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Do secondary hemiepiphytes exist?

Gerhard Zotz[1,2], Frank Almeda[3], Salvador Arias[4], Barry Hammel[5] and Emerson Pansarin[6]

[1]Carl von Ossietzky University, Institute of Biology and Environmental Sciences, Functional Ecology Group, Box 2503, D-26111 Oldenburg, Germany; [2]Smithsonian Tropical Research Institute, Box 0843-03092, Panama, Republic of Panama; [3]California Academy of Sciences, Institute for Biodiversity Science and Sustainability, 55 Music Concourse Drive, Golden Gate Park, San Francisco, California 94118, USA; [4]Botanical Garden, Instituto de Biología, Universidad Nacional Autónoma de México, México City 04510, México; [5]Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, MO 63110, USA and [6]Department of Biology, Faculty of Philosophy, Sciences and Literature of Ribeirão Preto, University of São Paulo, Av. Bandeirantes 3900, Ribeirão Preto, SP 14040-901, Brazil

Review Article

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Author for correspondence:
Gerhard Zotz, Email: gerhard.zotz@uol.de

Abstract

For decades, tropical ecologists distinguished primary (PH) and secondary hemiepiphytes (SH) as two structurally dependent life forms with an epiphytic phase at, respectively, the beginning or the end of their ontogeny. However, the use of these terms has been criticized repeatedly because the term "hemiepiphyte" suggests an unsubstantiated biological similarity in ontogeny, and worse, because it is often used without a qualifier, which makes unambiguous interpretation of the life history of such species impossible. In this paper, we go one step further and ask the question whether an ontogenetic trajectory as described by the term "secondary hemiepiphyte" does exist at all. We show that until now all evidence available for the three families that were traditionally listed as taxa with SHs (Araceae, Cyclanthaceae, Marcgraviaceae) falsifies such claims, but critically discuss reports of possible SHs in other families. In all these cases unambiguous conclusions about the existence of any SH are difficult, but our detailed discussion of potential candidates is meant to provide the basis for focused field studies. Irrespective of the outcome of these studies, we urge researchers to abandon the use of the term SH for the time being: Terminological issues can be discussed once there are data.

The tropics are well-known for their impressive diversity of plant species, but they are also outstanding globally in regard to the diversity of different life forms. Confronted with this hitherto unknown diversity prompted early explorers from the northern hemisphere (e.g. Schimper 1888; Schimper 1903; Went 1895) to come up with schemes to categorize the diversity of free-standing or mechanically dependent flora: Went (1895) separated hemiepiphytes from epiphytes because the former – after germination on other plants - produce feeder roots that connect the plant with the ground, representing a fundamental change in access to resources like water and nutrients. This may lead to structural independence as, e.g., in strangling figs, although a final freestanding stage is not typical for the bulk of hemiepiphytes (Zotz et al. 2021a). Schimper (1903) acknowledged another group, "pseudoepiphytes", i.e. plants that germinate on the ground, climb up a host tree with successive dieback of the proximal stem portion (for a detailed account of historical changes in terminology see Zotz 2013). At least since the mid-1980s the generally accepted terminology changed with the term primary hemiepiphytes (PH) being used for Went´s "hemiepiphytes" and secondary hemiepiphytes (SH) for Schimper´s "pseudoepiphytes" (Kress 1986; Putz & Holbrook 1986) – (note that the two terms had been introduced much earlier by Ellenberg & Mueller-Dombois 1965).

While we are not aware of any debate neither on the term "(primary) hemiepiphyte" nor on the general biology of the plants in this group, the term "secondary hemiepiphyte", and the underlying concept, have been debated for decades. Curiously, the two authors who may have popularized the term SH more than anyone else, partly revoked their classification in a later publication (Holbrook & Putz 1996), arguing that SHs are basically vine-like in physiology and morphology. Not much later, Lüttge (1997) argued against the use of SH because "hemiepiphytic" aroids in genera like *Monstera* or *Philodendron* maintain soil contact via adventitious roots, although he did not present any data to back up this claim. Moffett (2000) expressed similar reservations in his excellent treatise of the terms used in canopy biology. He noted that this dual usage of hemiepiphyte confounds two vastly different life cycle strategies. Zotz (2013) was the last to argue against the use of SH supporting Moffett´s suggestion to use the term "nomadic vine" for any climbing plant that germinates on or near the ground and may lose the proximal portion of its stem during ontogeny. Remarkably, none of these authors discussed a much more fundamental doubt. Why should a plant that starts life with a connection to the ground give up this connection entirely and sacrifice access to the soil as a large reservoir of water and nutrients in the first place? A much more parsimonious explanation for the dieback of the lower stem

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portion, e.g. in some climbing aroids, is not a transition to an assumed "epiphytic" phase but is rather a hydraulic strategy related to the fact that almost all reported so-called SH are monocotyledons. These lack secondary growth, and the use of adventitious roots may be the only option to allow sufficient long-distance flow to an increasing larger shoot, making the lower portion of the stem expendable (López-Portillo et al. 2000).

Several authors also noted the semantic problem that a single term is used for ecologically distinct plants, particularly relevant when descriptions in publications do not use a qualifier (Sperotto et al. 2020). This is the case in numerous studies (e.g. Barbosa et al. 2020; Fernández-Alonso & Hernández-Schmidt 2007; Mucunguzi 2007; Weigand et al. 2020). Since these studies also lack any definition of the term "hemiepiphyte", an unambiguous interpretation is impossible. For these reasons, Moffett (2000) proposed to abandon the term "secondary hemiepiphytes" and use the term "nomadic vine" instead. That term reflects the vine habit of these plants without making strict assumption on the site of germination and on rooting strategies. This rather vague circumscription highlights an issue that is much more important than semantics: there is a lack of good field data on the biology of these structurally dependent plants, with a real possibility that plants with the ontogeny associated with the term SH do not exist at all.

Kress (1986) defined SH by the following ontogenetic stages (Fig. 1): (1) germination on the ground; (2) ascent on a tree; (3) dieback of the older stem and severance of all (!) connections with the ground. The third requirement is particularly relevant, because otherwise these plants are simply vines: long-distance water transport is at least as effective in roots as in shoots (Zotz et al. 1997). In this context It is noteworthy that there are data for *Heteropsis* spp. (Araceae), which are typically called SHs: individual plants invariably die when their aerial roots are removed in commercial harvesting (Balcázar Vargas & van Andel 2005).

Two recent studies have further challenged the use of the term SH for members of this family. Zotz et al. (2020) investigated a community of climbing aroids in the lowland forest of Barro Colorado Island, Panama. They found that no species followed the ontogenetic trajectory of a SH. Species typically called SH and species typically called climber or vine (Croat 1978) differed by degree only as far as the proximal dieback of the stem was concerned, but invariably maintained connections to the soil via adventitious roots. Very similar results are reported by Bautista-Bello et al. (2021) who studied aroids in Los Tuxtlas, Mexico. Thus, we are currently not aware of any evidence that plants that fulfil the definition of SHs exist in Araceae. In contrast, there is increasing evidence that there are numerous species in the genera *Anthurium* and *Philodendron* with an epiphytic start that later establish root connections, i.e. species that qualify as (primary) hemiepiphytes (Zotz et al. 2021a, see also Meyer and Zotz 2004).

Reviews on PHs and SHs (Gentry & Dodson 1987; Putz & Holbrook 1986; Williams-Linera & Lawton 1995) listed two additional plant families with SHs, Cyclanthaceae and Marcgraviacae. Unfortunately, these reviews did not cite the primary literature to back up their claim. There are a substantial number of epiphytic taxa in Cyclanthaceae (Zotz et al. 2021b), but all claims of (secondary) hemiepiphytic occurrences (e.g. Irume et al. 2013; Leal & Forzza 2012) are unsubstantiated. Similar to the situation in Araceae, there are some observations that suggest a potential for (primary) hemiepiphytic growth, e.g. more or less baccate fruits with small seeds, the observation of at least occasional epiphytic germination (Zotz et al. 2021a), the copious production of adventitious roots. Detailed field observations are needed to document

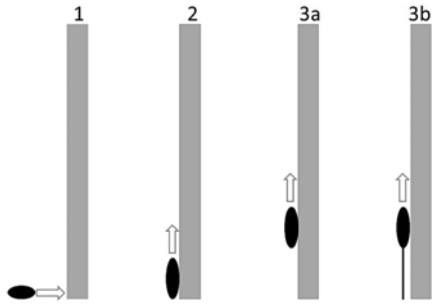


Fig. 1. Ontogeny of a secondary hemiepiphyte (SH) vs. a nomadic vine (NV). Both SH and NV germinate terrestrially and grow towards a tree (1) where they start to climb up (2). Both show dieback of their proximal stem portion, but while a (hypothetical) SH severs all its connections with the ground to become epiphytic (hence the name, 3a), a NV maintains a continuous connection with the soil via adventitious roots (3b).

the ontogeny of these species. There is good experimental evidence for at least one species of Marcgraviaceae (*Marcgravia serrae*), which, however, again does not support the classification as SH, but provides clear evidence for the life history of a (primary) hemiepiphyte (Massa 1996)! Numerous field observations of Diego Giraldo-Cañas (pers. comm.) suggest that this is also true for other Marcgraviaceae, i.e. that there are no SHs in this family (Zotz et al. 2021a). Thus, we are currently not aware of evidence that there are SHs in any of the three families that previous reviews had identified as having SHs (Araceae, Cyclanthaceae and Marcgraviaceae), although field data are still too scarce as to rule out the possibility.

However, although not listed in any of the three mentioned reviews there are species of at least four other families that have sometimes been called SHs, i.e. members of the families Acanthaceae, Cactaceae, Melastomataceae, and Orchidaceae. Systematic observations are scarce and unambiguous experimental evidence absent, so more rigorous investigations are needed to determine whether plants that fulfil Kress´ (1986) definition of SHs do exist in these groups. To facilitate such research efforts, we summarize in the following the relevant information for each family with promising taxa for further study.

Acanthaceae – As a first case, Cheek (1995) describes observations on several species of *Dischistocalyx* (Acanthaceae) from Mt. Cameroon that suggest the ontogenetic trajectory of a SH. Unfortunately, it is not entirely clear from his sketchy account whether these plants really sever all connections or whether the loss of the climbing stem is compensated by adventitious roots that reach the ground.

Cactaceae – This family includes between 1450 and 1870 species, with approximately 130 recognized in the broad sense as "epiphytes" (Barthlott et al. 2015; Hunt et al. 2006), which are found in at least five different evolutionary lines in the Americas.

While there are both epiphytic and lithophytic Rhipsalideae (*Hatiora*, *Lepismium*, *Rhipsalidopsis*, *Rhipsalis*, *Schlumbergera*) (Hunt et al. 2006; Korotkova et al. 2011), there is no claim of hemiepiphytic taxa in this species-rich clade. In contrast, apart from *Acanthocereus*, all genera of Hylocereeae [or Phyllocacteae, Hylocereinae] have developed a tendency to climb and have been described as epiphytes, lithophytes, or climbers (Anderson 2001; Hunt et al. 2006), but more recently also as facultative epiphytes or SHs (Calvente et al. 2011; Martínez-Quezada et al. 2020). Unfortunately, we are not aware of any study that has demonstrated that the site of germination is the soil and that there are no adventitious roots that retain some connection of these plants with the ground when there is partial dieback of the shoot.

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Similarly unclear is the situation in pitahaya and allies (*Selenicereus*, including *Hylocereus*, Anderson 2001; Ortiz-Hernández et al. 2012)(Figs. S1, S2). Particularly good candidates that possibly follow the scheme described by the term SH are found in the genus *Aporocactus*: these species start on the ground, but also on rocks, or the lower parts of trees but the base of their main stem usually dies and degrades (Figs. S3, S4). Whether soil contact is really severed permanently is unclear.

The term hemiepiphyte is quite frequently used in studies with cacti, but without detailed field studies it remains an open question whether this label is appropriate. Currently, conclusive evidence is lacking. Even the occasional observation of an individual without any connection to the ground does not indicate that this is the typical ontogenetic pattern, but may rather be an example of resilience. The polymorphic *Pereskia aculeata* is a case in point. This species has a wide ecological amplitude in South America (from dunes, dry forests to mesophytic forests, Leuenberger 1986), it germinates on the ground and climbs easily into the canopy, supported by the twisting of the flexible and slender stems, which can extend up to 10 m in length. When the ground connection is accidentally lost, the adventitious roots, the succulent leaves, and water-saving Crassculacean acid metabolism temporarily allow survival until a root connection is re-established.

Melastomataceae – Of the approximately 400 species of this family that have been described as "epiphytes" (Zotz et al. 2021a), most species in genera like *Adelobotrys*, *Catanthera*, *Gravesia*, *Heteroblemma*, *Kendrickia*, *Macrolenes*, and *Preussiella* may rather be nomadic vines that germinate terrestrially and retain some connection with the ground via adventitious roots. Others may qualify as SH: the climbers in the genus *Pleiochiton* are described as epiphytes with no connection to the ground (Reginato et al. 2013). However, in the same publication these authors note that roots of *P. blepharodes* do reach the ground. Unfortunately, herbarium specimen labels and species protologues do not provide the needed information to resolve such contradictions. The 18 species of *Gravesia* section *Scandentes* in Madagascar that are climbers with adventitious roots are also in need of additional field observations. *Gravesia thymoides* can sometimes be found with no apparent ground connection (Almeda, pers. obs.). This species stands out in the genus, because its leaves are distinctly succulent, one of the few species in the family with this characteristic. Careful observations are needed to document the ontogeny of this and other climbing species in the family, e.g. *Medinilla* and allied genera (*Catanthera*, *Heteroblemma*, and *Kendrickia*). In summary, life form categorization of Melastomes is often difficult, clear evidence for SHs in this family is missing.

Orchidaceae – apart from a few truly epiphytic species (e.g. *Vanilla palmarum*, Barberena et al. 2019) and a self-supporting terrestrial (Pansarin 2010), members of this genus are usually climbing plants. These are often described as "hemiepiphytes" (without qualifier) (e.g. Damian & Mitidieri 2020; Pansarin & Miranda 2016), but also as "secondary hemiepiphytes" (Rodrigues da Cruz & Nunes-Freitas 2019), "hemiepiphytic vines" (Gigant et al. 2011), "epiphytic vines" (Croat 1978), or "vines" (Stern & Judd 1999). In spite of the use of these different terms, substantial field observations indicate that all of these species germinate in the soil and climb up on a phorophyte (Pansarin, pers. obs., Fig. S5). *Vanilla* species typically have two types of roots, i.e. aerial or clasping roots, and feeder roots that enter the soil (Fig. S6). Aerial clasping roots are thin and velamentous, while the terrestrial roots are thick with absorbing hairs in the maturation zone. In some vanilla species (e.g. *V. parvifolia* group, *V. aphylla*), the velamentous aerial roots are short with determinate growth (Fig. S7). In these species, plants can die when the connection with the soil is lost. Members of other groups, such as species of the *Vanilla planifolia* group, have clasping aerial roots with undetermined growth. These aerial roots can reach the soil (Fig. S8) and function as absorbing roots (Fig. S9). When *Vanilla* plants are cultivated without a host tree, free aerial roots are produced that can establish secondary contact with the soil (Fig. S10).

In the majority of climbing vanillas, the stem remains connected to the soil for of the entire life span of the plant. However, in some species, such as in *Vanilla pompona* var. *grandiflora*, adult plants may lose the stem connection with the soil but plants stay connected by its roots. Taken together, current knowledge suggests that calling climbing *Vanilla* species (secondary) hemiepiphytes is incorrect, but some species do have the ability to survive severance of the connection with the soil at least temporarily.

Finally, there is also a recent report claiming that a bromeliad, *Billbergia euphemiae*, is a "secondary" hemiepiphyte (Zorger et al. 2019). This species, however, is well-known for its facultative terrestrial, lithophytic and epiphytic growth (Brazilian Flora 2020 in construction continuously updated). It features long stolons between individual rosettes, and may sometimes climb up a tree trunk in dry resting vegetation, and may or may not sever the connection to the remaining genet. We see the report by Zorger et al. (2019) as evidence for facultative epiphytism of an herb with clonal reproduction rather than the first demonstration of "secondary" hemiepiphytism in the family Bromeliaceae. Irrespective of different interpretations in this particular case, such observations highlight that our list of potential candidates is certainly not complete, take, e.g., possibly "hemiepiphytic" Gesneriaceae (Salinas et al. 2010) or Begoniaceae (Webster & Rhode 2001).

In conclusion, accumulating evidence unanimously contradicts the claim that there are plants that follow the ontogenetic pattern that defines a SH in any group that traditionally were associated with such a life cycle, i.e. Araceae, Cyclanthaceae, and Marcgraviaceae. However, we describe some observations that there may be plant species that follow the ontogenetic trajectory of SHs, with the most promising candidates in Cactaceae. For decades, we have applied neat labels of life form categories without testing our concepts with rigorously collected field data. This paper is intended to stimulate much needed research in structurally dependent plants in an effort to understand their biology. It is also a plea to avoid mixing observations with conjecture. Terminology that only biases our observations, but does not stimulate critical observation and experiments, has little heuristic value. Given the current uncertainty, we advocate – for the time being – to discontinue the use of SH as a label for a particular life form and the use of neutral terms like "nomadic vine" or "adpressed climber" for any plant that germinates on the ground and subsequently climbs up trees losing its proximal stem portion. Once we have a better understanding of the different facets of life cycles of structurally dependent plants (ideally studying epiphytes, hemiepiphytes, nomadic vines, climbers, and mistletoes together), there will be time to develop an appropriate terminological framework, but only if necessary. For the reasons outlined above, SH is not a good option.

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Literature cited

Anderson EF (2001) *The cactus family*. Timber Press.

Balcázar Vargas MP and van Andel T (2005) The use of hemiepiphytes as craft fibres by indigenous communities in the Colombian Amazon. *Ethnobotany Research & Applications* **3**, 243–260.

Barberena FFVA, Sousa TdS, Ambrosio-Moreira BdS and Roque N (2019) What are the species of phorophytes of *Vanilla palmarum* (Orchidaceae) in Brazil? An assessment of emblematic specificity with palm tree species. *Rodriguésia* **70**, e02732017.

Barbosa DEF, Basílio GA, Furtado SG and Neto LM (2020) The importance of heterogeneity of habitats for the species richness of vascular epiphytes in remnants of Brazilian montane seasonal semideciduous forest. *Edinburgh Journal of Botany* **77**, 99–118.

Barthlott W, Burstedde K, Geffert JL, Ibisch PL, Korotkova N, Miebach A, Rafiqpoor MD, Stein A and Mutke J (2015) Biogeography and biodiversity of cacti. *Schumannia* **7**, 1–205.

Bautista-Bello AP, Krömer T, Acebey AR, Weichgrebe L and Zotz G (2021) Variación biológica en las aráceas trepadoras. *Acta Botánica Mexicana* **128**, e1819.

Brazilian Flora 2020 in construction (continuously updated) - available in: <http://floradobrasil.jbrj.gov.br/>,. Rio de Janeiro Botanical Garden.

Calvente A, Zappi DC, Forest F and Lohmann LG (2011) Molecular phylogeny, evolution, and biogeography of South American epiphytic cacti. *International Journal of Plant Sciences* **172**, 902–914.

Cheek M (1995) *Dischistocalyx*: terrestrial herbs, climbers, then epiphytes! *Acanthus* **6**,3–4.

Croat TB (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford. 943 pp.

Damian A and Mitidieri N (2020) Living in the clouds: A new high-elevation species of *Vanilla* (Orchidaceae, Vanilloideae) from Peru. *Phytotaxa* **451**,154–160.

Ellenberg H and Mueller-Dombois D (1965) A key to Raunkiaer plant life forms with revised subdivisions. *Bericht über das Geobotanische Forschungsinstitut Rübel zu Zürich* **37**,56–73.

Fernández-Alonso JL and Hernández-Schmidt M (2007) Catálogo de la flora vascular de la cuenca alta del Río Subachoque (Cundinamarca, Colombia). *Caldasia* **29**,73–104.

Gentry AH and Dodson CH (1987) Diversity and biogeography of Neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* **74**,205–233.

Gigant R, Bory S, Grisoni M and Besse P (2011) *Biodiversity and evolution in the Vanilla genus*. In Grillo, O and Venora, G (eds.). *The dynamical processes of biodiversity: case studies of evolution and spatial distribution*. Rijeka: InTech, pp. 1–26.

Holbrook NM and Putz FE (1996) *Physiology of tropical vines and hemiepiphytes: plants that climb up and plants that climb down*. In Mulkey, SS, Chazdon, RL and Smith, AP (eds.). *Tropical Forest Plant Ecophysiology*. New York: Chapman & Hall, pp. 363–394.

Hunt D, Taylor N and Charles G (eds.) (2006) *The new cactus lexicon. Descriptions and illustrations of the cactus family*. dh Books, Milborne Port.

Irume MV, de Lourdes da Costa Soares Morais M, Zartman CE and do Amaral IL (2013) Floristic composition and community structure of epiphytic angiosperms in a terra firme forest in central Amazonia. *Acta Botanica Brasílica* **27**,378–393.

Korotkova N, Borsch T, Quandt D, Taylor NP, Müller KF and Barthlott W (2011) What does it take to resolve relationships and to identify species with molecular markers? An example from the epiphytic Rhipsalideae (Cactaceae). *American Journal of Botany* **98**,1549–1572.

Kress WJ (1986) The systematic distribution of vascular epiphytes: An update. *Selbyana* **9**,2–22.

Leal EdS and Forzza RC (2012) Cyclanthaceae in Para State, Brazil. *Acta Botanica Brasílica* **26**,822–835.

Leuenberger BE (1986) *Pereskia* (Cactaceae). *Memoirs of the New York Botanical Garden* **41**,1–141.

López-Portillo J, Ewers FW, Angeles G and Fisher JB (2000) Hydraulic architecture of *Monstera acuminata*: evolutionary consequences of the hemiepiphytic growth form. *New Phytologist* **145**,289–299.

Lüttge U (1997) *Physiological ecology of tropical plants*. Springer, Berlin. 384 pp.

Martínez-Quezada DM, Arias S, Korotkova N and Terrazas T (2020) The phylogenetic significance of the stem morpho-anatomy in the Hylocereeae (Cactoideae, Cactaceae). *Plant Systematics and Evolution* **306**,8.

Massa GW (1996) *Factors affecting the distribution of a neotropical hemiepiphyte. Department of Biology*. San Jose State University, San Jose.

Meyer CFJ and Zotz G (2004) Does growth and survival of aerial roots limit the vertical distribution of hemiepiphytic aroids? *Biotropica* **36**,483–491.

Moffett MW (2000) What's "up"? A critical look at the basic terms of canopy biology. *Biotropica* **32**,569–596.

Mucunguzi P (2007) Diversity and distribution of hemi-epiphytes and facultative herbaceous epiphytes in Kibale National Park, Uganda. *African Journal of Ecology* **45**,57–64.

Ortiz-Hernández YD, Carrillo-Salazar JA and Livera-Muñoz M (2012) Carbon exchange rate of pitahaya (*Hylocereus undatus* L. Harwort) in contrasting seasons and irrigation regimes. *Israel Journal of Plant Sciences* **60**,385–392.

Pansarin ER (2010) *Vanilla dietschiana*. *Orchids* **79**,106–107.

Pansarin ER and Miranda MR (2016) A new species of *Vanilla* (Orchidaceae: Vanilloideae) from Brazil. *Phytotaxa* **267**,84–88.

Putz FE and Holbrook NM (1986) Notes on the natural history of hemiepiphytes. *Selbyana* **9**,61–69.

Reginato M, Andrade Baumgratz JF and Goldenberg R (2013) A taxonomic revision of *Pleiochiton* (Melastomataceae, Miconieae). *Brittonia* **65**,16–41.

Rodrigues da Cruz AC and Nunes-Freitas AF (2019) Epífitas vasculares da mata de restinga da Praia do Sul, Ilha Grande, RJ, Brasil. *Rodriguésia* **70**, e03192017.

Salinas F, Arroyo MTK and Armesto JJ (2010) Epiphytic growth habits of Chilean Gesneriaceae and the evolution of epiphytes within the tribe Coronanthereae. *Annals of the Missouri Botanical Garden* **97**,117–127.

Schimper AFW (1888) *Die epiphytische Vegetation Amerikas*. Gustav Fischer, Jena. 162 pp.

Schimper AFW (1903) *Plant geography upon a physiological basis*. Clarendon Press, Oxford.

Sperotto P, Acevedo-Rodríguez P, Vasconcelos TNC and Roque N (2020) Towards a standardization of terminology of the climbing habit in plants. *The Botanical Review* **86**,180–210.

Stern WL and Judd WS (1999) Comparative vegetative anatomy and systematics of *Vanilla* (Orchidaceae). *Botanical Journal of the Linnean Society* **131**,353–382.

Webster GL and Rhode RM (2001) *Plant diversity of an Andean cloud forest - checklist of the vascular flora of Maquipucuna, Ecuador*. University of California Press, Berkeley.

Weigand A, Abrahamczyk S, Aubin I, Bita-Nicolae C, Bruelheide H, Carvajal-Hernandez CI, Cicuzza D, da Costa LEN, Csiky J, Dengler J, de Gasper AL, Guerin GR, Haider S, Hernandez-Rojas A, Jandt U, Reyes-Chavez J, Karger DN, Khine PK, Kluge J, Kromer T, Lehnert M, Lenoir J, Moulatlet GM, Aros-Mualin D, Noben S, Olivares I, Quintanilla LG, Reich PB, Salazar L, Silva-Mijangos L, Tuomisto H, Weigelt P, Zuquim G, Kreft H and Kessler M (2020) Global fern and lycophyte richness explained: How regional and local factors shape plot richness. *Journal of Biogeography* **47**,59–71.

Went FW (1895) Über Haft- und Nährwurzeln bei Kletterpflanzen und Epiphyten. *Annales du Jardin Botanique de Buitenzorg* **12**,1–72.

Williams-Linera G and Lawton RO (1995) Ecology of hemiepiphytes in forest canopies. In Lowman, MD and Nadkarni, NM (eds.). *Forest Canopies*. San Diego: Academic Press, pp. 255–283.

https://doi.org/10.1017/S0266467421000407 Published online by Cambridge University Press

Zorger BB, Arrivabene HP and Milanez CRD (2019) Adaptive morphoanatomy and ecophysiology of *Billbergia euphemiae*, a hemiepiphyte Bromeliaceae. *Rodriguésia* **70**,e00592018.

Zotz G (2013) "Hemiepiphyte" – a confusing term and its history. *Annals of Botany* **111**,1015–1020.

Zotz G, Almeda F, Bautista-Bello AP, Eskov AK, Giraldo-Cañas D, Hammel BE, Harrison RD, Köster N, Krömer T, Lowry II PP, Moran RC, Plunkett GM and Weichgrebe L (2021a) Hemiepiphytes revisited. *Perspectives in Plant Ecology Evolution and Systematics* **51**,125620.

Zotz G, Bautista-Bello AP, Kohlstruck J and Weichgrebe T (2020) Life forms in aroids - natural variability vs. terminological confusion. *Aroideana* **43**,315–333.

Zotz G, Patiño S and Tyree MT (1997) Water relations and hydraulic architecture of woody hemiepiphytes. *Journal of Experimental Botany* **48**,1825–1834.

Zotz G, Weigelt P, Kessler M, Kreft H and Taylor A (2021b) EpiList 1.0 - A global checklist of vascular epiphytes. *Ecology* **102**,e03326.

https://doi.org/10.1017/S0266467421000407 Published online by Cambridge University Press