Plant Spinescence: Architectural Modularity and Functional Plurality

Spinescence végétale : modularité architecturale et pluralité fonctionnelle

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Abstract

Spiny plant structures, commonly interpreted as defensive devices against herbivory, exhibit a morphological and positional diversity suggesting multiple origins and functions. Their ontogenetic and architectural distribution indicates that their previously proposed defensive effectiveness remains debatable. Morphological and ecological observations suggest that these structures may perform multiple roles, including leaf lamina stiffening, capture of organic matter and water, microclimatic regulation, water coalescence and drainage, spatial colonization for improved access to light, and modulation of abiotic constraints. In this context, spines may be integrated into a broader set of ecological functions that mitigate the growth–defense allocation trade-off. This article does not aim to experimentally demonstrate a single function for spiny structures, but rather to propose—based on diverse morphological and ecological examples—an expanded interpretative framework that may guide future functional investigations.

Résumé

Les structures piquantes des plantes, communément interprétées comme des dispositifs défensifs contre l'herbivorie, présentent une diversité morphologique et positionnelle suggérant des origines et des fonctions multiples. Leur distribution ontogénétique et architecturale indique que leur efficacité, préalablement proposée, défensive demeure discutable. Les observations morpho-écologiques suggèrent que ces structures pourraient jouer des rôles multifonctionnels : rigidification du limbe foliaire, captation de matière organique et d'eau, régulation microclimatique, coalescence et écoulement de l'eau, colonisation de l'espace pour l'accès à la lumière et modulation des contraintes abiotiques. Dans ce contexte, les épines pourraient s'intégrer dans un ensemble de fonctions écologiques atténuant le compromis allocationnel croissance–défense. Cet article ne vise pas à démontrer expérimentalement une fonction unique des structures piquantes, mais à proposer, à partir d'exemples morphologiques et écologiques variés, un cadre interprétatif élargi susceptible de guider de futures investigations fonctionnelles.

Keywords: abiotic constraints, functional ecology, herbivory, myrmecophytic plants, plant architecture, prickles, spines, thorns, trichomes.

Mots clés : aiguillons, architecture végétale, contraintes abiotiques, écologie fonctionnelle, épines, herbivorie, piquants, plantes myrmécophytes, trichomes.

Introduction

The interpretation of spines as primarily defensive devices against herbivory rests largely on a 19th-century conceptual legacy, in which spiny structures were spontaneously assimilated to passive weapons. This reading, inherited from an older interpretive tradition and sometimes aligned to zoological models, remains influential in contemporary literature. Although numerous studies have explored the defensive dimension of spines, their function is more often discussed on interpretive grounds than through systematic experimental or comparative demonstrations integrating the full ecological context.

In this synthesis, the comparative analysis of spiny organs in cacti, palms, roses, certain orchids, and many other plants shows that these structures cannot be systematically reduced to a simple defensive function against herbivores. This function sometimes appears late, secondary, or even hypothetical in light of available morphological and ecological observations: in many cases, spines or prickles are positioned on organs that do not effectively impede access to leaf tissue. Leaves remain largely accessible to herbivores, including small ones, without any need to cross the spiny zones.

In the particular case of cauline spines or prickles observed in certain species, a recurring hypothesis invokes a defensive function against now-extinct megafauna. This interpretation, however, assumes temporal coherence between the appearance of spiny structures and the presence of herbivores capable of exerting significant selective pressure on specific tissues—coherence that is not always clearly established within available phylogenetic frameworks. It also implies an explicit functional correspondence between prickle morphology and a precise mode of attack: a relationship that remains poorly demonstrated experimentally or comparatively. Finally, placed within a broader ecological framework, this hypothesis does not always fully account for the biogeographic diversity of spiny forms, nor for their occurrence in contexts where massive herbivory is not documented as a major structuring factor.

This spatial dissociation between spiny structures and the main photosynthetic organs calls into question their interpretation as simple anti-herbivore barriers. Conversely, examination of their morphology, position, and taxonomic constancy suggests that they may constitute, above all, "ecological tools" participating in leaf biomechanics, resource capture, water coalescence and drainage, thermal regulation, spatial colonization, and adaptation to abiotic constraints.

This evolutionary logic appears to recur in various forms across many plant families. This dynamic trajectory involves trunks and stipes, certain specialized stems, leaves, and some aerial roots.

Discussion

1. Specialized aerial roots: organ co-option beyond anchorage

Secondary, erect, rigid, and spiny aerial roots observed in several Orchidaceae (*Eriopsis biloba* Lindley [1847: t. 18], *Cymbidium finlaysonianum* Lindley [1833: t. 164], *Grammatophyllum speciosum* Blume [1825: 378]) do not serve for anchorage: they intercept organic debris and microorganisms, playing a predominantly active role in the indirect nutrition of the plant (Fig. 1). The absence of discussion on secondary roots highlights a functional bias in the literature, which is largely centered on water and ionic uptake (e.g., Went, 1940; Zotz & Winkler, 2013; Hauber *et al.*, 2020). Specialized aerial roots nonetheless constitute morphologically and mechanically distinct structures, justifying specific analysis within a broader reflection on spiny structures. Although simple observations suggest that they are initially homologous to classical aerial roots (presence of velamen, greening upon moistening, etc.), they nonetheless remain erect, with a more or less spiny root cap, sometimes markedly narrower than primary roots, long and densely branched, and ecologically distinct due to their permanent exposure to air currents and their almost constantly dry, subsclerified appearance.

Figure 1: *Grammatophyllum speciosum.* A – plant; B – secondary aerial roots with organic matter. Photos: Aurélien Sambin.

2. Specialized stems: structural investment over foliar defense

In plants with creeping, climbing, or prostrate habits, such as *Mimosa pudica* Linnaeus (1753: 518), *Rubus fruticosus* Linnaeus (1753: 493), or *Desmoncus polyacanthos* Martius (1824: 85, t. 68), stems frequently bear small uncinate outgrowths. In taxa such as *Rubus*, these correspond to epidermal prickles, whereas in *Desmoncus* they are better interpreted as epidermal–cortical outgrowths with a mechanically reinforced base and a zone of subbasal weakness. As suggested by several authors (e.g., Isnard & Rowe, 2008; Rowe & Speck, 2015; Lehnebach *et al.*, 2022), these structures may contribute to mechanical attachment and stabilization of the axes. In this context, such outgrowths can be interpreted as functional structures facilitating spatial colonization and access to light (Fig. 2).

Figure 2: Spinescence. A – *Mimosa pudica*; B – *Desmoncus polyacanthos*. Photos: Aurélien Sambin.

The strictly defensive interpretation of prickles deserves to be nuanced. They are abundant on stems, sometimes on petioles and leaf rachises, but remain very reduced or even absent on leaves or leaflets, particularly at the photosynthetic parts, which remain largely accessible to herbivory. Such an anatomical distribution does not correspond to a strategy primarily aimed at directly protecting assimilatory organs. It rather suggests that these structures first participate in the protection or maintenance of the structural axis by preserving the integrity of the load-bearing organs involved in plant growth and spatial expansion.

Experimental work carried out on *Rubus vestitus* (Weihe, 1825: 684) indicates that simulating herbivory does not lead to a significant increase in spine production (Gibson *et al.*, 1993), although this pattern has not been consistently recovered across studies, likely reflecting heterogeneous experimental conditions and variable

control of abiotic factors. Under repeated grazing conditions, resource allocation would tend instead to prioritize the maintenance of cauline growth at the expense of prickle development. These observations suggest that prickles constitute a potentially costly trait, whose expression depends on physiological state and resource availability, rather than a simple and immediate inducible response to herbivore pressure. Similarly, the morphological differences observed in *Rubus croceacanthus* Léveillé (1912: 33) between island and continental populations (Takei *et al.*, 2014), particularly prickle elongation in an insular context, cannot be unambiguously attributed to grazing pressure alone, in the absence of in-depth analyses of abiotic factors (soil, exposure, mechanical or water constraints). The lack of concomitant variation in other vegetative traits between insular and continental populations, noted by these latter authors, further suggests that prickle elongation cannot be interpreted as the simple expression of a univocal defensive mechanism, but could result from a set of ecological and developmental determinants that remain insufficiently discriminated. Comparable observations have been discussed in the Cactaceae, where variation in these characters also appears associated with environmental gradients independent of assumed herbivore pressure alone. In a synthesis devoted to the functions of cacti spines, Aliscioni *et al.* (2021) emphasize that these structures also intervene in the modulation of microclimatic constraints.

The leaves of species of *Rubus* are notably rich in phenolic metabolites, including catechin and quercetin, which have been well documented in terms of their occurrence and abundance (e.g., Oszmiański *et al.*, 2015). Although direct biochemical data on *Rubus* prickles are scarce, studies on related taxa such as *Rosa* Linnaeus (1753: 491) suggest a possible functional continuity based on similar biochemical mechanisms. The work of Swarnkar *et al.* (2021), conducted on hybrids of *Rosa*, provides direct evidence of this biochemical complexity: the authors show that prickles exhibit a specific organization of phenolic compounds within the secondary cell wall, as well as in intercellular spaces. The accumulation of secondary metabolites such as catechin and quercetin is associated with tissue hardening and prickle lignification. These molecules possess well-established in vitro antioxidant activities and are recognized for their contribution to plant tolerance to environmental stresses by modulating stress-associated metabolic responses (Zhuang *et al.*, 2023).

All these elements converge toward the idea that prickles of creeping or climbing plants cannot be reduced to a primary defensive function. Their anatomical distribution, their variability according to ecological context, and their biochemical composition indicate that this could be a structural trait whose expression results from functional trade-offs. On the one hand, their preferential location on load-bearing axes underlines a potential role in preserving the mechanical integrity of the organs ensuring growth and spatial expansion. On the other hand, experimental data show that their development depends on physiological state and available resources, suggesting integration into allocation strategies. Finally, the localized accumulation of phenolic compounds associated with lignification and stress responses, observed at least in *Rosa*, indicates that these structures also participate in metabolic processes related to environmental tolerance. Together, these elements argue in favor of a complex trait, simultaneously structural, ecological, and physiological, whose function cannot be interpreted in a univocal manner.

3. Agaves and Cacti: abiotic canalization as a primary driver

During the evolution of the Cactaceae, leaves were progressively reduced or transformed into spines, as evidenced by species of the genus *Pereskia* Miller (1754: s.p.), which still retain well-developed leaves (Butterworth & Edwards, 2008; Miravel-Gabriel *et al.*, 2024). This transformation occurs primarily in a context of severe abiotic constraints, notably to reduce transpiring surfaces, the limitation of water losses, and thermal dissipation. Mechanical defense by spines in cacti is often presented as a major function, although direct empirical evidence of its effectiveness is rare, fragmentary, or confounded with that of glochids—very reduced, multiple spines that clearly show strong interactions with animals, illustrating a high degree of functional specialization of the foliar system in the Cactaceae (e.g., Boke, 1980; Gibson & Nobel, 1986; Anderson, 2001).

Cacti possess spines that, first and foremost, for survival reasons, capture and channel water and create micro-shadows that reduce evaporation and limit thermal stress. To these already published demonstrations (e.g., Bai *et al.*, 2015; Liu *et al.*, 2015; Aliscioni *et al.*, 2021; Guo *et al.*, 2022), one may add the hypothesis that the spines of globular plants, often long, strongly uncinate, and laterally compressed, as illustrated by *Ferocactus peninsulae* (Weber, 1895: 320) Britton & Rose (1922: 133) or *Melocactus ferreophilus* Buining & Brederoo (1973: C VI d), could contribute to

stabilizing plants on unstable soils, preventing burial, and favoring the clearing of the collar and plant apex in the face of small stone displacements (Fig. 3).

In agaves, the apical and lateral spines likely play a major role in the architectural reinforcement of the leaf, particularly due to their high lignin content (Morán-Velázquez *et al.*, 2020). Although no functional study has so far demonstrated a secondary hydric role for these structures, several morphological observations suggest that the apical spines may also contribute to the interception of atmospheric water. These spines, generally rigid, erect, straight or sigmoid, are progressively widened, often laterally compressed toward the base, then distinctly caniculate on the ventral surface and sometimes decurrent.

Figure 3: Potential mechanical stability of *Melocactus ferreophilus*. A – plant; B – areole and spine cluster. Photos: Aurélien Sambin.

Micromorphological examination reveals a structured epidermal surface that varies according to species. Some present a verrucous and alveolate relief (Fig. 4A), while others show a regular longitudinal fibrillary network. In both configurations, the surface is most often associated with more or less dispersed trichomes (Fig. 4B) or, conversely, dense or cespitose ones (Fig. 4C). In certain species, the apical spines seem to become caducous during leaf maturation. When young, the spines are strongly constricted at the base, the epidermis is smooth and brownish, and the underlying tissues appear desiccated (Fig. 4D). When the leaves reach full deployment, the spines eventually detach, which suggests specific water management. This caducity clearly shows here a particular developmental phase rather than possible protection against herbivory.

On the mechanical level, the combination of an erect conical geometry, a

compressed and canaliculate base, and a fibrillar or verrucose-alveolate microtopography bearing trichomes appears to promote the initial adhesion of microdroplets, their progressive coalescence toward the base of the spine, and their subsequent flow onto the likewise canaliculate leaf (repeated personal observations, including field and microscopic observations, unpublished). Comparative morphological observations carried out on the spines of cacti *Opuntia cochenillifera* (Linnaeus 1753: 468) Miller (1768: OPU N° 6.) and *Opuntia gosseliniana* Weber (1902: 83) show subsimilar epidermal surfaces, notably the presence of longitudinal fibrillary structures associated with micro-trichomes. This morphological convergence between phylogenetically distant taxa reinforces the hypothesis of structures with possible hydric contributions.
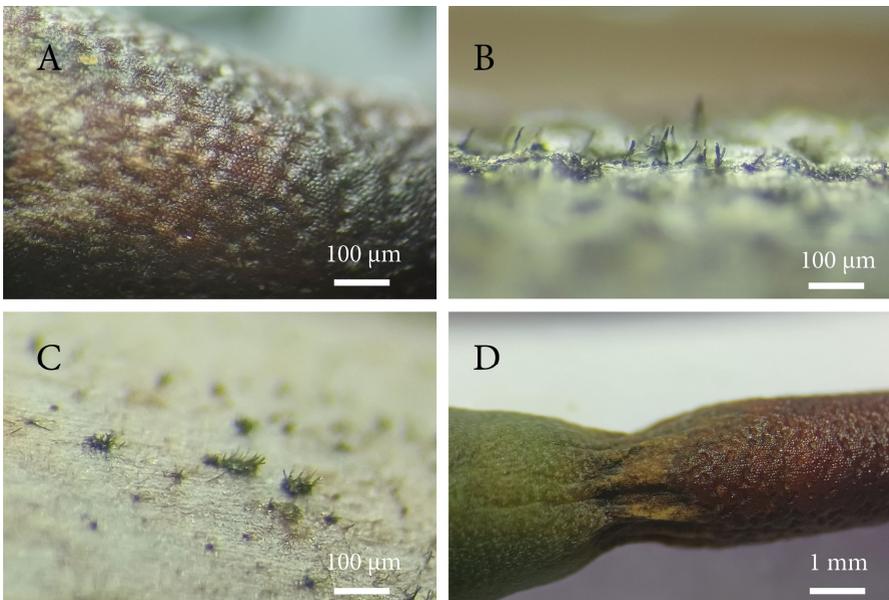

Figure 4: Various apical spine structures in agaves. A – verrucose and alveolate relief; B – dispersed trichomes on an alveolate surface; C – longitudinal fibrous network with cespitose trichomes; D – base of a juvenile apical spine with desiccated underlying tissues. Photos: Aurélien Sambin.

Desert cactus habitats harbor a limited but not insignificant diversity of herbivores, mostly generalist and weakly specialized, capable for the most part of circumventing or tolerating spines. The majority of documented phytophagous interactions concern flowers, fruits, seeds, or juvenile tissues, while consumption of adult parenchyma

remains rare, opportunistic, and associated with relatively low nutritional value (Gibson & Nobel, 1986; Nobel, 1988; Anderson, 2001). Although agaves and cacti produce various secondary metabolites—notably phenolic compounds and terpenoids, whose anti-herbivore role is well established (Maazoun *et al.*, 2019; Bermúdez-Bazán *et al.*, 2021; Conte *et al.*, 2025)—this pattern may also reflect effective deterrence by mechanical and chemical defences. However, the globally moderate and poorly targeted herbivory pressure on adult tissues calls into question the interpretation of spines as primary defensive devices in these systems.

Comparable arguments emerge in other nutrient-poor biomes. Grubb (1992), based on a comparative analysis of kwongan-type formations in western Australia—dominated notably by Proteaceae—and the South African fynbos, first highlights clear climatic differences (higher summer temperatures, weaker winds) likely to explain certain morphological divergences independently of herbivory. Although he subsequently invokes the hypothesis of historical pressure by now-extinct marsupials to explain the strong spinescence of Australian floras, this interpretation remains largely speculative and difficult to test, resting on extinct selective agents and indirect inferences. Furthermore, Grubb implicitly acknowledges that current marsupials, physiologically adapted to very low nutritional quality diets, continue to consume spiny plants, which suggests that these structures do not constitute effective barriers to herbivory.

This observation weakens the idea of a determining defensive function and invites consideration that spinescence may result, at least in part, from persistent abiotic constraints (water, thermal, or edaphic stress) and from developmental trajectories specific to the lineages concerned. In this framework, spines appear less as univocal adaptations to herbivory than as multifunctional, ecological and physiological structures, with a defensive role, when it exists, possibly secondary or contextual.

4. Palms: functional pluralism within a single lineage

In palms, the spiny structures often grouped under the generic term "spines" actually correspond to several distinct morphological types that moreover have systematic or diagnostic importance (Tomlinson *et al.*, 2011): (1) transformed leaf segments, as in *Phoenix* Linnaeus (1753: 1188), which clearly shows at the base shortened, strongly sclerified and sharp structures that progressively become, toward the apex,

increasingly long and flexible leaflets (Fig. 5A); (2) rigid, well-inserted spiny leaf appendages associated with sheaths, petioles, sometimes rachises and laminas, frequent in *Bactris* Jacquin ex Scopoli (1777: 70) or *Astrocaryum* Meyer (1818: 265) (Fig. 5B); (3) cauline epidermal-cortical outgrowths and leaf flagella—prolongations of modified rachis—notably in scandent palms such as *Desmoncus*: an exemplary case of leaf transformation oriented toward spatial colonization (Fig. 5C), discussed notably by Isnard & Rowe (2008); and (4) on the stipe, modified adventitious roots (Fig. 5D) and spiny structures that could be interpreted—since this is not explicitly formulated in accessible reference works—as subfoliar cauline spines (always inserted below the leaf sheath, either at the base, along, or at the summit of the internode) and sometimes morphologically distinct from leaf spines (Fig. 5E).
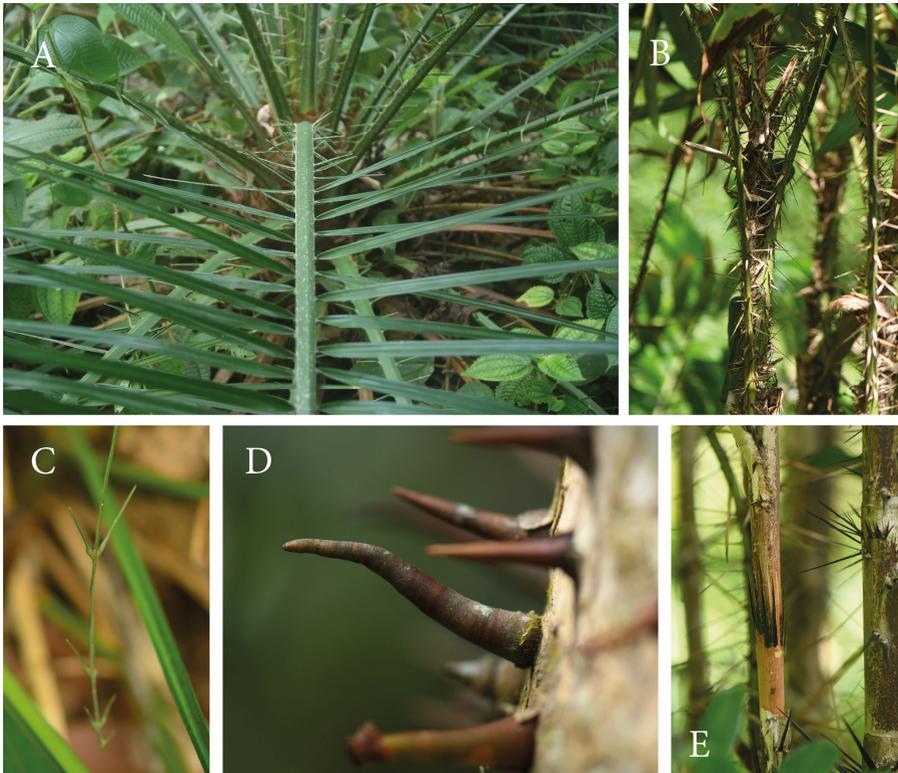

Figure 5: Different spines in palm species. A – transformed leaf segments; B – foliar spines; C – flagella; D – modified aerial root; E – subfoliar spines. Photos: Aurélien Sambin.

In spiny palms (*Bactris* and many others), the ontogenetic and spatial distribution of spines does not correspond to effective protection against foliar herbivory, particularly at the most vulnerable juvenile stages. If spines constituted the principal and sole defense mechanism, such ineffectiveness should logically lead to high juvenile mortality and, ultimately, significant demographic pressure. Many species are moreover of small size or slow growth, and although stipes may be heavily armed with subfoliar spines and leaves with spiny petioles or rachises, the leaf lamina, often unarmed, remain accessible from the ground to numerous herbivores. Given that leaves do not renew themselves and that the leaf lamina or leaflets remain accessible to herbivory, it is also legitimate to question the cost-effectiveness of such spine production on the sheath and the rigid structures of the rachis.

A complementary hypothesis, rarely explicitly discussed in the literature but compatible with the anatomy of the Arecaceae, is that certain spines, particularly foliar, could participate in the biomechanics of the leaf (Rowe & Isnard, 2009; Tomlinson *et al.*, 2011; Liu *et al.*, 2020). They are indeed generally strongly sclerified and solidly anchored in the fibrous tissues of the rachis or sheath, in zones corresponding to the main lines of mechanical constraints generated by rachis bending. In this context, spines could represent a morphological amplification of pre-existing fibrous tissues, locally participating in the peripheral stiffening of the leaf and in the distribution of mechanical constraints, particularly those induced by wind torsions and water flow.

The current persistence and diversity of spiny genera suggest that defense rests predominantly on chemical mechanisms (e.g., de Oliveira *et al.*, 2016; Hamini *et al.*, 2025; Husnudin *et al.*, 2025), while leaf and subfoliar spines could fulfill (1) a structural role (Fig. 6A); (2) various ecological functions, notably the capture and retention of organic resources (Fig. 6B–G)—a hypothesis proposed by Liu *et al.* (2020) for certain Asian palms at the origin of rattan—; (3) functions related to attachment and spatial colonization—already suggested by Grubb (1992) for this same group of plants—; and (4) a potential hydrological function, including runoff deflection and water removal at the level of the leaf sheaths and stipe (Fig. 6H–I). These processes could also contribute indirectly to maintaining the mechanical properties of the leaf by limiting the accumulation and stagnation of water in leaf sheaths, around the rachis and stipe.

Figure 6: Multifunctional roles of palm spines. A – lamina stiffening in *Bactris* sp.; B-G – capture and retention of organic matter in *Astrocaryum* spp. [B-C], *Phoenicophorium borsigianum* (Koch, 1859: 401) Stuntz (1914: 88) [D], and *Bactris* spp. [E-G]; H-I – coalescence and water flow on the dorsal side of the leaf rachis in *Pigafetta elata* (Martius, 1838: 216) Wendland (1878: 253) [H] and along the stipe in *Bactris* sp. [I]. Photos: Aurélien Sambin.

In their study conducted in western Amazonia, Trujillo *et al.* (2021) highlight a correlation between certain functional traits of palms, including armature, and hydrological and edaphic gradients. The authors interpret the presence of spines within a classical defensive framework, recalling that their production theoretically represents an allocation cost and suggesting that more fertile environments could compensate for these expenditures. This interpretation, however, rests on a general model of plant defense rather than on a direct measurement of the actual cost of spines in the studied species. The wide ecological distribution of many heavily armed palms, including in floodable or riparian environments, indicates that armature cannot be explained by hydrology alone. Thus, although the hypothesis of a high allocation cost remains theoretically plausible, its effective importance in armed palms remains to be empirically demonstrated. Spine production could, on the contrary, not constitute a strict defensive cost, but rather a multifunctional structural investment, whose evolutionary profitability would result from the integration of mechanical, hydrological, and ecological functions within a single morphological device.

4.1 Aerial roots: ontogenetic sclerification without clearly adaptive function

In certain palms, notably in the genera *Cryosophila* Blume (1838: 53) and *Mauritiella* Burret (1935: 609), stipes bear spines of root origin (Fig. 7). These aerial roots, well documented (e.g., Randall, 1995), are modified adventitious roots. From an anatomical standpoint, they retain the typical organization of monocot roots: a polyarch vascular cylinder, surrounded by a differentiated cortex. During their maturation, several transformations occur: the root cap detaches or degenerates, and the fundamental tissue undergoes progressive sclerification. In terms of distribution, these root spines are generally more abundant in the proximal portion of the stipe, then become rarer toward the distal part: the upper zone of the trunk is most often weakly armed, or even completely unarmed depending on the species.

The root spines observed in *Cryosophila* and *Mauritiella* can be interpreted, in light of the anatomical data and consistent with the phylogenetic framework proposed by Randall (1995), as non-functional adventitious roots that have become sclerified, resulting from a constitutive ontogenetic program. Their late ontogenetic appearance and distribution along the stipe correspond more to an internal developmental

dynamic than to a direct adaptation to herbivory or to a particular environmental factor. Although a secondary deterrent effect could theoretically be envisaged, ecological observation suggests that these spines do not significantly impede access to leaves or fruits, particularly for arboreal primates or small phytophages capable of moving between the sclerified structures. Their defensive role appears marginal here. The evolutionary persistence of these aerial roots could be more simply explained by a low production cost linked to this ontogenetic program, rather than by a demonstrated defensive selective pressure.

Figure 7: *Mauritiella armata* (Martius, 1824: 45) Burret (1935: 611). A – adventitious roots at stipe base; B – progressive sclerification of roots above the base; C – non-functional sclerification roots along the upper three-quarters of the stipe. Photos: Aurélien Sambin.

4.2 The particular case of the genus *Phoenix*: hydrological convergence with the agaves?

The main center of diversity of the genus *Phoenix* extends from India to Indochina, where eight species are recognized (Pintaud *et al.*, 2010). Several species of the genus today occupy arid or semi-arid environments in the Middle East, South Asia, and circum-Mediterranean regions, where nocturnal dews, mists, or fogs can constitute significant water inputs (Hill *et al.*, 2015; Bharali *et al.*, 2024). In certain coastal desert areas of the Arabian Peninsula, atmospheric fog even represents a hydrically exploitable component at the ecological scale (Valjarevic *et al.*, 2023).

Species of the genus show relative morphological homogeneity. The leaf crown appears to adopt a tripartite organization (Fig. 8A): (1) a basal portion with spreading to drooping leaves; (2) an apical portion with suberect to erect leaves; and (3) an intermediate zone that remains comparatively open (Fig. 8B).

This architectural configuration keeps the top of the stipe and the upper leaf bases visible, unlike other palms of comparable morphology in which the leaves more strongly obstruct the apical part. Without prejudging its functional origin, which may also relate to mechanical constraints or light optimization, this architecture could favor the direct exposure of leaf bases to mist or dew flows.
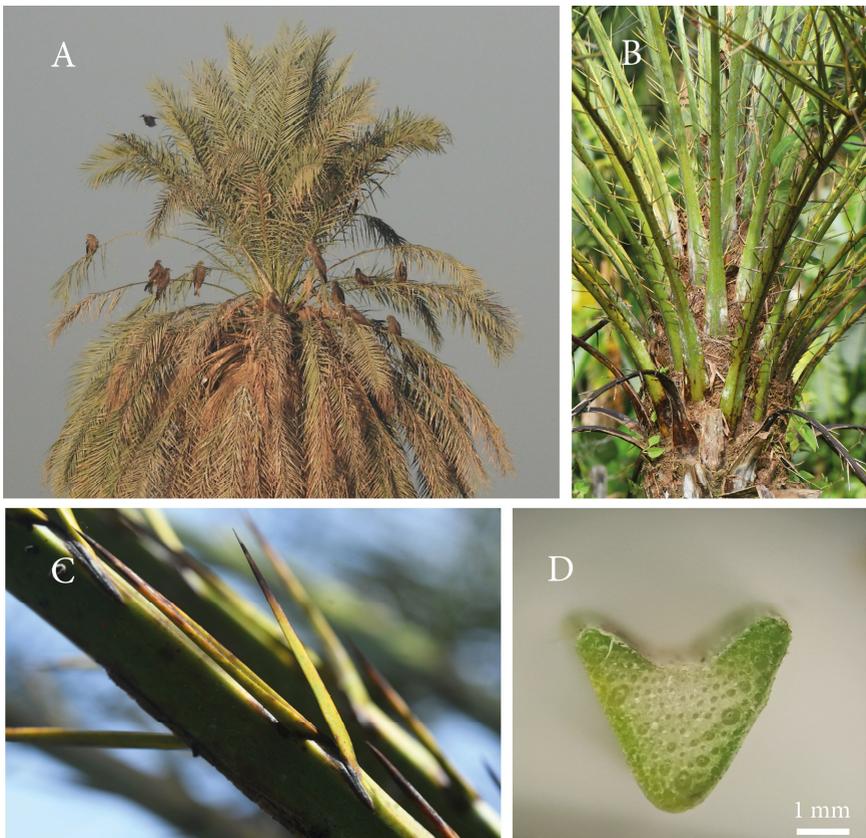

Figure 8: Tripartite leaf distribution and spines in *Phoenix dactylifera* Linnaeus (1753: 1188). A – leaf crown; B – median portion; C – spines; D – cross-section of a spine. Photos: A – lucapassalacqua [Available on iNaturalist: photos/468420991]; B-D – Aurélien Sambin.

The conduplicate leaflets, transformed into spines on the basal parts of the rachises, present a particularly structured morphology. Long, rigid, and smooth, they progressively become canaliculate, or even deeply canaliculate, on the three basal quarters of their ventral surface (Fig. 8C-D). This configuration recalls, by morphological analogy, that of the apical spines of *Agave* discussed above. In *Phoenix*, the combination of an elongated surface and a ventrally canaliculate structure oriented toward the base of the petiole could mechanically facilitate the adhesion, coalescence, and gravitational transport of atmospheric droplets toward the foliar base.

The vertical distribution of leaves within the crown could moreover reflect a functional differentiation associated with the age of the organs. Apical leaves, more recently formed and generally oriented upward, participate mainly in maximum light interception. The median part could, beyond the presence of inflorescences and as discussed above, represent a primary interface for the interception of dew or mist and water coalescence in close proximity to the stipe, notably via the spiny structures associated with the basal rachises of the leaves. Basal leaves, older, often persist for a long time before abscission and eventually dry out and progressively decompose along or near the stipe. This prolonged maintenance could contribute to proximal microclimatic and edaphic conditions of the individual. This organization suggests a possible vertical modular structuring in *Phoenix*, in which different leaf strata would participate in partially distinct ecophysiological functions, without these roles being considered exclusive or mutually independent.

No functional study has, to date, experimentally demonstrated such mechanisms for this genus. However, the phenotypic and anatomical plasticity of leaves in response to environmental constraints—notably drought, salinity, and high temperatures—has already been documented (Alnajjar *et al.*, 2022), suggesting that the foliar structures of *Phoenix* actively participate in adaptive responses to water stress.

5. Cortical prickles on trunks: structural traits and mismatch with herbivory

Ceiba pentandra (Linnaeus, 1753: 511) Gaertner (1791: 244, t. 133) belongs to a neotropical genus (Gómez-Maqueo & Gamboa-deBuen, 2022; POWO, 2026)

characterized by massive trunks, which can exceed 20 m in height and are often densely furnished with cortical cauline prickles.

The base of the trunk of *C. pentandra* presents prickles of variable sizes and morphologies, distributed heterogeneously on the bark surface, or even totally absent on mature trees (Fig. 9A). On a surface of approximately 50 × 50 cm, large prickles (up to ~6 cm in length) and distinctly smaller ones (~0.6 cm) can coexist without apparent organization or regular distribution. The organs are generally conical, most often slightly arched with a random orientation. The apex can be acute or obtuse, sometimes compressed, and frequently presents morphological anomalies: bifurcations, trifurcations, or multiple divisions giving coarse and irregular forms. Common longitudinal variations in thickness suggest non-uniform growth. The external surface is relatively hard, grayish, brown to orange, with a stratified organization of tissues that appear superficial. The internal region presents a less lignified cortical parenchyma, yellowish-white (Fig. 9B-C).

Figure 9: *Ceiba pentandra.* A – plant; B-C – cortical prickles. Photos: Aurélien Sambin.

The hypothesis according to which certain trunk spiny structures would constitute evolutionary relics of interactions with a now-extinct megafauna (Janzen & Martin, 1982), adopted by many authors (e.g., Dantas & Pausas, 2022), is sometimes advanced to explain the apparently low impact of current herbivores. This interpretation has been discussed in a more nuanced manner by Grubb (1992) in a comparative intercontinental framework, who highlights the explanatory limits of this type of reasoning. Such a hypothesis, however, presents several major

difficulties. First, it remains difficult to test experimentally or comparatively, since it rests on ecological interactions that have today disappeared and are therefore unobservable. Second, it assumes synchronous evolutionary morphogenetic responses between the appearance of cauline structures and the presence of specific herbivores.

Recent phylogenetic frameworks provide important context here. The molecular analyses of *Ceiba* proposed by Pezzini *et al.* (2021) indicate that the genus is monophyletic and that its diversification occurs mainly in the Miocene. This period corresponds, in neotropical America, to a phase of progressive climatic and ecological restructuring, including modifications of seasonality and hydric regimes (Scotese *et al.*, 2021). This chronology implies that the emergence and persistence of cauline spines in *Ceiba* occurred in an ecological context in which abiotic constraints—notably hydric and edaphic—already played a significant structuring role.

Available paleontological data indicate moreover that between approximately 20 and 12.5 million years ago (early to mid-Miocene), no known neotropical megaherbivore presents locomotor adaptations compatible with the active climbing of massive adult trunks. The large herbivores of this period (proboscideans, notoungulates, and other terrestrial forms) interacted with trees mainly from the ground, by browsing, bark stripping, or overturning, but without direct vertical access via the trunk (White, 1997; McDonald, 2007). Furthermore, in contemporary neotropical forests, a significant portion of herbivory and frugivory is carried out by arboreal organisms (birds, primates, and other mammals) that directly access leaves, fruits, and seeds via the canopy, without necessarily passing along the trunk. To date, no experimental or comparative demonstration shows that herbivore pressure exerted mainly on foliage could induce, at the evolutionary scale, the appearance of massive spiny structures localized on the trunk. This functional discordance therefore leads to questioning the existence of pressures acting specifically on cauline tissues, or to envisaging non-exclusively biotic determinants.

In Africa, massive bark stripping by large mammals, particularly elephants, is abundantly documented and recognized as a major structuring factor of woody plant dynamics, which can even lead to a significant reduction in tree density (Dublin *et*

al., 1990; Sukumar, 2003; Holvoet, 2021). Yet this intense and recurring pressure has not led to the generalized evolution of cauline spines in large African trees (e.g., *Adansonia* Linnaeus [1759: 1144]). It is notable that baobabs, like *Ceiba*, present trunks with relatively thin bark theoretically more vulnerable to bark stripping. Conversely, in neotropical forests, where bark stripping by mammals appears more sporadic and without clearly established demographic impacts, trees such as *Ceiba* develop particularly imposing cauline spines. These biogeographic and morpho-functional asymmetries weaken the argument of a simple and universal adaptive response to herbivore pressure and suggest that trunk spines do not constitute a trait systematically correlated with the intensity of bark stripping, nor with the sole apparent vulnerability of cauline tissues.

The defensive hypotheses discussed by Lefebvre *et al.* (2022) rest on the idea, in particular, that species with spiny trunks could protect organs that are relatively more nutritive than those of related non-spiny species. Their own comparative analyses, however, did not reveal a systematic difference in nutritional value between spiny and non-spiny species. In this context, no available substantiated data demonstrates that the bark or trunk of *Ceiba pentandra* constitutes a significant nutritional resource for herbivores. If seeds are well documented as rich in nutrients (Gómez-Maqueo & Gamboa-deBuen, 2022; Feedipedia, 2026) and leaves have been identified as an important source of proteins and minerals (Ibitoye, 2010), nothing indicates that bark—although presenting antioxidant activity (Gómez-Maqueo & Gamboa-deBuen, 2022)—constitutes a sought-after resource for substantial energy inputs.

In several species of *Zanthoxylum* Linnaeus (1753: 270), some of which present cortical prickles on the trunk comparable to those observed in *Ceiba*, antioxidant flavonoids such as quercetin and various derivatives have been identified in different vegetative tissues (Okagu *et al.*, 2021). In the absence of histochemical analyses specifically targeting cortical prickles, both in *Zanthoxylum* and *Ceiba*, these data do not establish a direct functional role. They nonetheless suggest that, if these metabolites are also present in spiny tissues—which is moreover the case in *Rosa* hybrids, as demonstrated by Swarnkar *et al.* (2021) and discussed above—they could potentially participate in protection against abiotic stresses via their antioxidant properties.

In *Ceiba*, just as probably in *Zanthoxylum*, the base of the prickles is moreover superficially inserted in the bark, and these structures can be detached with moderate or even no force (repeated personal field observations, unpublished). Their total absence or their limited anchorage, which constitutes only a partial obstacle to direct access to the bark, suggests that their effectiveness as a primary mechanical barrier could be restricted or even ineffective. This morphological configuration indicates that their function is not primarily mechanical and anti-herbivore, but rather associated with other roles, notably related to abiotic stress.

All these elements do not exclude a defensive contribution from cauline prickles. However, they suggest that defense against herbivory probably does not constitute the main selective pressure that led to their emergence and evolutionary maintenance. These structures could result from a combination of developmental (morphogenetic), physiological (resource allocation and stress responses), and ecological determinants, within which herbivore deterrence would represent only a secondary and context-dependent component.

6. Simple or branched cauline thorns: architectural canalization shaped by herbivore filtering

Lignified cauline thorns arising from transformed branches constitute determinate axes whose growth is precociously arrested and followed by terminal sclerification. This type of thorn, observed in several woody plants generally resistant to drought, such as *Haematoxylum campechianum* Linnaeus (1753: 384), is distinguished by its axillary meristematic origin and its integration into plant architecture: it must be interpreted as a specialized architectural structure rather than as a type of independent defensive appendage (Fig. 10).

Arid and oligotrophic environments generally favor slow growth strategies, associated with high tissue density and increased lignification (Wright *et al.*, 2004; Chave *et al.*, 2009). In these contexts, the frequent production of short, rapidly determined, and sparsely leafed axes already constitutes a coherent response to hydric and nutritive constraints. The dominance of sclerified short axes can thus emerge as an indirect consequence of abiotic limitations without requiring primary herbivore pressure.

At the macroecological scale, the frequency of spinescent plants increases in dry environments and on certain soil types, while showing marked phylogenetic structuring (Tomlinson *et al.*, 2025). This distribution suggests that spinescence is embedded in a broader ecological and functional syndrome, in which climate and edaphism, as observed in *Ceiba* or cacti, play a major structuring role.

If herbivory is not necessarily at the origin of the trait, it can nonetheless act as a powerful selective filter on existing architectures. Long-leaved axes, more exposed and more nutritive in the juvenile phase, are preferentially consumed. Conversely, short, rapidly lignified axes present low palatability, low accessibility, and strong structural persistence. Under repeated browsing, architectures dominated by long axes suffer disproportionate loss of biomass and functional meristems. Individuals producing a higher proportion of sclerified short axes retain more persistent organs. Over generations, this cumulative filtering favors architectures in which short axes dominate.

As discussed above, Lefebvre *et al.* (2022) did not reveal a systematic difference in nutritional value between spinescence-trunked and non-spinescent species. This absence of signal does not necessarily invalidate the defensive function of spinescences. Selection can, in effect, target rather than the average nutritional quality of tissues, the strategic protection of axillary meristems, young shoots, or the secondary cambium. Thorns, through their disposition, form a mechanical barrier around the emission zones of new axis emergence. Defense would then be directed toward preserving architectural potential rather than toward protecting potentially nutritive tissues.

Recent transcriptomic work on the development of branched thorns in *Gleditsia sinensis* Lamarck (1788: 465) shows that thorn formation involves active genetic regulation, notably of transcription factors associated with meristematic determination and lignification (MYB, TCP families) (Xiao F. *et al.*, 2023; Xiao D. *et al.*, 2025). These results indicate that cauline thorns are not growth accidents due to stress. Their formation involves the coordinated activation of genes controlling elongation arrest and lignification, indicating that these are programmed structures stabilized during evolution.

In an evolutionary context, it is plausible that (1) abiotic constraints favor an architecture rich in short axes; (2) herbivory preferentially eliminates architectures dominated by long axes; and (3) developmental pathways controlling early axis determination are progressively reinforced by selection: the branched thorns would then represent the stabilized form of an ancestral architectural structure.

Simple or branched cauline thorns could represent the culmination of an architectural canalization process primarily driven by abiotic constraints, then stabilized and amplified by continuous herbivore filtering. In these circumstances, herbivory would not be the origin of the trait, but a selection factor that favored architectures with short, lignified axes.
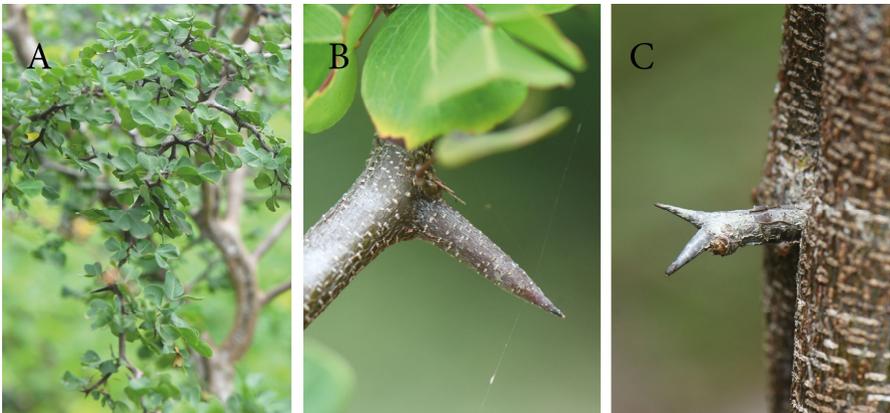

Figure 10: *Haematoxylum campechianum.* A – plant fragment; B – simple thorn; C – branched thorn on the trunk. Photos: Aurélien Sambin.

7. Stipular spines: developmental trajectories rather than defensive purpose

Stipules are expansions mostly interpreted as lateral parts of the leaf primordium (Bell, 2008). Stipular spines represent a morphologically distinct category of spiny organs derived from stipules in many angiosperms, particularly in certain Fabaceae.

As for prickles of specialized stems, cactus spines, cortical prickles of *Ceiba*, or cauline thorns, their evolution cannot be reduced to a simple response to herbivory. Like the stipular domatia interpreted by Davidson & McKey (1993) as initially non-mutualistic structures, subsequently integrated into biotic interactions, and whose

origin could relate to functions such as the hydraulic structuring of the lamina or passive protection against desiccation, stipular spines can be interpreted as the sclerified modification of a pre-existing basal foliar organ. In this perspective, their defensive function would represent less a primary purpose than a secondary specialization of a structure whose origin would relate to morphogenetic and physiological constraints, possibly linked to bud protection and local regulation of young tissues, without this initial role necessarily being generalizable to all concerned lineages.

In cactoid *Euphorbia* Linnaeus (1753: 450), at least two distinct configurations can be observed: (1) a single median spine compatible with a petiolar origin (Tomlinson *et al.*, 2025) and (2) a divergent infrapetiolar pair consistent with a stipular origin (Fig. 11).

Figure 11: Stipular spines of *Euphorbia lactea* Haworth (1812: 127). Photo: Aurélien Sambin.

The case of *Euphorbia* where sclerified stipules persist in pairs while leaves are strongly reduced, suggests a developmental dissociation between lamina and basal appendages. This configuration would indicate that the stipular spine can be maintained independently of a direct foliar defensive function and could result from a developmental trajectory associated with leaf reduction in a xerophytic context. In this framework, the defensive function, if present, would primarily concern the protection of meristematic and succulent tissues rather than the lamina itself.

Stipular spines could illustrate a process of secondary specialization of a basal foliar organ, whose sclerification and persistence would first be linked to architectural and ecophysiological constraints: with herbivory acting more as a stabilization or reinforcement factor than as the initial cause of the trait.

8. Myrmecophytic plants — beyond spinescence: analogous functional pluralism in biotic interactions

Plant–ant interactions offer an interesting parallel to the strictly defensive interpretations often advanced for other morphological structures, such as spines,

discussed above. In orchids of the genera *Myrmecophila* Rolfe (1917: 50) or *Caularthron* Rafinesque (1837: 40), although hollow pseudobulbs frequently house ant colonies or sometimes serve as refuge for small amphibians (Arrivillaga & Brown, 2019) or some gastropods (repeated field observations, unpublished), no active defensive mechanism has been demonstrated to date. The benefits for the plant seem rather to reside in the progressive accumulation of organic waste—excrement, insect carcasses, plant debris—favoring microbial mineralization processes and an indirect improvement of nitrogen and mineral nutrition, rather than in direct protection against herbivory.

This hypothesis finds particularly suggestive support in work conducted on the Melastomataceae *Maieta guianensis* Aublet (1775: 443, t. 176), whose leaves bear myrmecophilous domatia. In a study based on stable nitrogen isotope analysis, Solano & Dejean (2004) showed that the waste accumulated by ants, mainly of the genus *Pheidole* Westwood (1839: 219), inside these cavities constitutes a major nitrogen source for the plant, potentially representing a substantial proportion of its nitrogen budget. The authors interpret this enriched isotopic signal as the trace of an effective trophic transfer from animal waste to plant tissues, suggesting the existence of genuine myrmecotrophy.

Field observations, unpublished, suggest another example of potential myrmecotrophy in *Miconia tococa* (Desrousseaux 1797: 39) Michelangeli (2018: 116) (Fig. 12). In its domatia, small ants of the genus *Pheidole* deposit eggs within the foliar cavities (Fig. 12C) and construct, on the hirsute stems, carton nest structures (Fig. 12D). These arrangements are accompanied by a continuous deposit of organic matter at the base of the stems, likely to increase the nutritional inputs to the plant.

Without directly extrapolating this model to the Orchidaceae, this demonstration nevertheless establishes that, in certain myrmecophytic systems, hollow structures associated with ants are not limited to a shelter or indirect defense function, but participate in localized nutrient recycling. These cavities can moreover be interpreted within the framework of an evolutionary co-option comparable to that evoked above for stipular domatia (Davidson & McKey, 1993).

A horticultural observation provides a complementary element to this interpretation. In 2020, a young specimen of *Myrmecophila tibicinis* Rolfe (1917: 51) was deliberately installed on the trunk of *Jacaranda mimosifolia* Don (1822: t. 631), a substrate apparently poor in epiphytes and without visible fungal colonization. Despite a very reduced root system and a total absence of fertilizer input, the plant showed continuous growth, annually producing new pseudobulbs and regular flowering. Although this observation does not constitute an experimental demonstration, it reinforces the idea that the resources accumulated within pseudobulbs, notably by ants, could significantly contribute to plant nutrition, independently of abundant rooting in the substrate (Fig. 13).
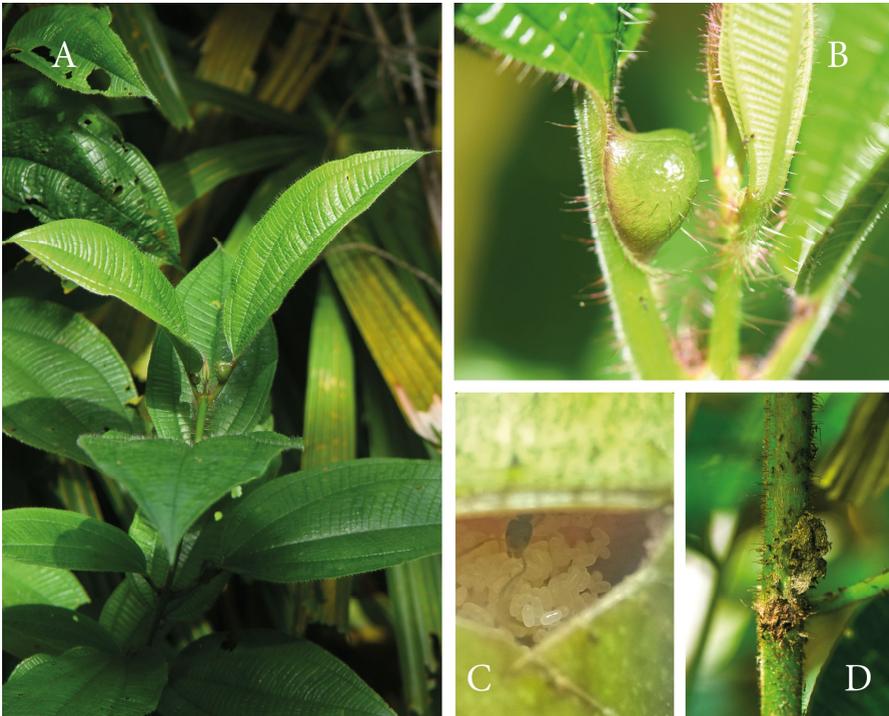

Figure 12: *Miconia tococa*. A – plant; B – domatia; C – brood management in a domatium; D – carton nest on the stem. Photos: Aurélien Sambin.

Cecropia Loefling (1758: 272), in the Urticaceae, is classically presented as an emblematic example of defensive myrmecophytism, involving aggressive

mutualistic ants (e.g., Davidson & McKey, 1993; Gianoli *et al.*, 2008). However, its leaves constitute a major food resource for herbivores such as sloths and frequently show substantial damage from small phytophages (Fig. 14). These observations indicate that, even in systems long considered quintessentially defensive systems— observations already nuanced by Fáveri & Vasconcelos (2004)—the protection conferred by ants remains clearly partial, contextual, and non-exclusive.

This parallel between *Myrmecophila*, *Caularthron*, *Maieta*, *Miconia*, and *Cecropia*, all from neotropical regions, and embedded in complex ecological exchange networks integrating trophic, microbial, and biochemical dimensions still insufficiently explored, suggests that plant–ant interactions cannot be interpreted as simple defensive devices. Like plant spinescence, they appear to relate to plural functional systems, whose evolutionary significance could far exceed a univocal protection function.

Figure 13: *Myrmecophila tibicinis* on *Jacaranda mimosifolia*. Photo: Aurélien Sambin.

Figure 14: Damaged leaves of *Cecropia obtusa* Trécul (1847: 79). Photo: Aurélien Sambin.

Conclusion

The morphological convergence of spiny structures across phylogenetically distant lineages does not correspond to a single functional convergence. If spines can limit herbivory, the morphological, phylogenetic, and developmental data examined here suggest on the contrary that spiny structures frequently emerge from pre-existing structural organizations whose sclerification and persistence result from specific ontogenetic trajectories with broad ecological consequences. In this context, herbivory does not necessarily constitute the main selective pressure that led to the emergence of spines and their evolutionary maintenance.

In several plant groups, spiny organs appear integrated into varied functions: attachment and spatial colonization in climbing plants notably, microclimatic regulation and water management notably in Cactaceae, and in some Asparagaceae and Arecaceae, capture and retention of organic matter in certain epiphytic Orchidaceae or numerous Arecaceae, reinforcement structural and participation in the local modulation of abiotic constraints (Tab. 1).

Recent transcriptomic analyses, at least in *Gleditsia*, confirm that spines do not constitute simple passive residues of reduced growth, but modules regulated by genetic networks involved in meristematic determination and secondary differentiation. Their defensive function, when clearly demonstrated, thus appears to be embedded within a broader framework where environmental constraints, structural economy, morphological configurations, and strategic protection of meristematic zones interact.

Rather than opposing the defensive explanation and the abiotic explanation, the available data invite consideration of spinescence as a multifactorial trait arising from an architectural canalization process, within which environmental and biotic pressures act at distinct and potentially successive levels. This perspective calls for integrative approaches combining comparative phylogenetic analyses, functional experiments, and careful developmental studies, in order to explicitly disentangle the respective roles of abiotic constraints, herbivore selection, and morphogenetic regulation.

Table 1. Functional diversity of spinescent structures across plant families discussed in this article.
* documented function; * partially documented function; * hypothetical function; ● secondary / context-dependent function ; (?) dubious function.

	Spatial colonization	Nutrient capture	Water management	Reinforcement and stability	Abiotic adaptation	Ontogenetic constraint	Herbivory deterrence
Orchidaceae		*					
Rosaceae	*			*	*		●
Fabaceae	*			*	*	*	●
Cactaceae			*	*	*	*	●
Asparagaceae			*	*	*		
Arecaceae	*	*	*	*	*	*	●–(?)
Malvaceae					*	*	●–(?)
Rutaceae					*	*	●
Euphorbiaceae				*	*	*	

Acknowledgements

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