylogenies were screened for clades with specific suites of epiphytic adaptations. Epiphytic genera were found to be significantly richer in species than terrestrial genera both for orchids and non-orchids. No evidence was found for a positive association between pollinator specialization and orchid species richness. Repeated associations between a small body size, short life cycle and specialized clinging roots of twig epiphytes in Bulbophyllinae and Oncidiinae were discovered. The development of twig epiphytism in the first group seems repeatedly correlated with speciation bursts.

Keywords: Bulbophyllinae; epiphytism; Oncidiinae; orchids; pollinator specialization; twig epiphytes

1. INTRODUCTION

Epiphytes are a characteristic component of modern tropical rain and cloud forests, both in terms of species diversity and biomass. Understanding when and how this particular life form diversified is vital to understanding the history of epiphytic biomes. Approximately 7.5% of all vascular plant species are epiphytes (Gentry & Dodson 1987; Bramwell 2002). Although many epiphytic species exist (more than 23 000), most of them are accounted for (Benzing 1990) by only a few higher taxa (876 genera in 84 angiosperm families). Apparently, relatively few lineages have been able to enter the epiphytic niche successfully. And out of those taxa that have evolved an epiphytic habit, only few have radiated into species-rich groups.

Benzing (1990) offered a possible explanation for the few large epiphytic vascular plant radiations. He postulated that a complex suite of adaptations is needed for an epiphytic habit. Canopy habitats are indeed difficult to colonize for four reasons. First, substrate stability is low (Nieder 2004). Structures such as multiple minute climbing roots that increase adhesion to the host are essential for survival. Second, nutrient and water supplies are limited owing to the frequently thin substrate cover with low water-carrying capacity (Chase 1987). Adaptations such as succulence, crassulacean acid metabolism sequential production of individual shoots operating as independent physiological units, and special absorptive tissues prolonging contact with transitory fluids such as velamentous roots, are required to overcome severe drought stress (Benzing 1990). Third, canopy habitats are not the most accessible for colonizing seeds owing to patchiness in the epiphytic biotope. Arrays of suitable branches within individual hosting crowns are usually scattered and sometimes far apart (Ibisch *et al.* 1996). Dust-like seeds, which are easily dispersed by wind and have a high germination success due to fungal intervention, significantly enhance successful propagation. Fourth, the population density of epiphytes is often low (Wolf & Flamenco 2003). Highly specialized pollination systems may be required for effective pollen transfer between such scattered populations.

The morphological and physiological adaptations mentioned above are most strikingly developed in the Orchidaceae. This is not surprising, given the fact that out of the almost 25 000 orchid species currently described, *ca.* 18 000 are epiphytes (Royal Botanic Gardens, Kew 2003). In addition, almost half of the 47 largest epiphytic genera are orchids (Benzing 1990). The question arises as to whether orchids, in contrast to other vascular plant

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One contribution of 16 to a Discussion Meeting Issue 'Plant phylogeny and the origin of major biomes'.

doi:10.1098/rstb.2004.1529

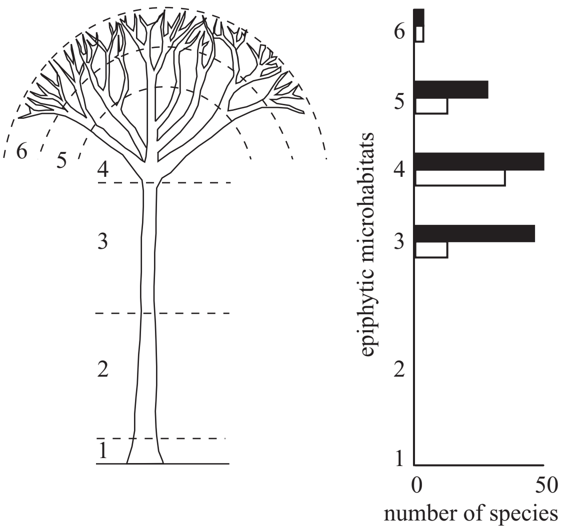

Figure 1. Vertical distribution of orchid species (open bars) and individuals (black bars) in four of the six different epiphytic microhabitats as first described by Johansson (1974). Picture modified from Ek *et al.* (1997) and Nieder (2004).

families, managed to radiate so explosively owing to their predominantly epiphytic habit.

Several hypotheses for the large species richness of orchids have been described. The first theory was postulated by Gentry & Dodson (1987), who proposed that the high species diversity of orchids might be correlated with their exceptionally fine niche partitioning. Floristic inventories by Pittendrigh (1948), Johansson (1974), Ter Steege & Cornelissen (1989), Ek *et al.* (1997), Wolf & Flamenco (2003) and Nieder (2004) indeed demonstrated microhabitat specialization in the tropical epiphytic environment and show that the total bark and branch surface area available for occupation by epiphytic species greatly exceeds that of the ground area. These studies also show that many more orchid species and individuals are crowded into the tree crown and branches as compared with a similar ground area. Four main epiphytic microhabitats exist (figure 1). The first consists of the shaded and humid tree base, where species growing directly on the bark survive. The second microhabitat encompasses the upper trunk, where epiphytes grow only when suitable germination sites are present. The third microhabitat comprises the inner canopy, which is a heterogeneous assemblage of the environment of the upper tree trunk and outer canopy. Here, shade-adapted species can survive in the inner forks and branches next to hemi-epiphytes growing in packages of moss and humus and species that can endure sites in direct sun. The observation that the largest numbers of epiphytic species and crown-foraging pollinators are usually found here might be correlated with the large diversity of this environment. The fourth microhabitat is the outer canopy, with high levels of disturbance, prolonged periods of drought and large fluctuations in temperature, where largely xeromorphic species are present rooting directly on the outer well-illuminated twigs. Speciation may be increased since specialized morphological adaptations allow a survival advantage in each of these four microhabitats. In addition, the high diversity in tropical tree species might stimulate further niche differentiation owing to host specificity.

A second hypothesis explaining the large species richness of orchids is given by Benzing (1990). He describes the highly fragmented nature of the epiphytic substratum, especially in mid-montane rainforest, as an ideal speciation condition since it should promote allopatric speciation. According to Benzing (1990), this would explain why not only orchids, but also epiphytic aroids and bromeliads are so species-rich despite their different morphological adaptations to the arboreal habitat. This argument is contradicted by Ibisch *et al.* (1996), who mention that, in plant families that have evolved epiphytism other than the Orchidaceae, the terrestrial species have higher rates of speciation. They use this observation as support for their hypothesis that the fragmented nature of the epiphytic substratum cannot be the main driver for diversity in the orchids.

A third hypothesis explaining the large species richness of orchids is pollinator specialization. Orchids are widely believed to have the highest degree of pollinator specialization when compared with other families of flowering plants (Tremblay 1992; Ibisch *et al.* 1996). Clearly, a high degree of prezygotic ('ethological') isolation can be imposed if each group of plants receives visits from only one, unique pollinator species, and this can easily lead to reproductive isolation and thus potentially speciation with, or without, physical barriers to gene flow. The orchids are well known for certain pollination strategies that are argued to cause such highly specialized relationships between plant and pollinator. For example, flowers of species of *Ophrys* in Europe and several Australian genera are thought to produce highly specific suites of olfactory and visual stimuli that each attract a unique species of pollinator, usually a male bee or wasp (Dafni & Bernhardt 1990). The insect confuses these stimuli with the conspecific female and pollinates through repeated mistake copulations. It is suggested that high speciation rates within these genera are because different species of bees use slightly different olfactory stimuli to attract mates, so only a small number of mutations in orchid olfactory stimuli genes should be sufficient to cause adaptation to a new species of pollinator and thus reproductive isolation (Schiestl & Ayasse 2002). Even in moderately specialized 'pollinator syndromes'—such as those associated with bumble-bee and hummingbird pollination, where a plant species is pollinated by a small number of bumble-bee or hummingbird species—one major gene mutation may be all that is required to cause an adaptive switch between the two syndromes (Bradshaw & Schemske 2003). Thus chance mutations within plant species that are only moderately specialized on pollinators could also potentially drive speciation. Gentry & Dodson (1987) consider bee, fly, hummingbird, hawkmoth, bat and small mammal pollination syndromes all to be moderately specialized in terms of the number of pollinator species attracted. Epiphytic taxa with these types of pollination systems are present in Apocynaceae (Asclepiadaceae), Bignoniaceae, Bromeliaceae, Cactaceae, Ericaceae, Gesneriaceae, Marcgraviaceae and Rubiaceae. Apart from Bromeliaceae, these families have much lower species diversities compared with the Orchidaceae, and therefore this does not necessarily support the hypothesis that pollinator specialization *per se* has driven speciation. However, for many authors the specialized pollination mechanisms displayed in some orchid genera are sufficient to warrant this argument. Tremblay (1992) attempted to test the pollinator specialization hypothesis by comparing information on numbers of pollinator species per orchid available from the literature. Out of the 456 orchid species for which pollinators were known in 1992, he argued that 67% were pollinated by a single pollinator. A much lower proportion of orchid species were pollinated by two (14%) or more (17%) species. Only a few orchids ($< 5\%$) exploit pollinators indiscriminately, suggesting high pollinator specialization. Further, Tremblay (1992) averaged the numbers of pollinator species across the orchid subfamilies recognized by phylogeneticists at the time, and argued that more recently derived subfamilies have fewer pollinators, suggesting that pollinator specialization could drive speciation. However, the information from both orchid phylogenetics and on pollinating species has increased since 1992. It is also recognized that time spent studying a single plant species often increases the number of pollinator species recognized, and that including casual observations can erroneously categorize species as specialized (Ollerton & Cranmer 2002).

A fourth hypothesis for the large species richness of orchids is given by Vasquez *et al.* (2003). They use long-distance dispersal modes as an explanation for the high species diversity of orchids by using the argument that their dust seeds enable the establishment of innumerable small and dispersed founder populations, and thus high rates of allopatric speciation. Benzing (1990) also uses this argument as the explanation for high species richness amongst epiphytic ferns. Kessler (2002) however, shows that bromeliad taxa with adaptations to long-distance dispersal (dust seeds) have lower species numbers as compared with taxa with short-distance dispersal modes (winged seeds and berries). He attributed this to the hypothesis that long-distance dispersal is much more efficient in colonizing canopy habitats and preventing population differentiation owing to a high gene flow.

A fifth hypothesis for the large species richness of orchids can be deduced from Wikström & Kenrick (2000, 2001). They correlate development of a closed-canopy vegetation of broad-leafed angiosperm forests during the Late Cretaceous and Early Tertiary with an increase in the ranges of light and humidity conditions. According to these authors, this had a positive effect on epiphytic diversification and a negative effect on terrestrial species diversity because the quality and intensity of light reaching the forest floor was greatly reduced. The Orchidaceae, with their highest percentage of epiphytism, might have had the best chances of diversification in this new environment with light in the canopy and shade at the forest floor. That epiphytic diversification in the Early Tertiary is not a general phenomenon for vascular plants, however, is pointed out by Benzing (1990). He states that many species-rich, canopy-based orchid and non-orchid genera such as *Anthurium, Peperomia, Rhododendron* and *Tillandsia* are concentrated in geologically young montane habitats, which suggests that much of the current epiphyte diversity dates from the Pliocene/Pleistocene only. Molecular dating studies on the diversification of the epiphytic orchid genus *Coelogyne* from terrestrial allies in the Himalayan and southeast Asian region performed by Gravendeel (2004) support this hypothesis.

2. GENERAL AIMS

We have highlighted that there is a debate as to whether the epiphytic habit promotes speciation rates in the Orchidaceae. Pollinator specialization has been advanced as a main alternative to this hypothesis. We test these contrasting hypotheses from both a statistical and a phylogenetic standpoint.

(i) To test statistically whether epiphytism could have driven speciation, species numbers of 100 randomly chosen epiphytic and terrestrial genera were compared. This was carried out for both orchids and non-orchids to test whether epiphytic species have a significantly different number of species compared with terrestrial species. (ii) To test statistically whether pollinator specialization could have driven speciation, pollinator numbers of all orchid species described in Van der Cingel (1995, 2001) of the (predominantly terrestrial) subfamilies Apostasioideae, Cypripedioideae, Orchidoideae and (climbing) Vanilloideae were compared with the numbers of pollinators per species of the (predominantly epiphytic) subfamily Epidendroideae.

For the second approach, two different phylogenies of tropical epiphytic orchids were used to investigate whether (iii) special suites of epiphytic adaptations characterize specific clades; (iv) how many times these combination of characters evolved; and (v) whether these characters are repeatedly associated with main speciation bursts.

3. MATERIAL AND METHODS

(a) *Concept of epiphytism used*

The designation 'epiphyte' is here reserved for rain-fed 'atmospheric' vascular plants, germinating on their host (which can either be trees or rocks) to which they are anchored by a few roots only and which never become host vasculature- or ground-connected so that they can allocate resources for growth and reproduction that soil-based terrestrials have to allocate to self-support (Benzing 1987, 1990). For practical reasons, we included epilithic species in our survey as well, although some epilithic orchids are restricted to rocks only. The term 'obligate twig epiphytes' is used for those epiphytes that occur predominantly on less than 2-year-old ultimate branchlets and twigs (Chase 1987).

(b) *Statistical analyses*

To determine whether epiphytes have significantly more species compared with terrestrial orchids, the epiphytic genera listed in table 1.1 of Benzing (1990) were numbered. Subsequently, 100 numbers were generated (using the random number generation option as implemented in Microsoft EXCEL v. 2002) for both orchid and non-orchid genera. Out of the 100 genera in each dataset, the next terrestrial genus according to the alphabet was looked up in Mabberley (1998). Out of all genera, the number of species was recorded (table 1). Genera found were sorted from small to large species numbers and subsequently subdivided into 10 classes of 10 observations each.

A likelihood-ratio test for goodness of fit (or *G*-test), as described by Sokal & Rohlf (1995), was subsequently performed to compare the distributions of species over genera between epiphytes and terrestrials, both for orchids and non-orchids.

To determine whether a high degree of pollinator specialization is correlated with a large orchid species diversity, the number of

Table 1. Species numbers of 100 randomly chosen (*a*) orchid genera and (*b*) non-orchid genera from the list of epiphytes as given in Benzing (1990) and the next terrestrial genus according to the alphabet in Mabberley (1998).

(*a*) orchid genera

epiphytic genus	species number	terrestrial genus	species number
Acineta	10	*Acrolophia*	9
Aeranthes	30	*Altensteinia*	9
Ancistrochilus	2	*Androcorys*	4
Ancistrorhynchus	13	*Androchilus*	1
Angraecopsis	14	*Anoectochilus*	35
Ansellia	2	*Anthogonium*	1
Armodorum	2	*Arnottia*	2
Basiphyllaea	3	*Baskervilla*	7
Benzingia	2	*Beloglottis*	1
Bogoria	4	*Bonatea*	20
Bollea	7	*Brachystele*	18
Bolusiella	10	*Brachionidium*	35
Brachypeza	7	*Brownleea*	7
Bulbophyllum	1000	*Burnettia*	1
Caucaea	1	*Centrostigma*	5
Ceratochilus	2	*Cheirostylis*	15
Chamaeangis	15	*Chiloglottis*	18
Chamaeanthus	10	*Chloraea*	47
Chitonanthera	7	*Chusua*	17
Chondrorhyncha	16	*Chrysoglossum*	6
Chroniochilus	5	*Coeloglossum*	1
Chysis	6	*Collabium*	10
Cleisocentrum	1	*Claderia*	2
Cleisostoma	95	*Cleistes*	55
Clowesia	5	*Codonorchis*	3
Coryanthes	20	*Corybas*	100
Cryptopus	3	*Cryptostylis*	20
Cycnoches	17	*Cynorkis*	125
Cymbidiella	3	*Cyrtosia*	5
Cyrtorchis	18	*Cyrtostylis*	5
Dendrobium	900	*Diceratostele*	1
Dilomilis	4	*Diphylax*	1
Dimerandra	2	*Diplomerus*	2
Diothonaea	7	*Diplolabellum*	1
Dracula	93	*Drakaea*	4
Dressleria	4	*Duckeella*	3
Dryadorchis	2	*Eleorchis*	1
Drymoda	2	*Ephippianthus*	1
Encyclia	130	*Epiblema*	1
Eparmatostigma	1	*Epipactis*	22
Epidendrum	500	*Epipogium*	3
Eria	500	*Eriaxis*	3
Gongora	40	*Goniochilus*	1
Hagsatera	2	*Hancockia*	1
Hofmeisterella	1	*Holothrix*	55
Hygrochilus	1	*Hylophila*	6
Hymenorchis	9	*Isotria*	2
Ischnogyne	1	*Ipsea*	2
Jacquiniella	11	*Kreodanthus*	6
Laelia	69	*Kuhlhasseltia*	6
Leptotes	5	*Ligeophila*	8
Lockhartia	29	*Ludisia*	1
Lopharis	25	*Lyperanthus*	5
Macroclinium	25	*Malaxis*	300
Mediocalcar	20	*Megalorchis*	1
Mendoncella	11	*Mexipedium*	1
Mesospinidium	7	*Microtis*	11
Neofinetia	1	*Neottia*	9
Neogyna	1	*Neotinea*	2
Notylia	75	*Odontorrhynchus*	5

(*Continued.*)

Table 1. (*Continued.*)

Oncidium	430	*Ophrys*	25
Otoglossum	8	*Otostylis*	3
Pachyphyllum	25	*Pachyplectron*	2
Papperitzia	1	*Papuaea*	1
Pedilochilus	15	*Pelexia*	73
Peristeranthus	1	*Peristylus*	70
Phloeophila	7	*Phragmipedium*	14
Pinelia	3	*Piperia*	4
Platyrhiza	1	*Platythelys*	8
Plectrophora	6	*Pogonia*	2
Polyotidium	1	*Ponthieva*	53
Ponera	9	*Porphyrostachys*	2
Porphyrodesme	3	*Prasophyllum*	60
Porphyroglottis	1	*Prescottia*	21
Pseudacoridium	1	*Pseudocentrum*	6
Quisqueya	4	*Raycadenco*	1
Rangaeris	6	*Rhamphorhynchus*	1
Renanthera	14	*Rhizanthella*	2
Rhipidoglossum	4	*Rimacola*	1
Rhyncholaelia	2	*Risleya*	1
Rossioglossum	5	*Sarcanthopsis*	7
Rudolfiella	2	*Sarcoglottis*	40
Sanderella	2	*Serapias*	13
Sepalosiphon	1	*Sertifera*	6
Smitinandia	3	*Spiculaea*	1
Sphyrarhynchus	1	*Stenoglottis*	4
Stenia	1	*Satyridium*	1
Stolzia	4	*Solenocentrum*	3
Summerhayesia	2	*Symphyosepalum*	1
Sunipia	25	*Tainia*	14
Systeloglossum	5	*Thulinia*	1
Taeniophyllum	187	*Thaia*	1
Tetramicra	11	*Thelymitra*	46
Thelasis	10	*Thelyschista*	1
Trevoria	4	*Triphora*	19
Trias	2	*Tropidia*	35
Trichoceros	8	*Trudelia*	5
Trichopilia	21	*Tsaiorchis*	2
Trichosalpinx	84	*Tubilabium*	2
Tuberolabium	5	*Tylostigma*	3

(*b*) non-orchid species

family	epiphytic genus	species number	family	terrestrial genus	species number
Melastomataceae	*Adelobotrys*	21	Lamiaceae	*Adelosa*	1
Gesneriaceae	*Agalmyla*	15	Apocynaceae	*Aganonerion*	1
Gesneriaceae	*Alloplectus*	25	Asteraceae	*Allopterigeron*	1
Gesneriaceae	*Alsobia*	2	Icacinaceae	*Alsodeiopsis*	11
Araceae	*Amydrium*	4	Euphorbiaceae	*Amyrea*	2
Polypodiaceae	*Anathropteris*	1	Brassicaceae	*Anastatica*	1
Caryophyllaceae	*Arenaria*	1	Palmae	*Arenga*	20
Polypodiaceae	*Arthromeris*	6	Poaceae	*Arthroostachys*	1
Aspleniaceae	*Asplenium*	400	Asteraceae	*Asplundianthus*	17
Cyclanthaceae	*Asplundia*	60	Brasssiceae	*Asta*	2
Begoniaceae	*Begonia*	30	Sapindaceae	*Beguea*	1
Burmanniaceae	*Burmannia*	2	Campanulaceae	*Burmeistera*	80
Campanulaceae	*Burmeistera*	5	Alismataceae	*Burnatia*	1
Ericaceae	*Calopteryx*	1	Restionaceae	*Calorophus*	1
Melastomataceae	*Calvoa*	4	Asteraceae	*Calycadenia*	11
Bromeliaceae	*Catopsis*	20	Bombacaceae	*Catostemma*	11
Asclepiadaceae	*Ceropegia*	3	Palmae	*Ceroxylon*	15
Campanulaceae	*Clermontia*	10	Clethraceae	*Clethra*	64
Melastomataceae	*Clidemia*	11	Rosaceae	*Cliffortia*	115
Liliaceae	*Clivia*	1	Myrtaceae	*Cloezia*	8

(*Continued.*)

Table 1. (*Continued.*)

Ericaceae	*Costera*	8	Cyperaceae	*Costularia*	20
Moraceae	*Coussapoa*	20	Rubiaceae	*Coussarea*	100
Polypodiaceae	*Crypsinus*	40	Poaceae	*Crypsis*	8
Asclepiadaceae	*Cynanchum*	2	Apiaceae	*Cynapium*	1
Cyperaceae	*Cyperus*	1	Acanthaceae	*Cyphacanthus*	1
Gesneriaceae	*Cyrtandra*	10	Amaryllidaceae	*Cyrthanthus*	47
Melastomataceae	*Dalenia*	2	Fabaceae	*Dalhousiea*	3
Davalliaceae	*Davallia*	40	Asteraceae	*Daveaua*	1
Polypodiaceae	*Dendroconche*	2	Annonaceae	*Dendrokingstonia*	1
Polypodiaceae	*Diblemma*	1	Rubiaceae	*Dibrachyionostylus*	1
Ericaceae	*Didonica*	2	Rubiaceae	*Didymaea*	5
Dioscoreaceae	*Dioscorea*	1	Menispermaceae	*Dioscoreophyllum*	3
Ericaceae	*Disterigma*	15	Juncaceae	*Distichia*	3
Solanaceae	*Ectozoma*	1	Poaceae	*Ectrosia*	11
Rapateaceae	*Epidryos*	3	Orobanchaceae	*Epifagus*	1
Asteraceae	*Eupatorium*	7	Sapindaceae	*Euphorianthus*	1
Cyclanthaceae	*Evodianthus*	1	Rutaceae	*Evodiella*	2
Onagraceae	*Fuchsia*	15	Apiaceae	*Fuernrohria*	1
Gnetaceae	*Gnetum*	3	Thymelaeaceae	*Gnidia*	140
Liliaceae	*Hippeastrum*	2	Asteraceae	*Hippia*	8
Bromeliaceae	*Hohenbergia*	20	Malvaceae	*Hoheria*	5
Solanaceae	*Juanulloa*	10	Palmae	*Jubaea*	1
Ericaceae	*Lateropora*	2	Scrophulariaceae	*Lathraea*	7
Gentianaceae	*Leiphaimos*	1	Aizoaceae	*Leipoldtia*	10
Bromeliaceae	*Lymania*	4	Ericaceae	*Lyonia*	35
Gesneriaceae	*Lysionotus*	2	Epacridaceae	*Lissanthe*	6
Gentianaceae	*Macrocarpaea*	2	Melastomataceae	*Macrocentrum*	15
Rubiaceae	*Malanea*	2	Olacaceae	*Malania*	1
Polypodiaceae	*Marginariopsis*	1	Apiaceae	*Margotia*	1
Melastomataceae	*Medinilla*	300	Sarcolaenaceae	*Mediusella*	1
Myrtaceae	*Metrosideros*	3	Palmae	*Metroxylon*	5
Polypodiaceae	*Microgramma*	13	Asteraceae	*Microgynella*	1
Vittariaceae	*Monogramma*	2	Chenopodiaceae	*Monolepis*	6
Myrsinaceae	*Myrsine*	12	Myrtaceae	*Myrtastrum*	1
Bromeliaceae	*Navia*	2	Malvaceae	*Nayariophyton*	1
Polypodiaceae	*Neocheiropteris*	10	Fabaceae	*Neochevalierodendron*	1
Melastomataceae	*Neodissochaeta*	10	Urticaceae	*Neodistemon*	1
Davalliaceae	*Nephrolepis*	15	Menyanthaceae	*Nephrolephyllidium*	1
Polypodiaceae	*Oleandropsis*	1	Asteraceae	*Olearia*	75
Liliaceae	*Pamianthe*	1	Asteraceae	*Pamphalea*	6
Pandanaceae	*Pandanus*	4	Chenopodiaceae	*Panderia*	1
Gesneriaceae	*Paradrymonia*	8	Euphorbiaceae	*Paradrypetes*	2
Melastomataceae	*Phainantha*	4	Orchidaceae	*Phaius*	45
Polypodiaceae	*Photinopteris*	1	Loranthaceae	*Phragmanthera*	6
Urticaceae	*Pilea*	20	Myrtaceae	*Pileanthus*	3
Bromeliaceae	*Pitcairnia*	75	Fabaceae	*Pithecellobium*	37
Polypodiaceae	*Pleopeltis*	10	Rutaceae	*Plethadenia*	2
Ericaceae	*Plutarchia*	6	Poaceae	*Poa*	200
Polypodiaceae	*Polypodiopteris*	3	Poaceae	*Polypogon*	10
Epacridaceae	*Prionotes*	1	Brassicaceae	*Prionotrichon*	4
Urticaceae	*Procris*	10	Amaryllidaceae	*Proiphys*	3
Bromeliaceae	*Pseudaechmea*	1	Euphorbiaceae	*Pseudagrostistachys*	2
Solanaceae	*Rahowardiana*	1	Asteraceae	*Raillardella*	3
Rubiaceae	*Relbunium*	2	Poaceae	*Relchela*	1
Clusiaceae	*Renggeria*	1	Rubiaceae	*Rennellia*	4
Araceae	*Rhaphidophora*	100	Rubiaceae	*Rhaphidura*	1
Liliaceae	*Rhodocodon*	1	Bignoniaceae	*Rhodocolea*	6
Ericaceae	*Rusbya*	1	Aizoaceae	*Ruschia*	360
Marcgraviaceae	*Ruyschia*	7	Flacourtiaceae	*Ryania*	8
Gesneriaceae	*Sarmienta*	1	Sarraceniaceae	*Sarracenia*	8
Bignoniaceae	*Schlegelia*	18	Sapindaceae	*Schleichera*	1
Rubiaceae	*Schradera*	12	Oleaceae	*Schrebera*	10
Araceae	*Scindapsus*	20	Apiaceae	*Sciothamnus*	4
Polypodiaceae	*Scleroglossum*	6	Chenopodiaceae	*Sclerolaena*	64
Davalliaceae	*Scyphularia*	8	Scytopetalaceae	*Scytopetalum*	3

(*Continued.*)

Table 1. (*Continued.*)

Solanaceae	*Solanum*	15	Alliaceae	*Solaria*	2
Cyclanthaceae	*Stelestylis*	2	Caryophyllaceae	*Stellaria*	200
Araceae	*Stenospermation*	30	Acanthaceae	*Stenostephanus*	6
Gesneriaceae	*Streptocarpus*	10	Poaceae	*Streptochaeta*	3
Vitaceae	*Tetrastigma*	2	Olaceae	*Tetrastylidium*	3
Polypodiaceae	*Thayeria*	1	Euphorbiaceae	*Thecacoris*	20
Cyclanthaceae	*Thoracocarpus*	1	Ericaceae	*Thoracosperma*	10
Bromeliaceae	*Tillandsia*	400	Myrtaceae	*Tillospermum*	36
Melastomataceae	*Triolena*	2	Burseraceae	*Triomma*	1
Ericaceae	*Vaccinium*	95	Amaryllidaceae	*Vagaria*	4
Vittariaceae	*Vaginularia*	6	Apocynaceae	*Vahadenia*	2
Bromeliaceae	*Vriesea*	200	Orchidaceae	*Vrydagzynea*	40
Cactaceae	*Werckleocereus*	2	Brassicaceae	*Werdermannia*	4
Bromeliaceae	*Wittrockia*	4	Alseuosmiaceae	*Wittsteinia*	3
Agavaceae	*Yucca*	2	Rubiaceae	*Yutajea*	1

Table 2. Species numbers of taxa in Bulbophyllinae investigated, their taxonomic rank and estimated number of species (based on Schlechter 1912, 1925; Vermeulen 1987).

genus	section	species number
Bulbophyllum	*Altisceptrum*	9
	Aphanobulbon	110[a]
	Careyana	33
	Cirrhopetalum	78
	Desmosanthes	50
	Globiceps	48
	Hybochilus	33[a]
	Hymenobractea	5
	Intervallatae	74
	Leptopus	45
	Macrobulbon	7
	Macrouris	27[a]
	Oxysepalum	19[a]
	Pelma	22[a]
	Polyblepharon	90[a]
	Sestochilus	90
Drymoda		3
Pedilochilus		36[a]
Sunipia		27
Trias		15

[a] Groups containing obligate twig epiphytes.

pollinators of orchid species belonging to the (predominantly terrestrial) subfamilies Apostasioideae, Cypripedioideae, Orchidoideae, (climbing) Vanilloideae, and (predominantly epiphytic) subfamily Epidendroideae was recorded from Van der Cingel (1995, 2001). We excluded casual observations regardless of plant species, focusing on quantitative pollinator studies. For comparison, the mean number of pollinators and standard error were calculated per subfamily. Overall mean number of pollinator species per orchid, and relationships between more recently derived subfamilies and mean pollinator numbers, were also compared using a *G*-test. For comparison, the mean number of pollinators and standard deviation were calculated per subfamily.

(c) *Selection of phylogenetic datasets*

Phylogenies of the largely epiphytic Bulbophyllinae (B. Gravendeel, unpublished data) and Oncidiinae (Williams *et al.* 2001) were selected because of the availability of floristic, molecular phylogenetic, and macromorphological data.

(d) *Phylogenetic analysis*

The character states of morphological characters at internal nodes were reconstructed with Mesquite v. 1.0 (Maddison & Maddison 2003) using the 'likelihood ancestral states' option. This likelihood reconstruction finds, for each node, the state assignment that maximizes the probability of arriving at the observed states in the terminal taxa under a *Mk1* (gains and losses are equally likely) model of evolution, and allows the states at all other nodes to vary. The relative likelihoods found are indicated as pie diagrams in the cladograms analysed.

4. RESULTS

(a) *Statistical analyses*

The results of the *G*-tests show that epiphytic genera are significantly richer in species than terrestrial genera ($p < 0.01$) both for orchids and non-orchids (figures 2 and 3). The magnitude of the epiphyte–terrestrial imbalance is greater for orchids than for non-orchids, especially in classes 9 and 10.

Overall, the mean number of pollinators amongst the orchids was 3.98 ± 0.97 per species, with 46% of species having one pollinator ($n = 424$). Excluding those genera proposed to have specialized pollination, such as pseudocopulation, there were 5.4 ± 1.8 pollinators per species, with only 38% of species having just one pollinator ($n = 232$). The mean number of species pollinating each subfamily, along with species richness per subfamily (number of species currently described per subfamily), are shown in figure 4. There was a trend for more recently derived subfamilies to have a larger mean number of pollinators per species, but this correlation was not significant ($r_{\mathrm{p}} = 0.59$, $p > 0.05$). Further, there was a trend for the mean number of pollinators per species within subfamilies to increase with subfamilial species richness, although this correlation was again not significant ($r_{\mathrm{p}} = 0.50$, $p > 0.05$). The predominantly epiphytic Epidendroideae tended to have more pollinators per species when compared with the other families, which are predominantly terrestrial (Apostasioideae, Cypripedioideae, Orchidoideae), or climbing (Vanilloideae), but again this was not significant (Epidendroideae: 4.61 ± 1.80 pollinators per species; others: 3.27 ± 0.25 pollinators per species; $t_{422} = 0.69$, $p > 0.05$).

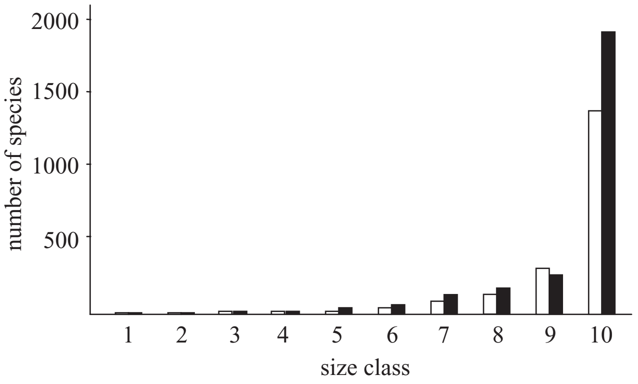

Figure 2. Species numbers of randomly sampled epiphytic (filled bars) and terrestrial (open bars) orchid genera sorted from small to large and subsequently divided into 10 classes of 10 observations each. The two distributions differed significantly from each other according to the *G*-test (d.f. $= 9$; $\chi^2 = 1015$; $p < 0.01$).

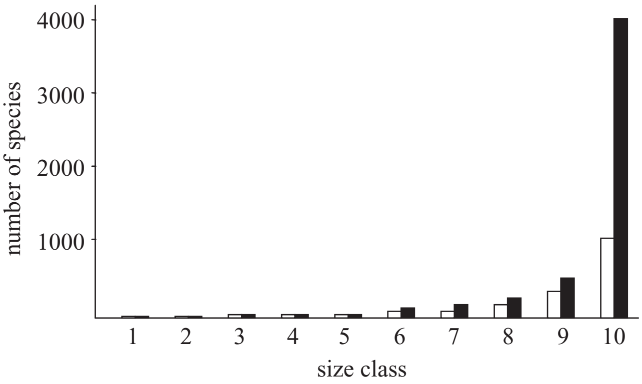

Figure 3. Species numbers of randomly sampled epiphytic (filled bars) and terrestrial (open bars) non-orchid genera sorted from small to large and subsequently divided into 10 classes of 10 observations each. The two distributions differed significantly from each other according to the *G*-test (d.f. $= 9$; $\chi^2 = 99$; $p < 0.01$).

(b) *Phylogenetic analyses*

When optimized on the molecular phylogenies presented in figures 5 and 6, several clades are characterized by a small body size, short life cycle and climbing roots with multiple adhesion points. This suite of epiphytic adaptations seems to be present in obligate twig epiphytes only and evolved multiple times in the Bulbophyllinae and Oncidiinae.

In Bulbophyllinae, *Bulbophyllum* sections *Aphanobulbon, Coelochilus, Fruticicola, Hybochilus, Lepanthanthe, Macrouris, Monilibulbus, Nematorhizis, Oxysepalum, Pelma, Pedilochilus, Peltopus* and *Polyblepharon* contain obligate twig epiphytes. In particular, sections *Aphanobulbon, Coelochilus* and *Polyblepharon* are species-rich as compared with the other sections and genera in Bulbophyllinae (table 2) and show independent associations between twig epiphytism and speciation bursts.

The twig epiphytic groups in Oncidiinae are confined to 31 genera, of which *Comparettia, Erycina, Ionopsis, Macroclinium, Notylia, Rodriguezia,* and *Tolumnia* were included in the molecular phylogeny of Williams *et al.* (2001). It is impossible to say whether the number of species of these twig epiphytic genera is high or low because many of the traditionally recognized genera of Oncidiinae are polyphyletic and in need of revision (Chase & Palmer 1992; Williams *et al.* 2001).

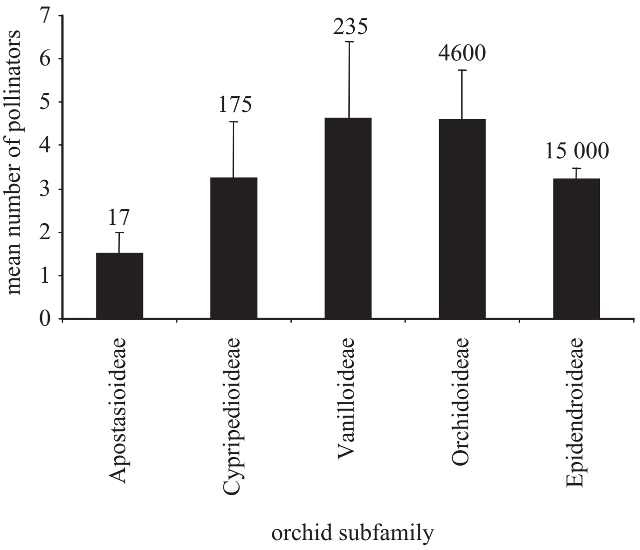

Figure 4. Mean number of pollinators calculated from observations listed in Van der Cingel (1995, 2001) for orchid species belonging to subfamilies Apostasioideae ($n = 2$), Cypripedioideae ($n = 8$), Vanilloideae ($n = 4$), Orchidoideae ($n = 184$) and Epidendroideae ($n = 227$) with corresponding standard errors. Subfamilial species richness (numbers of species currently described per subfamily; Royal Botanic Gardens, Kew 2003) is indicated above the corresponding bars.

5. DISCUSSION

(a) *Higher diversity of epiphytic genera*

Our results show that epiphytic genera are significantly richer in species than terrestrial genera, both in orchids and non-orchids. It must be stressed, however, that a random sample of only 100 genera might be too small to represent trends in the more than 13 000 genera of vascular plants currently described. We think, however, that a random sample of 100 of the 438 epiphytic orchid genera currently described should be sufficient to discover trends in species richness.

The larger taxonomic diversification found for epiphytes contradict Ibisch *et al.* (1996), who state that in plant families which have evolved epiphytism other than the Orchidaceae, the terrestrials have more elevated levels of speciation. The correlation found here between high species diversity and epiphytism supports the hypotheses of Gentry & Dodson (1987) and Benzing (1990) who postulate that the epiphytic habitat offers more possibilities for speciation owing to its larger number of niches and more fragmented nature compared with the forest floor.

Another factor that could explain this difference in species richness is that, within a forest, total bark surface area greatly exceeds ground area and can be more densely packed with plants. One square metre of ground area can be equivalent to more than 10 m^2 of canopy area immediately above it. The larger the area, the more

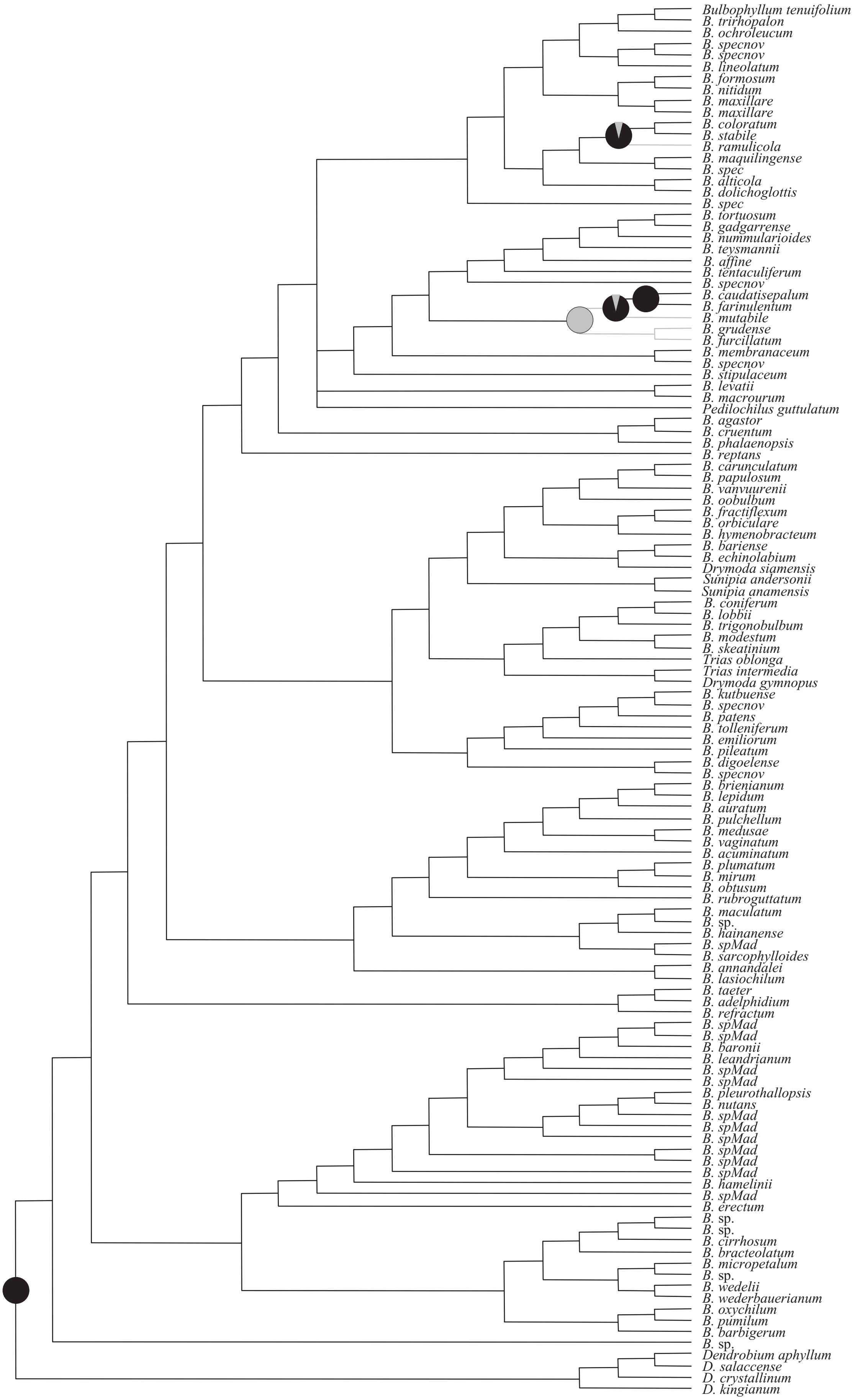

Figure 5. One of more than 10 000 maximum parsimonious trees (randomly chosen) based upon matK sequences of Bulbophyllinae (B. Gravendeel, unpublished data). Trunk epiphytes, black circles; twig epiphytes, grey circles. Pie diagrams depict the relative likelihoods found.

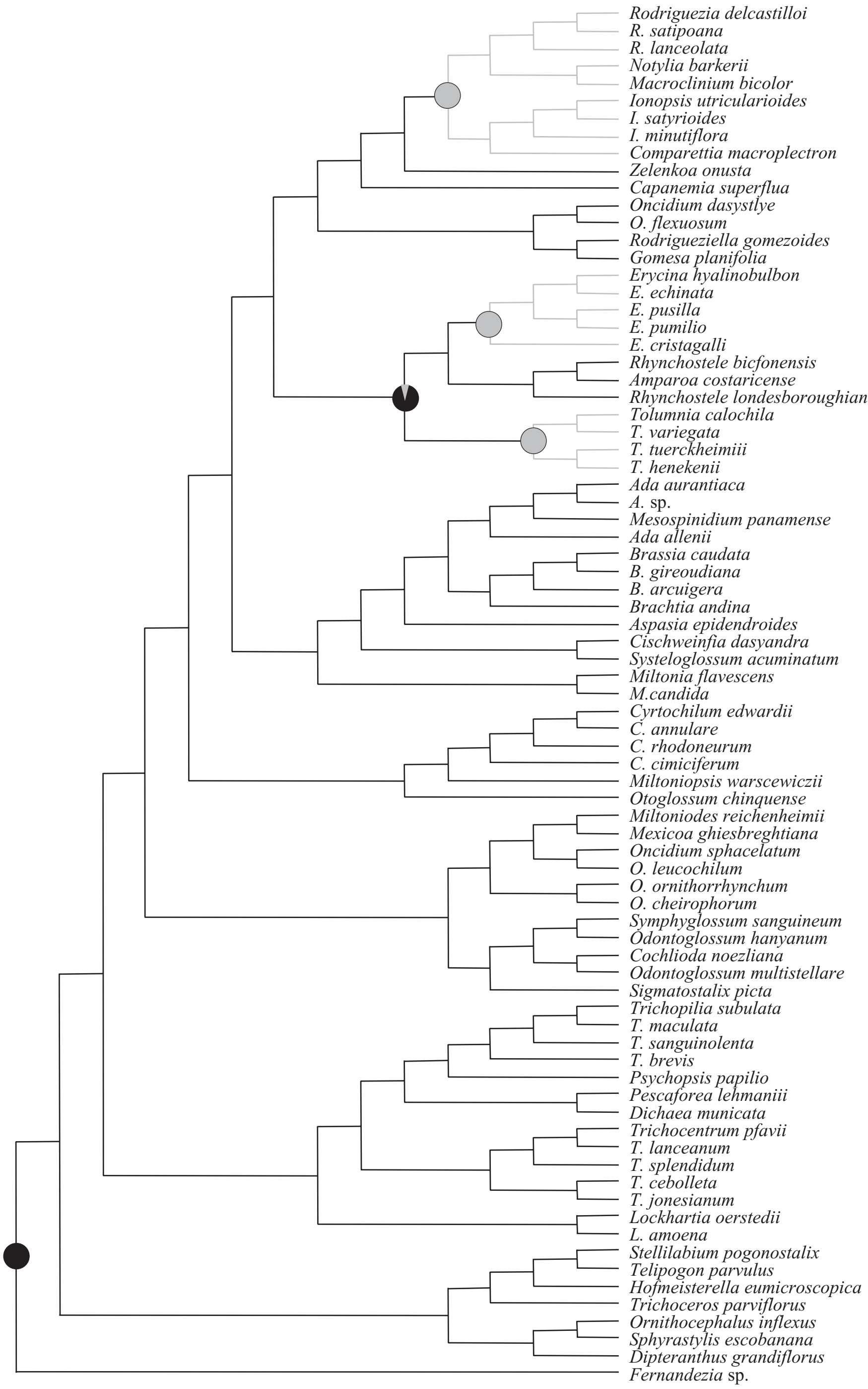

Figure 6. Single maximum parsimonious tree based upon nuclear (nrITS1–5.8S–ITS2) sequences of Oncidiinae (Williams *et al.* 2001). Trunk epiphytes, black circles; twig epiphytes, grey circles. Pie diagrams depict the relative likelihoods found.

different species can coexist in this area. A hypothetical species–area curve should therefore become saturated at a higher maximum number of species of epiphytes compared with terrestrial ones (figure 7).

Epiphytic orchids are overwhelmingly tropical, whereas terrestrial orchids are tropical and temperate. The general increase in species diversity in the tropics could be another explanation for the significant difference in species diversity found between epiphytes and terrestrials. This hypothesis is not supported, though, by the species diversity of subfamily Orchidoideae, which is largely terrestrial in the tropics as well and evenly diverse in both temperate and tropical regions.

(**b**) *Correlation between pollinator specialization and species richness*

Our analysis has found no evidence that pollinator specialization has driven speciation in the Orchidaceae. Instead, we have found that more recently derived subfamilies tended to show decreased, rather than increased, pollinator specialization (cf. Tremblay 1992). Similarly, species richness tended to decrease with increased pollinator specialization. The predominantly epiphytic subfamily Epidendroideae is the most species-rich, but does not have a significantly different level of pollinator specialization from other subfamilies (indeed, if anything there is a trend for decreased rather than increased pollinator

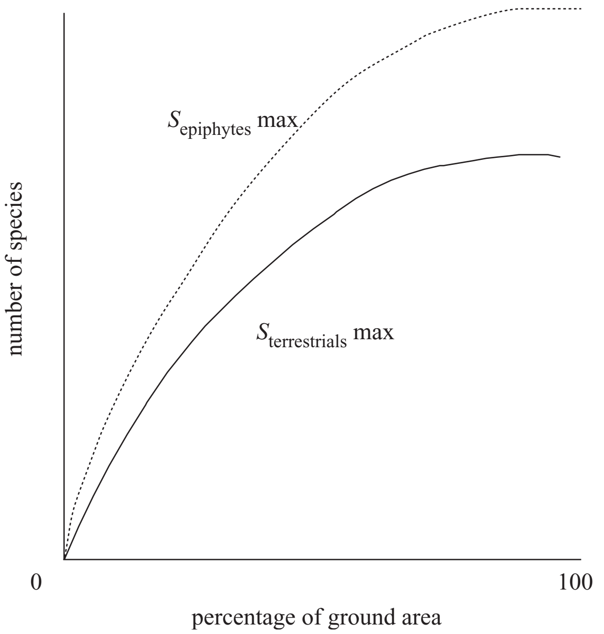

Figure 7. Hypothetical species–area curve for epiphytes (dotted line) and terrestrials (solid line).

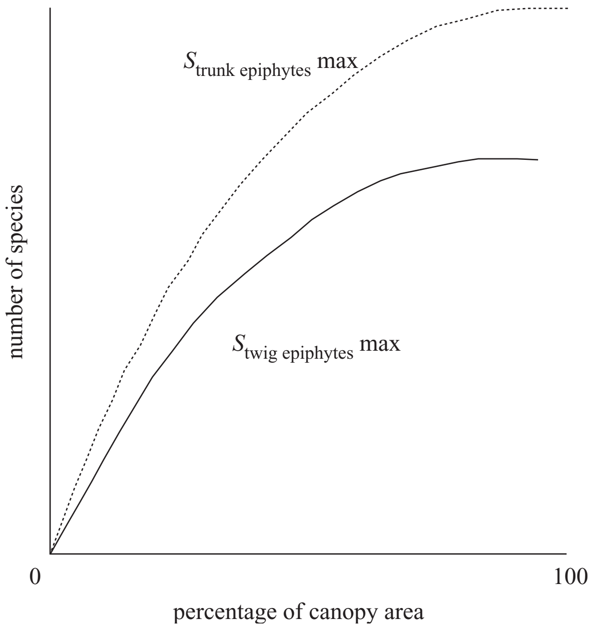

Figure 8. Hypothetical species–area curve for twig epiphytes (solid line) and trunk epiphytes (dotted line).

specialization). Orchids generally are less pollinator-specialized than is generally assumed—most species have more than one pollinator.

It must be stressed that certain groups of orchids may be underrepresented within our dataset, and that the results presented here might be influenced by the fact tha pollination has been most extensively studied in European orchids. The sample size within Apostasioideae is particularly small, and we encourage further studies within this subfamily. Further, we cannot rule out the hypothesis that specialization has been important for speciation in some orchid clades, nor that some pollinator-associated mechanisms more complex than mere specialization may have driven speciation. We feel, however, from this analysis that pollinator specialization *per se* is unlikely to have driven orchid speciation.

(c) *Twig epiphytism*

Twig epiphytes appeared to have several unique features that make them highly specialized for growth and survival on outermost branchlets. The first is a small body size to make efficient use of space in the canopy. According to Nieder (2004), a small body size allows some orchids to grow on extremely tiny twigs.

The second feature is related to the fact that twigs are short-lived habitats: they either break off or develop into larger branches with a more textured surface and thicker substrate layer. During these two processes, they become unsuitable habitats for twig epiphytes and are colonized instead by ‘trunk epiphytes’ with long-lived life cycles (Dungeon 1923; Benzing 1990). A short life cycle forces twig epiphytes to ensure that they colonize, mature and reproduce before the twig they are growing on is either abscised or develops into a large branch with different substrate characteristics. Many of the twig epiphytes in the Oncidiinae and Bulbophyllinae mature within the course of a single season (Chase 1986; G. Fischer, personal communication).

A third factor is the large amount of vegetative reduction that most twig epiphytes display. Growth forms can be laterally flattened and small in size. Leaves are unifacial or completely absent (Chase 1987). In addition, shoot development is limited, whereas root production is increased. Bloom *et al.* (1985) postulated that this vegetative reduction is meant to mitigate specific resource scarcities. According to Chase (1987), a leafless habit is a more efficient way for small plants to deal with water/surface area relations compared with standard habits.

A fourth factor is also related to the fact that twigs are short-lived habitats. Many twig epiphytes have clinging roots with one or more secondary points of attachment, which have the effect of increasing the number of growing seasons before they are shed by their hosts. These host trees can often be found with several twig epiphytic plants loosely dangling by their clinging roots (Chase 1986).

A fifth factor is owing to the fact that tiny twigs only have a very thin or completely absent substrate cover with very limited absorbent capacities. Chase (1986) and Benzing (1990) therefore postulate that the restriction of species to twigs might reflect tolerances for certain moisture levels. On young bare twigs, humidity is low, whereas humidity increases on older branches with thicker layers of substrate (Winter *et al.* 1985).

(d) *The number of times twig epiphytism has evolved*

Different orchid groups have independently developed a surprising number of parallel adaptations related to twig epiphytism throughout the tropics. In South American orchids, obligate twig epiphytism developed significantly in the Oncidiinae and Pleurothallidinae (Chase 1986). In southeast Asia, it developed in some species groups of *Bulbophyllum* (Bulbophyllinae) and *Taeniophyllum* (Aeridinae). In Africa, this habit also occurs in *Microcoelia* (Aerangidinae).

(e) *Species-rich clades*

Epiphytism evolved multiple times in the Orchidaceae. Rather than a key innovation, we are inclined to define epiphytism as the result of a suite of key innovations among which are the ability to cope with nutrient-poor and temporarily very dry conditions. The development of twig epiphytism seems repeatedly associated with several speciation bursts in Bulbopyllinae. In contrast with general epiphytic radiations, however, the total number of twig epiphytes in both Bulbophyllinae and Oncidiinae is lower than the number of trunk epiphytes. This is not surprising as the larger axes in the canopy have a much higher total surface area as compared with the twigs (Johansson 1975). A hypothetical species–area curve therefore should become saturated at a higher maximum number of species of trunk epiphytes as compared with twig epiphytes (figure 8).

6. CONCLUSIONS

Our results show that epiphytic genera are significantly more species-rich as compared with terrestrial genera, both for orchids and non-orchids. Species diversity could not be explained by a high degree of pollinator specialization. A small body size, short life cycle and highly specialized clinging roots evolved multiple times and independently in unrelated orchid clades. Furthermore, clades with these suites of traits seem to have undergone extensive speciation in one the orchid groups investigated on more than one occasion. It seems therefore that epiphytism stimulated the development of a high taxon diversity in the Orchidaceae.

Evidence for an adaptive value of twig epiphytism was not provided, as phylogenetic techniques are not suitable for this. Correlations between twig epiphytism and repeated bursts of speciation in the orchid groups investigated, however, do indicate that several groups of tropical orchids are so species-rich thanks to, and not despite, their predominantly arboreal habit. Only future studies that also include other plant families containing epiphytes, such as bromeliads, can show whether repeatedly occurring correlations between twig epiphytism and lineage diversifications as presented here are a general phenomenon within epiphytic floras.

Bill Baker, Freek Bakker, Mark Chase, John Dransfield, Marcel Eurlings, Gunter Fischer, Peter Hovenkamp, Peter Linder, and Niels Raes are gratefully acknowledged for stimulating discussions, literature suggestions, help with the molecular and statistical analyses, and critically reading drafts of this manuscript.

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