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Towards a Standardization of Terminology of the Climbing Habit in Plants

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Abstract
In science, standardization of terminology is crucial to make information accessible and allow proper comparison of studies' results. Climbing plants and the climbing habit have been described in numerous ways, frequently with imprecise and dubious terms. We propose a standardization of terms regarding the climbing habit, with special attention to climbing mechanisms. We abide by previous suggestions that the terms "primary" and "secondary" hemiepiphyte be substituted by "hemiepiphyte" and "nomadic climber" respectively, thus emphasizing the relationship of the latter to the climbing habit. We also suggest that "climbing plant" or "climber" be used to describe plants displaying the climbing habit, and "liana" and "vine" be left for describing woody and herbaceous climbers respectively. As for climbing mechanisms, we propose an eight-category classification comprised of two major categories: passive climbing, containing scrambling, hooks or grapnels, and adhesive roots; and active climbing, containing twining, tendrils, prehensile branches, twining petioles, and twining inflorescences.

Portuguese
Na ciência, a padronização de terminologia é crucial para tornar informações acessíveis e possibilitar a comparação adequada dos resultados de estudos. Trepadeiras e o hábito trepador vêm sendo descritos de diversas maneiras, frequentemente com termos imprecisos e dúbios. Nós propomos uma padronização da terminologia relativa ao hábito trepador, com atenção especial aos mecanismos de escalada. Nós acatamos sugestões anteriores de que os termos "hemiepífita primária" e "secundária" sejam substituídos por "hemiepífita" e "trepadeira nômade" respectivamente, enfatizando assim a relação desta última com o hábito trepador. Nós também sugerimos que "trepadeira" seja utilizado para descrever plantas apresentando o hábito trepador, e "liana" e "trepadeira herbácea" sejam utilizados somente para descrever trepadeiras lenhosas e herbáceas respectivamente. Quanto aos mecanismos de escalada, nós propomos uma classificação com oito categorias

compreendidas em duas grandes categorias: trepadeiras passivas, contendo os mecanismos apoiante, ganchos e raízes grampiformes; e trepadeiras ativas, contendo os mecanismos volúvel, gavinhas, ramos preensores, pecíolos volúveis e inflorescências volúveis.

Keywords climbing plants · lianas · vines · climbing mechanisms · standardization · terminology

Palavras-chave trepadeiras · lianas · mecanismos de escalada · padronização · terminologia

Introduction

In an ideal scenario of any biological study, the terms of scientific language and the concepts they express should be clear and precise to avoid ambiguities, which are a barrier to scientific progress (McIntosh, 1991). The task of developing good terminology, though, is not an easy one. Biologists must use classifications that are concise, but because evolution is complex and gradual, it is often difficult to define where are the outmost limits of a classification that deals with continuous forms. Thus, good terminology must be both inclusive (i.e., allowing some flexibility to the user), intuitive and accurate, so that there is a minimum overlap among distinct terms. This means that good terminology has a better chance of being employed by the scientific community, leading to its standardization, which is essential to better communicate and compare the results of our works. Furthermore, in this era of big-data and increasing use of machine learning and data mining, standardizing terminology is also crucial for evolutionary and comparative studies (e.g., Kaur et al. 2019). Bio-ontologies are a valuable resource when it comes to this matter: they are terminological resources, or controlled structured vocabularies, designed to assemble, describe and classify entities within a given domain while also describing the relationships among them (Ilic et al. 2007; Avraham et al. 2008; Walls et al. 2012). By doing so, ontologies like the Plant Ontology (Walls et al. 2012), Gene Ontology (Gene Ontology Consortium, 2012) and Protein Ontology (Natale et al. 2007; Bult et al. 2011) make large amounts of information available in a standardized manner that can be used for computerized logical inference (Walls et al. 2019).

The lack of adequate and standardized terminology is fairly common amongst the many fields of biology and has been addressed by numerous workers (McIntosh, 1991; Hall et al. 1997; Barthlott et al. 1998; Moffett, 2000; Colautti & MacIsaac, 2004; Kljuykov et al. 2004; Hodges, 2008; Marzinek et al. 2008; Prenner et al. 2009; Castel et al. 2010; Endress, 2010; Winegardner et al. 2012), including those studying climbing plants (e.g., Groppo & Pirani, 2005; Hu & Li, 2015). Since first described in the scientific literature by Plumier (1693), climbing plants have been referred to in many ways (Villagra & Neto, 2014). Because studies of them have lagged behind in comparison to other plants, they constitute one of the most neglected and understudied groups of plants (Gentry, 1991). This fact may have led to the great variety of terms and the lack of standardization we see today, as authors had relatively fewer publications to base their descriptions of the climbing habit on. After the first comprehensive and pioneer studies on climbers by Darwin (1865) and Schenck (1892, 1893), only few authors have made an effort to actually define and explain the terminology they use (e.g. Hegarty, 1991; Acevedo-Rodríguez, 2003, 2005; Isnard & Silk, 2009; Vaughn & Bowling, 2011; Villagra & Neto, 2014). However, these definitions do not always concur in a number of aspects.

Several recent floristic projects have adopted a loose terminology when referring to climbing plants (e.g., Checklist of Bolivia, Ecuador, Peru by Missouri Botanical Gardens). One good example is the Flora do Brasil 2020, an extensive and extremely important project aiming to catalogue and describe all Brazilian plant, algae and fungi species by 2020, where the option "Liana/Twiner/Climber[1]" is used in reference to climbing plants (Flora do Brasil, 2020, [under construction]). This option considers as equivalents three terms that actually mean different things. "Liana" means climbers in general or, preferably (as it will be discussed along this review), woody climber; "twiner" refers to plants whose climbing mechanism is by the twining of the main stem; and "climber" is a term equivalent to climbing plant in general, regardless of climbing mechanism or woodiness. This lack of terminology standardization on the climbing habit becomes obvious as we study plant collections. For instance, the climbing mechanism, a potentially pivotal character on the ecology and evolution of climbing plants (Gianoli, 2015), is often missing from voucher labels. In addition, confusing or redundant terminology is often used, in expressions such as "scandent with tendrils", "climbing liana" or "twining scandent vine" (Sperotto pers. obs.).

Thus, this work analyzes the terms on climbing habit by performing a thorough review of major studies on climbing plants in order to standardize the terminology and propose a general classification for climbing mechanisms. In order to facilitate the access and comprehension of climbing plant literature, we provide an equivalence table of terminologies, including translations to several languages (English, Spanish, Portuguese and German).

What can be considered a climbing plant?

We suggest that climbing plants be considered as all plants that germinate on the ground, and after a certain point in their growth, cannot mechanically sustain their stems without the aid of an external support. After establishing themselves on the supports, the connection to the ground may or may not be lost due to stem dieback (Ray, 1992; Moffett, 2000). This definition includes the commonly called "secondary hemiepiphytes", a term denoting plants that germinate on the ground, climb onto a support and eventually lose contact with the soil and become epiphytic (Putz & Holbrook, 1986; Kress, 1986). This distinction between "primary" (i.e. plants that germinate on other plants and later establish contact with the soil via aerial roots, like many *Ficus* species; Putz & Holbrook, 1986; Kress 1986) and "secondary hemiepiphytes" has generally been accepted and widely

[1] During the writing of this work, this option was changed in Flora do Brasil's English website version to "Liana/Scandent/Vine", but the Portuguese and Spanish versions still remain as "Liana/volúvel/trepadeira" and "Liana/voluble/bejuco" respectively, which are equivalent to "Liana/twiner/climber".

used, although not without criticism (for a history and discussion on the term "hemiepiphyte", see Zotz, 2013).

Moffett (2000) reviewed the terminology on canopy biology and pointed out that even though both "primary' and "secondary hemiepiphytes" share a life cycle phase of epiphytism, this phase is acquired via different strategies or "growth programs", and therefore it was not adequate to consider them variants of the same category. After assessing the physiological implications of the two strategies, Holbrook and Putz, the same authors that popularized the terms "primary" and "secondary hemiepiphytes", also became hesitant in their definitions (e.g., Holbrook & Putz, 1996). Thus, Moffett (2000) suggested replacing the term "secondary hemiepiphyte" with "nomadic vine" or "nomadic climber", while "hemiepiphyte" would be exclusive to" primary hemiepiphytes" *sensu* Putz and Holbrook (1986).

Therefore, we endorse the suggestion made by Moffett (2000), meaning that the term "climber" or "climbing plant" should include climbing plants to which soil connection is mandatory ('true' climbers or climbers *sensu stricto*) as well as plants that germinate on the ground and later become epiphytic (nomadic climbers) (Fig. 1). This adjustment would emphasize the relationship and proximity of strategies between nomadic and climbers *sensu stricto*, and reduce the ambiguity associated with the term "hemiepiphyte" that is often seen in the literature (Zotz, 2013).

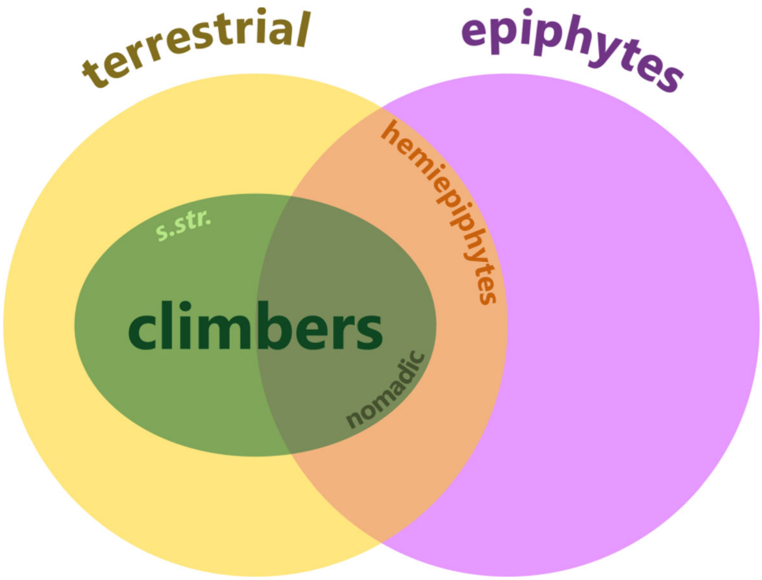

Fig. 1 Diagram representing where climbing plants (i.e., climbers) stand in regard to both terrestrial (yellow) and epiphytic (purple) habits. Lighter green represents the *sensu stricto* climbers, to which soil connection is mandatory and is never lost. Darker green represents the nomadic climbers (i.e. secondary hemiepiphytes sensu Putz & Holbrook (1986)), to which soil connection is eventually lost. Orange represents the hemiepiphytes (i.e. primary hemiepiphytes sensu Putz & Holbrook (1986))

What are their growth forms?

Although we prefer using terms in their original sense, an exception is made when referring to growth forms. We recommend the use of **liana** when referring to climbers that are woody throughout the entirety of their length; **vines** for herbaceous or non-woody climbers; and **climbing plants** or **climbers** as a general term for plants presenting a climbing habit (the term "scandent" is also acceptable as a synonym of "climber" or "climbing plant", but its use may be confounded with a climbing mechanism, as it will be discussed later).

According to Villagra & Neto (2014), the term "liana" was first described in the scientific literature by Plumier in his 1693 book *Descriptions des Plantes L'Amérique*, in which he devoted a section to *des Lianes*, i.e., climbing plants in a general sense. *Liane* comes from the French verb *lier*, which means "to bind or to attach". Plumier called climbers *Lianes* because of their utility in building of houses and general constructions by the natives living in the American islands (Plumier, 1693). It wasn't until much later that the expression "climbing plant" appeared on the scene with Darwin's 1865 *On the Movements and Habits of Climbing Plants*. Nevertheless, prominent works still used "liana" as a general term for climbing plants (e.g, Raunkiaer, 1934, 1937). As for "vine", it is a term first coined in reference to grape plants, which are woody, but later acquired the connotation of a herbaceous climber (Gentry et al. 1973; Croat, 1978). Even though both "liana" and "vine" had originally other meanings, the application of these terms as summarized in Gentry (1991) can make communication more straightforward since the characteristics "woody" and "herbaceous" are already comprised by "liana" and "vine" respectively. This dismisses the need to characterize these plants in a compound expression (i.e. "woody vines" or "herbaceous vines"). Using "lianas" and "vines" also makes sense given that both growth forms seem to have different distributions and abundances either within vegetation gradients or biogeographic regions (Gentry, 1991; Durigon & Waechter, 2011; Durigon et al. 2014, 2019).

What are their climbing mechanisms?

Climbing mechanisms are the means by which plants climb onto and stay attached to their supports. These involve behavioral or structural modification of various organs such as roots, stems, leaves or inflorescences in order to climb. They are pretty much taxon-specific (Hegarty, 1991; Burnham & Revilla-Minaya, 2011) and therefore are a useful character for the identification of families, genera and even species. Although most species present a single climbing mechanism, some may present more than one, making it difficult to classify them exactly in a given category (Hegarty, 1991). Though, when in the field, a good first step would be to observe if any part of the plant is twining (and then follow the flowchart presented in Fig. 2).

The vast majority of extant climbers are angiosperms and, expectedly, the highest diversity of climbing mechanisms can be found in this group. However, it is interesting to note that some of these climbing mechanisms may have appeared way before the angiosperms in the evolutionary history of land plants. Enough evidence has accumulated in the fossil record to show that climbers were diverse before the Cretaceous

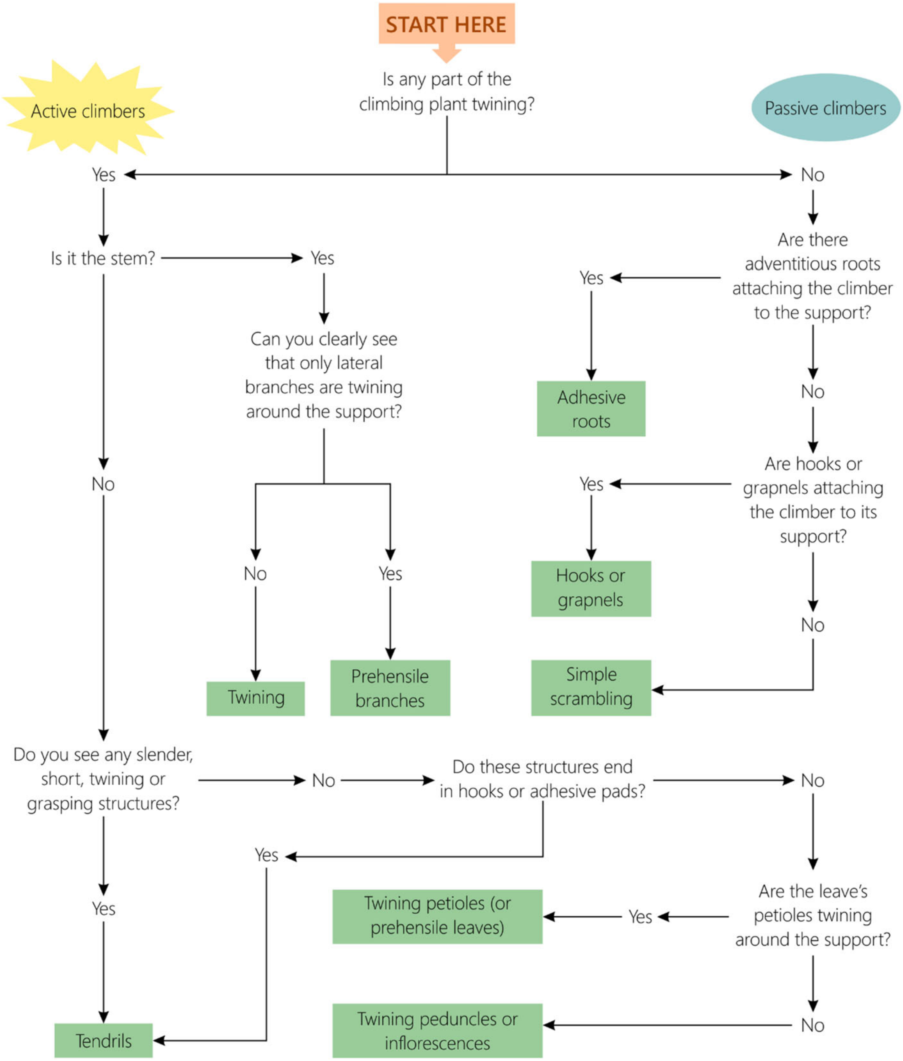

Fig. 2 Flowchart for identifying the different climbing mechanisms of climbing plants

radiation of flowering plants (Burnham, 2009). For instance, in the case of pteridosperms, a late Paleozoic group of gymnospermous plants with foliage resembling ferns (Krings et al. 2003), climbing mechanisms such as hooks, tendrils, and tendrils terminating in adhesive pads can be clearly recognized from compression fossil data (Huth, 1912; DiMichele et al. 1984; Krings & Kerp, 1997, 1999).

Given such diversity of climbing modes in groups with different biologies, classifications on climbing mechanisms vary substantially throughout literature, ranging from three categories (Vaughn & Bowling, 2011) to as high as nine in some cases (Addo-Fordjour & Rahmad, 2015). After literature review, we here propose and characterize two major categories encompassing a total of eight subcategories. To our concern, these categories represent the most intuitive way to classify the diversity of climbing mechanisms: **passive climbing**, comprising scrambling (or clambering, leaning), hooks or grapnels, and adhesive roots; and **active climbing**, comprising twining, tendrils, prehensile branches, twining petioles, and prehensile peduncles and inflorescences. All taxa cited as examples hereafter can be found summarized in Table 1. Terms translated to Spanish, Portuguese, and German can be found in Table 2 and a terminology equivalence table with some main studies on climbing plants is provided in Table 3.

Passive climbing

Passive climbers do not actively search for a support, rather they just grow over it without any searching movements such as circumnutation. Passive climbers may have adhesive roots or specialized grapnels or hooks to ensure their attachment to supports. "Scandent" is a term commonly used to describe climbing plants that passively grow over supports. However, that is a problematic term. Its origin dates from the late 17th century (Merriam-Webster Dictionary) and comes from the Latin verb *scandere*, meaning "to climb" (Font-Quer, 2001). With the further development of the science of morphology in the 18th century, *scandens* was applied by Linneaus (1753, 1788), together with *grimpante* (French for "climber"), to describe the stems of climbing plants (Villagra & Neto, 2014) in a general manner. Today, "scandent" is used to describe two different things: the climbing habit itself (Beentje, 2010; Oxford Dictionary; Merriam Webster Dictionary, n.d) and a climbing mechanism. These two meanings often get confused. For example, climbing *Disterigma* (Ericaceae) are referred to as "scandent" in Flora Neotropica even though they are root climbers (Pedraza-Peñalosa, 2010). So in this context, the term is being employed as a synonym for "climbing plant". In contrast, Fishbein et al. (2018) used "scandent" when discerning scrambling Apocynaceae species from twining or tendrilled ones, thus the term characterizes a climbing mechanism. Therefore, we agree that "scandent" should only be used as a synonym for "climber", which is in concordance with its original meaning. Still, we recommend prioritizing "climbing plant" or "climber" instead of "scandent" to avoid confusions involving climbing mechanisms.

Simple scrambling (or clambering, leaning)

In this mechanism, the climbing plant grows over the support without any active mechanism or specialized structure (Schenck, 1892). It is also less frequently referred to as "rambling" (Beentje, 2010). This has been said to be the least specialized climbing mechanism (Schenck, 1892; Hegarty, 1991) since it does not involve any major changes in the plant's structure (Acevedo-Rodríguez, 2003, 2005) besides adjustments in the vascular tissue, such as wide xylem vessels (Ewers et al. 1991) (Fig. 3a,b). Scrambling plants can also have thorns (e.g., *Byttneria*, Malvaceae, Fig. 3c), spines (e.g., *Celtis*, Cannabaceae, Fig. 3e), or coarsely barbed leaves (e.g., *Scleria*, Cyperaceae, Fig. 3d) that can prevent them from slipping down and/or falling from the support. This climbing mechanism is sometimes separated into two categories: simple scrambling and scrambling with the aid of spines, hooks and thorns (Acevedo-Rodríguez, 2005; Isnard & Silk, 2009; Burnham & Revilla-Minaya, 2011; Durigon et al. 2014, 2019). Differently from Schenck (1892), Darwin (1865) did not consider

Table 1 List of taxa cited throughout this work, alongside their respective climbing mechanisms

Family	Genus	Climbing mechanism
Apocynaceae	*Ibatia* Decne.	Twining
	Landolphia P. Beauv.	Twining inflorescence
	Matelea Aubl.	Twining
	Pacouria Aubl.	Twining inflorescence
Araceae	*Philodendron* Schott	Adhesive roots
Arecaceae	*Desmoncus* Mart.	Hooks or grapnels
Aristolochiaceae	*Aristolochia* L.	Twining
Asteraceae	*Dasyphyllum* Kunth	Simple scrambling
	Hidalgoa La Llave	Twining petioles
Bignoniaceae	*Dolichandra* (L.) L.G. Lohmann	Tendrils
	Perianthomega vellozoi Bureau	Twining petioles
Cannabaceae	*Celtis* L.	Simple scrambling
Celastraceae	*Hippocratea* L.	Prehensile branches
	Peritassa Miers	Prehensile branches
Connaraceae	*Connarus* L.	Prehensile branches
Cucurbitaceae	*Fevillea* L.	Tendrils
Cyperaceae	*Scleria* P.J.Bergius	Simple scrambling
Euphorbiaceae	*Dalechampia* L.	Twining
	Tragia L.	Twining
Ericaceae	*Disterigma* (Klotzsch) Nied.	Adhesive roots
Fabaceae	*Machaerium* Pers.	Prehensile branches; simple scrambling
	Senegalia Raf.	Tendrils (or cirrhus); simple scrambling
Gnetaceae	*Gnetum* L.	Twining
Loganiaceae	*Strychnos* L.	Tendrils
Malpighiaceae	*Mascagnia* (Bertero ex DC.) Bertero	Twining
Malvaceae	*Byttneria* Loefl.	Simple scrambling
Marcgraviaceae	*Marcgravia* L.	Adhesive roots
Melastomataceae	*Adelobotrys* DC.	Adhesive roots
Menispermaceae	*Abuta* Aubl.	Twining
Orchidaceae	*Oncidium* Sw.	Twining inflorescence (possibly)
	Vanilla Mill.	Adhesive roots
Piperaceae	*Piper* L.	Adhesive roots
Plantaginaceae	*Antirrhinum* L.	Twining peduncles
Polemoniaceae	*Cobaea* Cav.	Tendrils
Polygalaceae	*Securidaca* L.	Prehensile branches
Ranunculaceae	*Clematis* L.	Twining petioles
Rhamnaceae	*Reissekia* Endl.	Tendrils
Rubiaceae	*Uncaria* Schreb.	Hooks or grapnels
Sapindaceae	*Paullinia* L.	Tendrils
Smilacaceae	*Smilax* L.	Tendrils
Solanaceae	*Solanum* L.	Twining petioles (Dulcameroid clade); simple scrambling; root climbing
Tropaeolaceae	*Tropaeolum* L.	Twining petioles; twining peduncles (rarely)
Vitaceae	*Cissus* L.	Tendrils (sometimes ending in adhesive pads)

Table 2 Terminology of the climbing habit translated to Spanish, Portuguese and German

English	Spanish	Portuguese	German
climber; climbing plant	trepadora; bejuco[a]	trepadeira; cipó[a]	Kletterpflanz
climbing mechanism	mecanismo de trepado	mecanismo de escalada	Klettermodus
climb	trepar; subir	trepar; escalar	klimmern; klettern
nomadic climber	Not yet translated. Suggestion: "trepadora nómada"	Not yet translated. Suggestion: "trepadeira nômade".	Not yet translated. Suggestion: "Nomadenkletter"
hemiepiphyte	hemiepífita	hemiepífita	Hemiepiphyt
liana	liana	liana	Liane
vine	trepadora herbacea	trepadeira herbácea	krautiger Kletterpflanz
scandent	escandente	escandente	Kletternd
scrambling	apoyante	apoiante	Spreizklimmer; Spreizkletter
spine	espina	espinho	Spreitz
prickle	acúleo	acúleo	Dorn
Hook or grapnel	gancho	gancho	Haken
root climber	/	/	Wurzelkletter
adhesive roots	raíces adhesivas	raízes adesivas (ou grampiformes)	Haftwurzeln
circumnutation	circumnutación	circunutação	Nutation
twiner	enredadera; voluble	volúvel	Schlingpflanz; Windenpflanz
prehensile branches	ramas prensiles	ramos preensores	Kletterzweigen
tendril	zarcillo	gavinha	Ranke
circinated tendril	zarcillo circinado	gavinha circinada	Uhrfederranke
coiled tendril	zarcillo espiralado	gavinha espiral	Fadenranke
adhesive pads	discos adhesivos	discos adesivos	Haftscheiben
twining petioles	peciolos volubles	pecíolos volúveis	windende Blattstiele
prehensile leaves	hojas prensiles	folhas preensoras	kletternde Blätter
leaf climber	/	/	Blattklimmer; Blattkletter
twining inflorescences	inflorescencias volubles	inflorescências volúveis	windende Blütenstände

[a] : terms that are used in a more popular manner but may appear in scientific literature

simple scrambling in his work, only scrambling with the aid of any spines, hooks and thorns, which he put under the category "hook-climbers". In this review, we do separate scrambling plants bearing grapnels or hooks and place them in their own category (see below), while scramblers that may or may not have spines and thorns are kept together under "simple scrambling". This is due to the fact that those structures may be present for reasons other than climbing, such as protection against predators. For example, all *Dasyphyllum* species (Asteraceae) bear spines and prickles, but the majority of them are shrubs, not climbers (Ferreira, 2015). The same happens in *Mimosa* species (Fabaceae); many are thorny but are not necessarily climbers (Barneby, 1991). These patterns

Table 3 Equivalence table between here proposed terminology and some main works on climbing plants. * indicates a term is being used in the same sense both in the cited literature and in this work. Empty cells mean there is no reference to the term in the cited literature

	Climbing plant/ climber	Hemiepiphyte	Nomadic climber	Liana	Vine	Scandent	Simple scrambling
Darwin (1865)	*				Generally used meaning the grape-giving climber of the Vitaceae family, and very rarely as a synonym of "climber"		Spiny and prickly scramblers included in "Hook-climbers", but there is no mention to unarmed scramblers
Schenck (1892)		Treated as "Epiphyt" (i.e., epiphyte)	Schenck acknowledges the close relationship between the epiphytic and climbing habits seen in nomadic climbers but does not name them in any special way	Used as a synonym of "climbing plant"		*	Included in "Die Spreizklimmer"
Putz (1984)	*			*	*		Considered in the same category here called "Hooks or grapnels"
Putz & Holbrook (1986)	*	Treated as "primary hemiepiphytes"	Treated as "secondary hemiepiphytes"				
Putz & Chai (1987)				*			
Gentry (1991)	*	The author contextualizes and classifies hemiepiphytes based on their woodiness, not soil connection		*	Even though "Vine" is defined as a herbaceous climber, the term is largely used as a synonym of "climber" throughout the text	*	

Table 3 (continued)

Hegarty (1991)					Used with no distinction from "climbing plant"		Included under "Scrambling (+ − hooks/thorns)"
Moffett (2000)	*	*	*	*	Used with no distinction from "climbing plant"	*	
Krings et al. (2003)	*			*	*		Included under "Scrambling and hook-supported scrambling/climbing"
Acevedo-Rodríguez (2005)	*	*		*	*	Sometimes used as a synonym for "climber", sometimes as a climbing mechanism (i.e., scrambling)	Scrambling plants with no spines or prickles are placed under "Clambering plants", while spiny/thorny plants are placed under "Cauline or foliar spines"
Isnard & Silk (2009)	*			*	Mainly used as a synonym for "climbing plant"		Spiny and prickly scramblers included in "Hook-climbers", but there is no mention to unarmed scramblers
Burnham & Revilla-Minaya (2011)	*			Used with no distinction from "climbing plant"	Used with no distinction from "climbing plant"		Included in "Thorny/ spiny stems and scramblers"
Zotz (2013)	*	*	As "Nomadic vines"	*	Used mainly as a synonym for "climbing plant"		
Villagra & Neto (2014)	*			As "trepadeira lenhosa" (Portuguese, meaning "woody climber")	As "trepadeira herbácea" (Portuguese, meaning "herbaceous climber")	Used as a climbing mechanism, includes "arbusto pendente, não possui sustentação, apoia-se sobre	Spiny scramblers included in "Espinhosa" (Portuguese, meaning "spiny")

Table 3 (continued)

						algum suporte" (Portuguese, meaning "pending shrubs, not self supported, leaning over some support)	
Durigon et al. (2014)	*			*	*		Divided into two categories: "Scramblers" and "Hook-climbers" (i.e., scrambler with any spines, prickles, hooks or grapnels)
Addo-Fordjour & Rahmad (2015)				*			Separated into "Leaning climber" (which would be the unarmed scramblers) and "Thorn climber"
Sousa-Baena et al. (2018b)	*			*	*	*	
	Hooks or grapnels	**Adhesive roots**	**Twining**	**Prehensile branches**	**Twining petioles (or prehensile leaves)**	**Tendrils**	**Twining peduncules or inflorescences**
Darwin (1865)	Included in "Hook-climbers" together with other scrambler bearing spines or thorns	*	*		Included in "Leaf-climbers"	Included in "Tendril-bearers"	
Schenck (1892)	Climbing palms with hooks or grapnels were included in "Die Spreizklimmer", but climbing *Uncaria* were included in "Die Rankenpflanzen"	*	*	Included in "Die Rankenpflanzen" (German, meaning "the tendrilled plants") under "Zweigklimmer"	Included in "Die Rankenpflanzen" (German, meaning "the tendrilled plants") under "Blattkletter"	Large category including what we consider here as "Prehensile branches", "Twining peitoles (or prehensile leaves)", "Tendrils"	Included in "Die Rankenpflanzen" (German, meaning "the tendrilled plants") under "Blattkletter"

Table 3 (continued)

	(German, meaning "the tendrilled plants") under "Hakenkletter" (German, meaning "hook climbers)			(German, meaning "branch climbers")	(German, meaning "leaf climbers")	and "Twining peduncles or inflorecences"	(German, meaning "leaf climbers")
Putz (1984)	Considered in the same category as here called "Simple scrambling"	Placed together with adhesive-tendril climbers	*	*		All tendril climbers were placed in the same category except for adhesive-tendril climbers, which were place together with root climbers	
Putz & Holbrook (1986)							
Putz & Chai (1987)	Included in "Tendrils or hooks", except for climbing palms (rattans), that were placed under their own category	As "Adventitious roots"	Divided into "Twining stems (indeterminate)", "Twining stems (determinate)" and "Twining branches"	Included in "Twining branches"		Included in "Tendrils or hooks"	
Gentry (1991)	*	*	*	*	* (but also treated as "sensitive petioles")	*	
Hegarty (1991)	Included under "Scrambling (+ − hooks/thorns)"	*	Included in "Apices" under "Twining"	Included in "Branches" under "Twining"	Included in "Petiol(ul)es" under "Twining"	Divided into "Coiled" and "adhesive or hooked"	
Moffett (2000)							
Krings et al. (2003)	Included under "Scrambling and hook-supported scrambling/climbing"	*	*			*	
Acevedo-Rodríguez (2005)		As "Adventitious roots"	*	Included in "Sensitive branches or leaves"	Included in "Sensitive branches or leaves"	Tendrils are subcategorized by their postion, i.e.	

Table 3 (continued)

						"Axillary tendrils", "Tendrils opposite to the leaves", "Tendrils in the inflorescence", "Foliar tendrils" and "Tendrils derived from the leaf sheath"
Isnard & Silk (2009)	*Uncaria* species included in "Leaf climbers and irritable organs", but climbing palms included in "Hook-climbers"	Included in "Clinging climbers" together with adhesive-tendril climbers	*		Included in "Leaf climbers and irritable organs"	All tendril climbers were placed in the came category except for adhesive-tendril climbers, which were place together with root climbers under "Clinging climbers"
Burnham & Revilla-Minaya (2011)	Included in "Thorny/ spiny stems and scramblers"	*	Addressed as "Stem twining"	Included in "Stem twining"		Authors separated tendrils in three categories according to their origin: "Axillary tendrils: stem/inflorescence modification", "Tendrils: modified leaf and petiole" and "Spines/tendrils: modified stipules"
Zotz (2013)						
Villagra & Neto (2014)	Probably would be included in "Ganchosa" (Portuguese, meaning "hooky"), whose description is "planta com caule resistente e preensora, seus ganchos podem ser retos ou curvos"	*	*			*

Table 3 (continued)

	(Portuguese, meaning "prehensile plants with resistent stem, its hooks can be straight or curved")						
Durigon et al. (2014)	Included in "Hook-climbers"	*	*	*	*	*	
Addo-Fordjour & Rahmad (2015)	Separated into "Hook climber" and "Grappler climber", the last including "horizontal or recurved branches to grasp the host"	*	As "Stem twining climber"	As "Branch twining climber"	Included in "Leaf tendril climber"	Divided into "Stem tendril climber" and "Leaf tendril climber"	
Sousa-Baena et al. (2018b)					Treated as Tendrils	Divided into 17 categories of tendrils depending on their ontogenetic origin	Treated as Tendrils

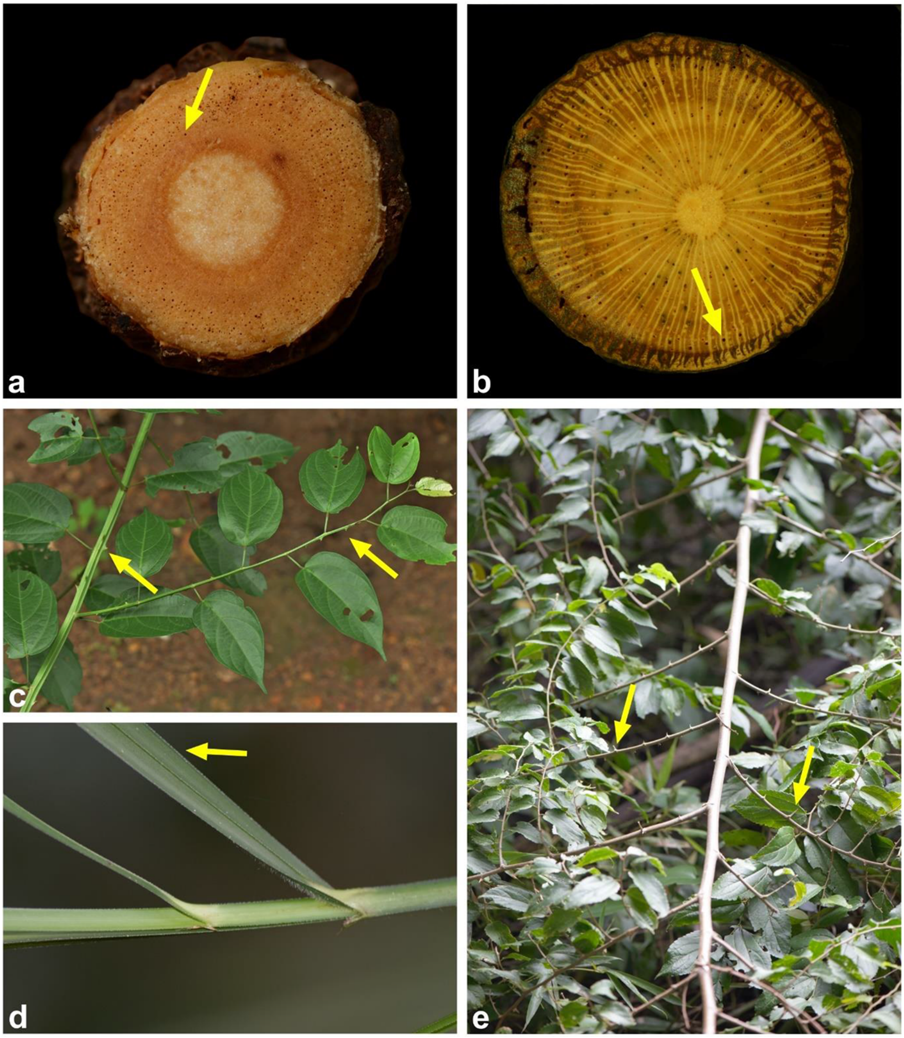

Fig. 3 Simple scramblers. a) and b) cross-sections of *Bougainvillea* sp. (Nyctaginaceae) and *Guatteria scandens* Ducke (Annonaceae), respectively, where the enlarged xylems vessels are visible (arrows); c) prickles in *Byttneria* (Malvaceae) (arrows); d) close up of the coarsely barbed leaves of a *Scleria* (Cyperaceae) (arrow); e) spines in *Celtis iguanaea* (Jacq.) Sarg. (Cannabaceae) (arrows). (all photos by Pedro Acevedo-Rodríguez)

suggest that these structures were not necessarily selected across evolution to improve climbing, even though they facilitate the plant's attachment to its support.

Hooks or grapnels

This climbing mechanism is similar to simple scrambling, in that plants bearing grapnels or hooks are also passive climbers. However, unlike the above, hooks or grapnels are specialized structures present in climbing palms, such as *Desmoncus* (Arecaceae) (Fig. 4a,b), or species of *Uncaria* (Rubiaceae) (Fig. 4c,d), that are clearly

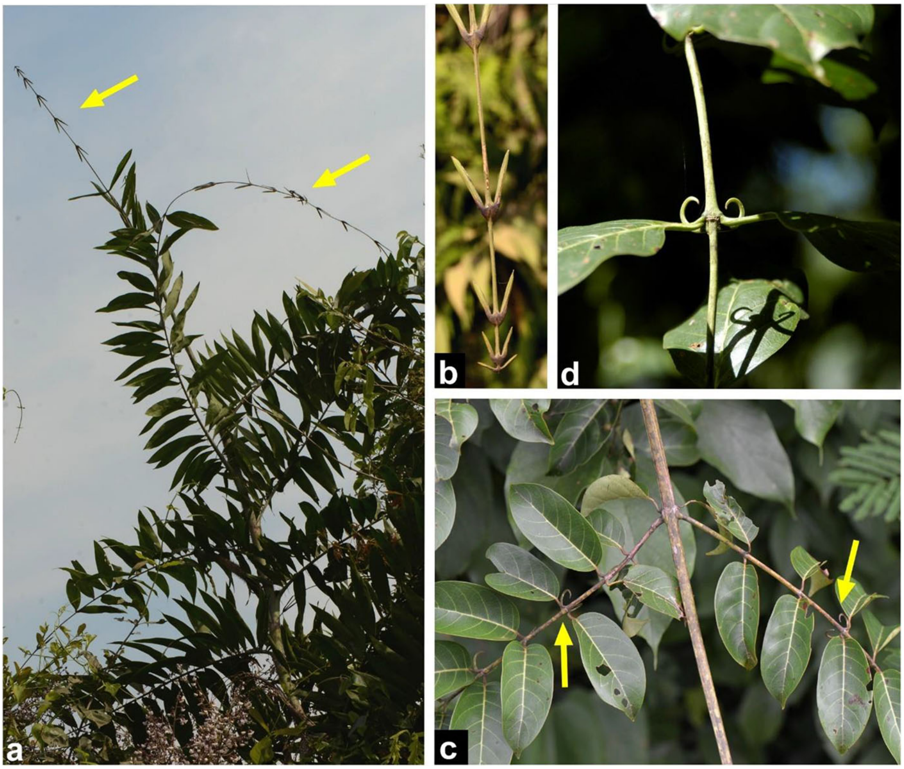

Fig. 4 Hooks or grapnels, the specialized structures of passive climbers. a) acanthophyll grapnels in *Desmoncus leptoclonos* Drude (Arecaceae) (arrows); b) close up of grapnels; c) and d) hooks of *Uncaria guianensis* (Aubl.) J. F. Gmel. (Rubiaceae) (arrows). (all photos by P. Acevedo-Rodríguez)

developed by the plant to aid in its attachment to the supports. In the case of climbing palms, the distal part of their leaves is modified into acanthophylls, which are short, stiff and act like grapnels that very efficiently anchor the plant onto surrounding vegetation (Isnard & Rowe, 2008). In their work on the biomechanics of climbing palms, Isnard and Rowe (2008) noted that all observed climbing palm species did not develop such grapnels in their juvenile self-supported phase, so these structures can be considered as specializations for the climbing habit. Thus, it felt more appropriate to place them under their own category. As for the hooks of *Uncaria* (Rubiaceae), they are modified branches and may even thicken when in contact with a support (Treub, 1883).

Adhesive roots

Root climbers are plants that climb through adhesive roots emerging from their stems (i.e. adventitious roots), such as *Marcgravia* (Marcgraviaceae) (Fig. 5a), *Philodendron* (Araceae) (Fig. 5b), *Adelobotrys* (Melastomataceae) (Fig. 5c), *Piper* (Piperaceae) (Fig. 6a,b) and *Vanilla* (Orchidaceae) (Fig. 6c,d). Also, all nomadic climbers climb through adhesive roots. This is a fairly consistent category of climbing mechanism that has been recognized since Darwin (1865). It is also easily recognizable in the field because root climbers need to be adpressed to their support (Hegarty, 1991), leading this mechanism

Fig. 5 Adhesive roots in climbing plants. a) flowering branches in *Piper* sp. (Piperaceae) and its young roots (arrows); b) close up of older adhesive roots in the same *Piper* sp.; c) *Vanilla palmarum* (Salzm. ex Lindl.) Lindl. climbing up the leaf rachis of a palm in the Brazilian Caatinga; d) *Vanilla barbellata* Rchb. f. and its long adhesive roots (arrow). (a, b and d: photos by P. Acevedo-Rodríguez; c: photo by Tiago Vieira)

to be recognized from the forest understory even if the plant climbs several meters in height. For this same reason, they are less mobile in comparison to plants that present other climbing mechanisms, which is also the case with tendril climbers whose tendrils end in adhesive pads (Putz et al. 1991).

The presence of root climbers was found to be associated with higher mean annual precipitation and shorter dry-season periods at a global scale (Durigon et al. 2013). This distribution pattern contrasts to the apparent pattern for climbers as a whole, in which they were found to be increasingly abundant with decreasing mean annual precipitation and longer dry-season periods (Schnitzer, 2005; DeWalt et al. 2010). Nonetheless, species that go against this trend observed in root climbers do exist: *Vanilla* (Orchidaceae) species, for

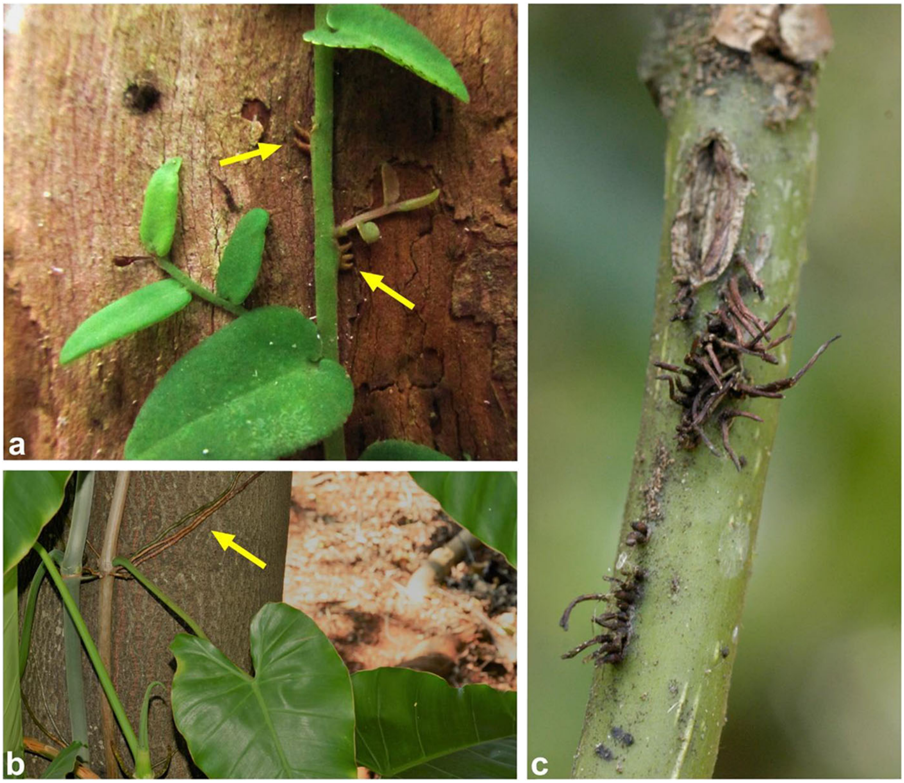

Fig. 6 Adhesive roots in climbing plants. a) young rootlets of a juvenile *Marcgravia* sp. (Marcgraviaceae) (arrows); b) a *Philodendron* sp. (Araceae) and its long adhesive roots (arrow); c) a close up of the short roots of an *Adelobotrys adscendens* (Sw.) Triana (Melastomataceae). (a: photo by Patrícia Sperotto; b and c: photos by P. Acevedo-Rodríguez)

example, do not seem to be constrained in the same way as reported by Durigon et al. (2013), with species seen creeping over shrubs in open coastal vegetation (i.e. “restinga”) or climbing up small palms in the Brazilian Caatinga (Fig. 6c), a characteristically hot and dry tropical biome (Alvares et al. 2013). This phenomenon may apply to climbing Cactaceae as well.

Active climbing

Unlike passive climbers, active climbing plants display a support-searching behavior such as circumnutation, an endogenous growth-related rhythmic movement in which leader shoots (i.e., shoots produced to search for supports) sweep through the air in arcs (Darwin, 1865; Hegarty, 1991; Carlquist, 1991; Putz et al. 1991; Isnard & Silk, 2009). This greatly increases the plant’s chance in finding suitable supports. This movement is also performed by tendrils that are still unanchored to supports (Putz et al. 1991).

Twining

Twining plants, or “twiners”, are plants that coil their main stem around a support (Darwin, 1865; Gentry, 1991; Hegarty, 1991; Burnham & Revilla-Minaya, 2011), such as many Menispermaceae (e.g., *Abuta*, *Cissampelos,* Fig. 7a,e), virtually all New World climbing Apocynaceae (e.g., *Matelea*, *Ibatia*, Fig. 7b,f), Aristolochiaceae (e.g., *Aristolochia*, Fig. 7c) and Malpighiaceae (e.g., *Mascagnia*, Fig. 7d) amongst numerous others, even the gymnospermous genus *Gnetum* (Gnetaceae). This climbing mechanism has been consistently shown to be the most common, regardless of geographic region (Putz, 1984; Putz et al. 1987; Hu & Li, 2010; Durigon et al. 2014; Addo-Fordjour & Rahmad, 2015; Addo-Fordjour et al. 2017), vegetation (DeWalt et al.

Fig. 7 Climbing plants with twining main stems. a) *Abuta* sp. (Menispermaceae); b) *Metastelma* sp. (Apocynaceae); c) *Aristolochia* sp. (Aristolochiaceae); d) *Mascagnia* sp. (Malpighiaceae); e) *Cissampelos* sp. (Menispermaceae); f) *Ibatia maritima* (Jacq.) Decne. (Apocynaceae). (c: photo by P. Sperotto; a, b, d, e and f: photos by P. Acevedo-Rodríguez)

2000; Gianoli et al. 2010; Durigon et al. 2019) and even phylogenetic placement (Mohl, 1827; Palm, 1827; Darwin, 1865; Schenck, 1892; Gentry, 1991; Hegarty, 1991; Sperotto et al., in. prep.). Interestingly, most twining stems seem to be dextral, i.e., they twine from left to right, (Edwards et al. 2007; Burnham & Revilla-Minaya, 2011) and this twining chirality is consistent within families, suggesting that it is phylogenetically correlated (Burnham & Revilla-Minaya, 2011).

Prehensile branches

This climbing mechanism is similar to twining in the sense that the plant climbs by using its stem. However, there are fundamental differences between the two that justify considering them as separate mechanisms. Prehensile-branch climbers do not employ their main stem in the task of climbing, but actually their lateral leaf-bearing branches, which they twine around the support (Putz, 1984; Hegarty, 1991; Burnham & Revilla-Minaya, 2011). These branches act like tendrils in that they are sensitive and twine when encountering a support (Hegarty, 1991) but differ from actual tendrils because they do not undergo any kind of structural modification (Acevedo-Rodríguez, 2005). They are still leaf-bearing branches that also acquire the function of securing the climber onto the support. Even though some prehensile-branch climbers can also twine their main stems, most of their support comes from the branches (Putz, 1984). Furthermore, prehensile branch climbers seem to be capable of establishing themselves on higher diameter trellises (supports) than both tendril climbers and twiners (Schenck, 1892; Putz, 1984), thus sustaining the separation of these plants in their own category of climbing mechanism. Prehensile branch climbers can be found in *Securidaca* (Polygalaceae, Fig. 8a), *Connarus* (Connaraceae, Fig. 8b), *Peritassa* and *Hippocratea* (Celastraceae, Fig. 8c,e) and *Machaerium* (Fabaceae, Fig. 8d), amongst others.

Tendrils

Here we adopt a stricter definition of tendril, which is of terminal, haptotropic (i.e., irritable, touch-responsive) and threadlike structures that are used exclusively for climbing (Darwin, 1865; Font-Quer, 2001; Sousa-Baena et al. 2018a). They have been defined as the most specialized climbing mechanism of all (Gentry, 1991) although this could be debated facing the existence of previously discussed grapnels and hooks.

Tendrils are highly variable in morphology, ontogeny and have “evolved multiple times during the history of angiosperms, representing a beautiful case of convergent evolution” (Sousa-Baena et al. 2018b, p. 2). They can vary from simple-ended (e.g., *Gouania*, Rhamnaceae, Fig. 9a) to much branched (e.g., *Cobaea*, Polemoniaceae, Fig. 9b); be circinated (e.g., *Paullinia*, Sapindaceae, Fig. 9c), coiled in spring-like shape (e.g., *Fevillea*, Cucurbitaceae, Fig. 9d) or present no particular shape (e.g., *Smilax*, Smilacaceae, Fig. 9e); end on hooks (e.g., *Dolichandra unguis-cati* (L.) L.G. Lohmann, Bignoniaceae, Fig. 10a), adhesive pads (e.g., *Cissus*, Vitaceae, Fig. 10d) or no special structure; and remain herbaceous or become lignified over time (e.g., *Strychnos*, Loganiaceae, Fig. 10e) (Fig. X). An interesting case is the structures present in *Senegalia* (Fabaceae) (Fig. 10d,e), which seem to be intermediate between prehensile branches and tendrils. They are not very slender or threadlike, and are armed with prickles resembling some prehensile branches of *Machaerium* (Fabaceae). At the same

Fig. 8 Prehensile branches in climbing plants. a) *Securidaca* sp. (Polygalaceae); b) *Connarus* sp. (Connaraceae); c) arrows pointing to the lateral prehensile branches of a *Peritassa* sp. (Celastraceae); d) prehensile branch of a *Machaerium* sp. (Fabaceae) (arrow); e) arrows indicating the main stem of a *Hippocratea volubilis* L. (Celastraceae) (left arrow) and one of its prehensile branches twining around the support (right arrow). (a: photo by Andrea Gandara; c: photo by P. Sperotto; b, d and e: photos by P. Acevedo-Rodríguez)

time, they are axillary to leaves, do not bear leaves and coil around supports, making it clear that their only purpose is to aid the plant in the task of climbing. On account of this last argument, we decided to keep these "cirrhi", as they are sometimes called

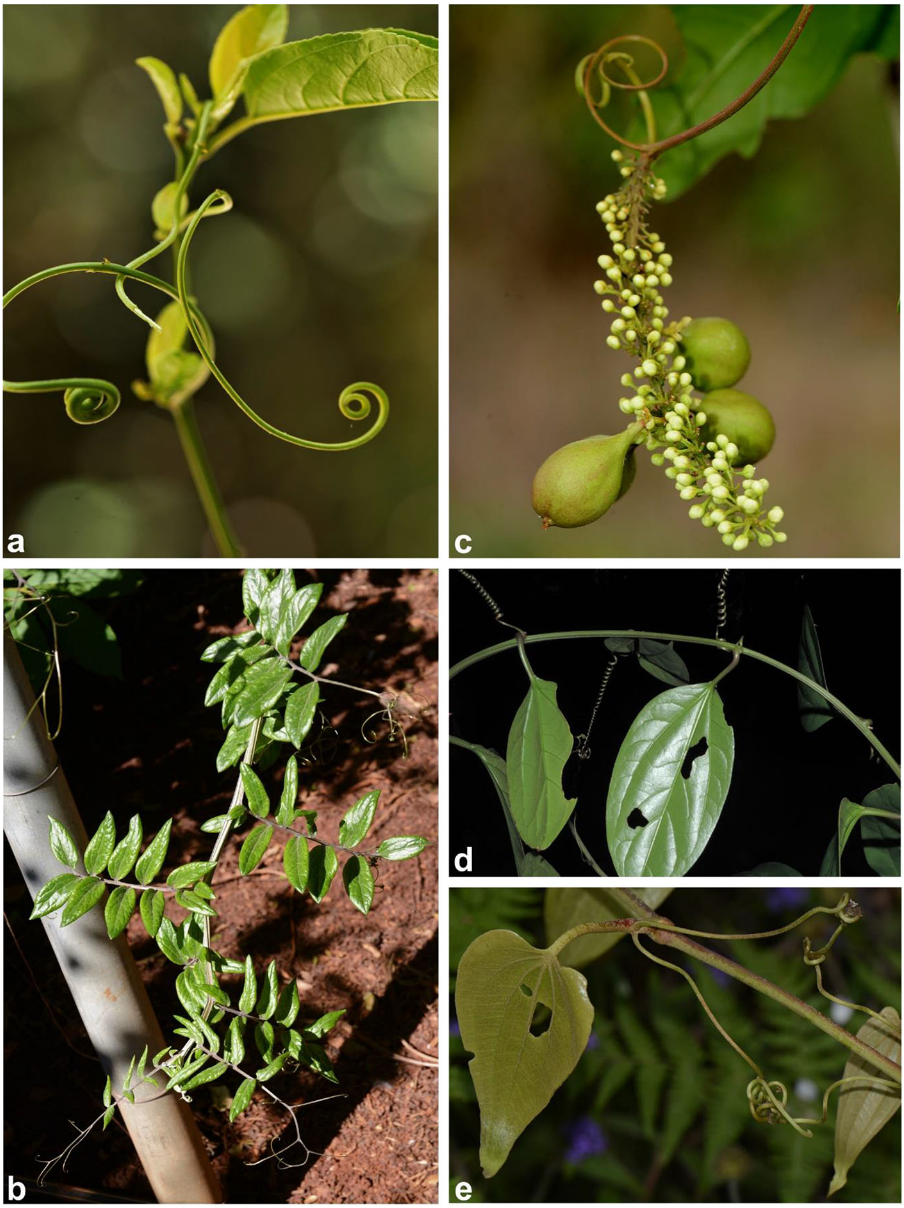

Fig. 9 Different tendril morphologies. a) simple-ended tendrils of a *Gouania* sp. (Rhamnaceae); b) branched tendrils in *Cobaea* sp. (Polemoniaceae) at the end of the leaves; c) pair of circinated tendrils in *Paullinia clavigera* Schltdl. (Sapindaceae) at the base of the inflorescence; d) coiled tendrils in *Fevillea passiflora* Vell. (Cucurbitaceae); e) tendrils in *Smilax* sp. (Smilacaceae) twining in no particular configuration. (all photos by P. Acevedo-Rodríguez)

(Acevedo-Rodríguez et al. 2015 [onwards]), under the "tendrils" category until further investigation is done to properly characterize these unusual structures.

The ontogenetic origin of tendrils can be from modified stems, petioles, stipules, whole leaves, leaflets, leaf rachis, leaf tips and inflorescences (Acevedo-Rodríguez,

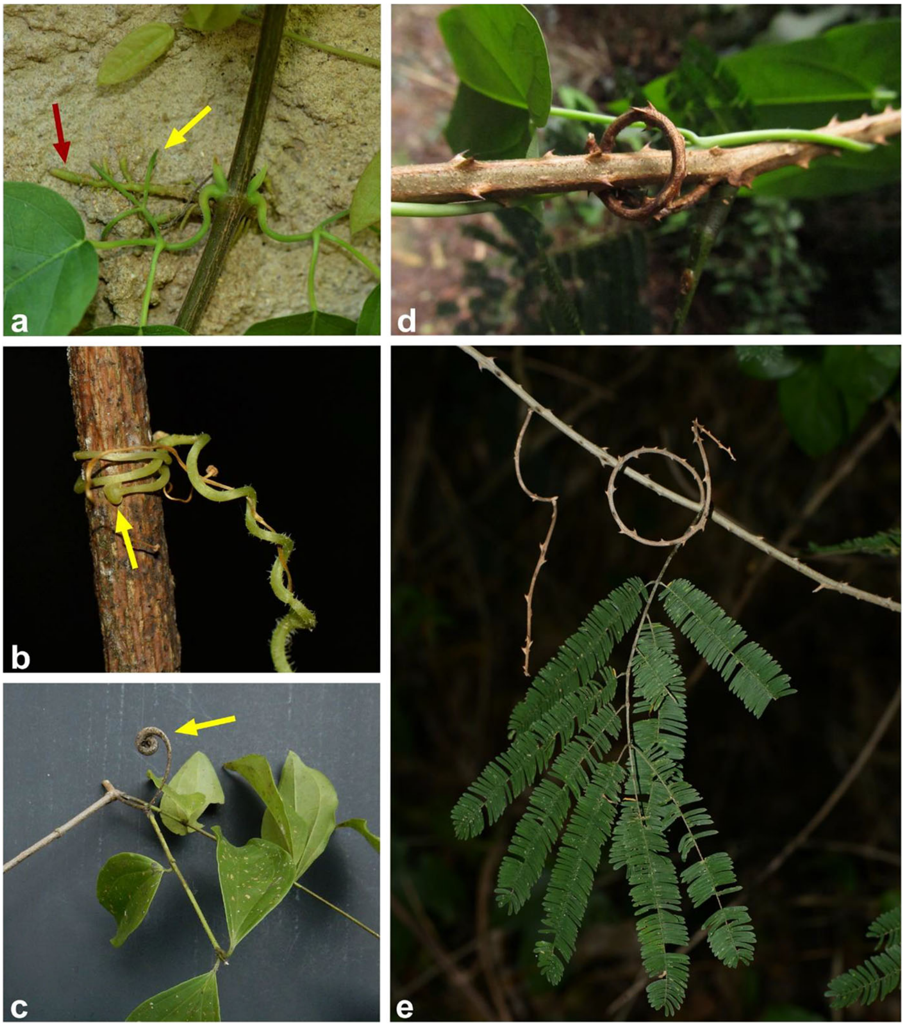

Fig. 10 Different tendril morphologies. a) *Dolichandra unguis-cati* (L.) L.G. Lohmann (Bignoniaceae) displaying two climbing mechanisms: its characteristic short, trifid tendril terminating in hooks (yellow arrow) and adhesive roots (red arrow); b) tendril in *Cissus sulcicaulis* (Baker) Planch. (Vitaceae) terminating in an adhesive pad (arrow); c) a lignified tendril in *Strychnos* sp. (Loganiaceae); d) and e) Different *Senegalia* sp. (Fabaceae) with “cirrhi”. (a, b, c, and e: photos by P. Acevedo-Rodríguez; d: photo by P. Sperotto)

2003, 2005; Cooper et al. 2018; Sousa-Baena et al. 2018b). Their true identity is sometimes difficult to interpret, thus generating different published opinions; however, developmental studies aid in solving these questions (Bell & Bryan, 2008). Tendril bearing plants also circumnutate in search of a support, but they differ from twiners in their faster, more irregular movements and the presence of irritability (Isnard & Silk, 2009), which is what makes tendrils coil.

In their comprehensive ontogeny-based work, Sousa-Baena et al. (2018b) considered a broad definition of tendril, leading to the identification of 17 tendril types including what we consider here as twining petioles (see below) and prehensile branches (see above). We disagree with the inclusion of twining petioles and prehensile branches under the same category of tendrils because they fail to fit the definition of an organ modified exclusively for climbing. The leaves whose petioles twine continue to bear a photosynthetic lamina, and the prehensile branches continue to bear leaves. Hence, both organs still fulfill their main function after acquiring a new one (i.e. climbing), which is not the case with tendrils.

Climbing plants with hook-ended and adhesive-pad-ended tendrils are not limited by the diameter of the supports like other tendril climbers: such tendrils circumvent the need to exclusively coil around the support, instead clinging themselves directly onto it. This could have ecological implications such as liana community assemblage (Putz, 1984; Putz et al. 1987; Seger et al. 2017) and has led some authors to accommodate climbers presenting these types of tendrils alongside root climbers under a different category, the "clinging-climbers" (Isnard & Silk, 2009).

Twining petioles (or prehensile leaves)

In this category we place plants that climb through twining their petioles around supports (Darwin, 1865; Bell & Bryan, 2008; Hegarty, 1991; Acevedo-Rodríguez, 2005; Durigon et al. 2014, 2019). These are also sometimes called "leaf climbers" (Darwin, 1865). This climbing mechanism is present in six angiosperm orders (Sousa-Baena et al. 2018b) including Asterales (e.g., *Hidalgoa*, Asteraceae) (Fig. 11a) and Solanales (e.g., species of the *Solanum* Dulcamaroid clade, Solanaceae, Knapp, 2010, 2013), but most twining petiole climbers are concentrated in Ranunculales (e.g., *Clematis*, Ranunculaceae) (Fig. 11b,c) and Brassicales (e.g., *Tropaeolum*, Tropaeolaceae). "Twining petioles" is not much of a consistent category of climbing mechanisms throughout the literature as is twining or root climbing. While Darwin

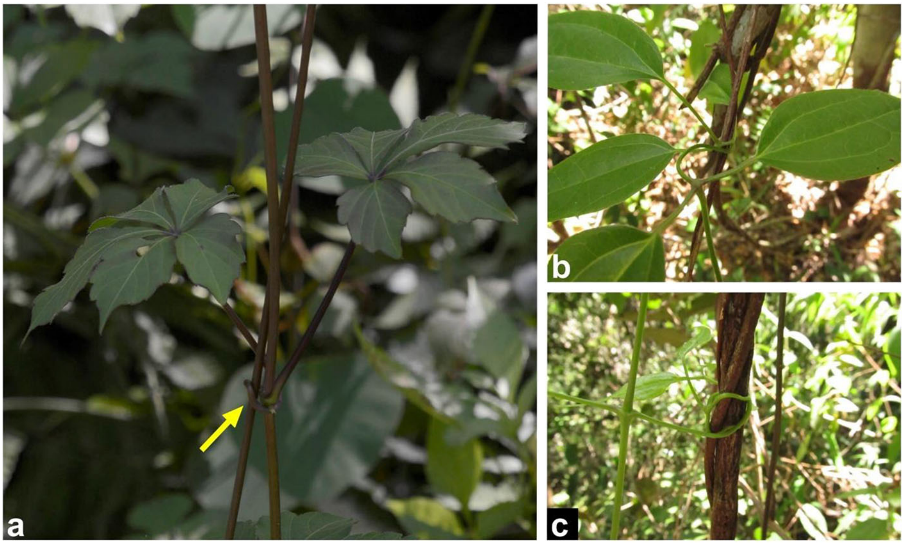

Fig. 11 Climbers displaying prehensile leaves. a) *Hidalgoa pentamera* Sherff (Asteraceae), arrow pointing at twining petiole of the leaf on the left; b) and c) prehensile leaves in *Clematis* sp. (Ranunculaceae). (a: photo by P. Acevedo-Rodríguez; b and c: photos by P. Sperotto)

(1865) classified plants with twining petioles under their own category (i.e. “leaf climbers”), Schenck (1892) placed them in the same category as plants that climb through tendrils, prehensile branches and irritable hooks, arguing that all these mechanisms are irritability based. This position was later followed by Isnard and Silk (2009), while Hegarty (1991) put leaf climbers under “other twiners” alongside prehensile branches, and Sousa-Baena et al. (2018b) considered twining petioles as tendrils. We follow Darwin (1865) and consider twining petiole climbers under their own category since they do not fit the concept of tendril discussed above. However, there definitely seems to be a relationship between twining petioles and tendrils, at least in Bignoniaceae: *Perianthomega vellozoi* Bureau is sister to the whole of extant Bignoniae and the only member of the tribe that climbs through twining petioles, not tendrils (Sousa-Baena et al. 2014). All tendrils in the Bignoniae tribe are derived from leaves (Sousa-Baena et al. 2018a, 2018b).

Twining peduncles and inflorescences.

This is the climbing mechanism of plants whose inflorescence rachides or flower peduncles are irritable and twine around a support when in contact with it. It is probably the less common climbing mechanism and can be found in some *Pacouria* and *Landolphia* (Apocynaceae), *Antirrhinium* (Plantaginaceae) and possibly in one orchid belonging to the genus *Oncidium* (Sousa-Baena et al. 2018b). Following the same logic applied to prehensile branches and twining petioles, twining peduncles and inflorescences behave like tendrils (i.e. coil around supports) but are not entirely specialized structures whose only purpose is to aid the plant in climbing. Therefore, we have chosen to place this mechanism it in its own category, even though it is a very infrequent one. Unfortunately, there is no data or discussion on maximum support diameter or any ecological aspects regarding this climbing mechanism since it is fairly uncommon. Since we lacked images of this climbing mechanism, we recommend the reader to see Sousa-Baena et al. (2018b).

Conclusions

Climbing plants can present themselves in a great variety of shapes and forms. In the Neotropics alone, impressively 10% of the around 90.000–110.000 species of seed plants (Antonelli & Sanmartín, 2011) are climbers (Acevedo-Rodríguez et al. 2015 [onwards]), and they have long been recognized as characteristic components of tropical forests (Richards, 1952; Gentry, 1991; Schnitzer & Bongers, 2002, 2011; Schnitzer et al. 2015). Furthermore, in a world of aggravating climate change, on-the-rise forest disturbance and elevated CO_2 emissions, liana abundance in forested ecosystems is expected to increase (Schnitzer & Bongers, 2011), although the subject is still controversial. This would be particularly concerning given that lianas affect tree growth and survival to the point of jeopardizing carbon accumulation and storage (van der Heijden et al. 2015). At the same time, lianas still play an important role as a food source and pathway for canopy fauna (Emmons & Gentry, 1983; Gentry, 1991).

The importance of climbers in floristic compositions of extratropical regions (Gianoli et al. 2010; Ladwig & Meiners, 2010; Gallagher & Leishman, 2012;

Valladares et al. 2011) and non-forested vegetations (Durigon et al. 2014, 2019) has lately been highlighted, but our knowledge of climbers in such regions and environments still lags behind tropical ecosystems, especially forests.

We believe that the terminology here presented, especially of climbing mechanisms, can be applied to climbers of any region, or, at least, be a good starting point in recognizing additional undescribed climbing mechanisms or structures. Even though research interest and studies on climbers have boomed somewhat in the last 30 years (e.g., Carter & Teramura, 1988; Putz, 1991; Balfour & Bond, 1993; Morellato & Leitão-Filho, 1996; Citadini-Zanette et al. 1997; Andrade et al. 2004; Gianoli, 2004; Rowe et al. 2004; Gilbert et al. 2006; Angyalossy et al. 2011; Parthasarathy, 2015; Schnitzer et al. 2015) there is still plenty to be learned. We hope that this publication can facilitate future research on climbing plants through the standardization of terms to improve mutual understanding and communication among researchers in this exiting field of investigation.

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