

PODARIUM (PODARIA) – A CONTROVERSIAL BOTANICAL TERM

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Abstract: Succulent plants and especially cacti require specific botanical terms for their morphological description. *Podarium* is one such term, used mostly to designate the spine-bearing formations in cacti and thorny succulent euphorbias. The analysis of specialized literature reveals its use by various authors with different meanings. The term is present in dictionaries or specialised glossaries only in the last 30 years, and the definitions are quite varied. The synonymous terms used over time in different languages show that there is no unity regarding the definition of the term, but also regarding the way in which the formation it defines is understood.

Key words: botanical terms, Cactaceae family, *Euphorbia*, Lemaire, spine-shield, tubercle.

Introduction

Botanical terminology, like all specialized terminology, has certain characteristics that differentiate it from common language. In the general sense, scientific terms are characterized by clarity and lack of ambiguity. These aspects are not always obvious and are not understood by all specialists in the same way [SLISKO & DYKSTRA, 1997]. Often terms evolve during their use in one or more fields, and sometimes they are rejected for various reasons (there are accepted synonyms, they are not clearly represented, etc.).

There is an ongoing concern to standardize botanical terms and make their use uniform. In some botanical families, the problem of terms has given rise to numerous efforts, due to the morphological peculiarities of some species, e.g. Poaceae [JACQUES-FÉLIX, 1972], Cucurbitaceae [NESOM, 2012], Loganiaceae [CONN, 1995].

Cacti are also among the plants with a novel structure, so it was only natural that there would be a variety of theories and terms to explain it. The need for terminological uniformity in the treatment of the Cactaceae family is eloquently highlighted by a comment on “Flora Argentina”, in which STUCKERT (1899) draws attention to the fact that the author names the cactus family **Cactáceas**, but also **Cácteos**, which constitutes “una falta de uniformidad”/ a lack of uniformity.

Podarium (pl. *podaria*) is a botanical term used to describe structure specific to cacti species, but also other succulents. We consider it deserves attention for several reasons: it is little known (in some languages it is not used and there is no corresponding term), it designates a formation present in few plants, it has a precise “moment of birth” and, last but not least, it appears very rarely in dictionaries or glossaries of specialized terms.

In this paper we wish to draw attention both to the botanical term *podarium* and to the inconsistencies, misunderstandings and chaos created around the use of terms, out of the desire

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to describe (especially in cactus and euphorbia families) similar morphological formations. At the same time, we point out that in the case of the two mentioned families, cacti and euphorbias, respectively, the botanical terms “spines” and “thorns”, especially in German literature, are often mistaken (“stacheln” = “dornen” = “thorns”, for both cacti and euphorbia, while for roses, for example, it is “stacheln” = “thorns”, “prickles”, in English).

Moreover, the description of some formations that appeared as a result of the convergent evolution of the characters, in different plant families, on different continents, as well as the ignorance of some authors on all the descriptive works published to the date, have resulted over the years in the accumulation of many inconsistencies and confusion in the use of terms.

Material and methods

In order to clarify the term *podarium*, numerous bibliographic references have been consulted (most of them available online) looking for aspects regarding the chronological use of the term since its first documented use, its presence in works written in widely spoken languages (English, German, French, Spanish, Italian) and / or the presence of the translation of this term in relation (especially of synonymy) with other terms.

The analysis of the bibliographic material is not exhaustive, as it is impossible to verify all the works that refer to or mention the term *podarium*.

For a more accurate analysis, the authors have turned to some classic works in the field of terminology. From these works we selected two definitions to represent initial working hypotheses:

“The term ... is a linguistic symbol that is assigned to one or more concepts, which are defined by related concepts” [FELBER, 1984].

“[The term] is a lexical unit that consists of one or more words that represent a concept within a field” [BESSÉ & al. 1997].

Results and discussions

Podarium (plural, *podaria*) is a botanical term with limited use, which in the Romanian scientific literature is practically unknown.

Its etymology is from the Greek language: *podos* – foot; it has been taken up in various languages as follows:

French: sg. *podaire* / pl. *podaires*; English: sg. *podarium* / pl. *podaria*; German: sg. *podarium* / pl. *podarien*; Spanish: sg. *podario* / pl. *podarios*; Latin: sg. nominative *podarium* / pl. dative *podariis*.

The frequency of appearance of this term in specialized works, especially regarding the Cactaceae family, is closely correlated with the number of cacti and succulent enthusiasts.

Charles Lemaire and the need for proper botanical terms

The history of this term begins in 1858, when Lemaire uses the term “podaires” (French) as a synonym for “teeth” in the description of the species *Euphorbia hermentiana* [LEMAIRE, 1858a], but also to designate the protuberances present on *Pelecypora aselliformis* [LEMAIRE, 1858b]. In fact, to designate the protuberances specific to cacti, Lemaire proposes another term – *cýrtome*. He shows that the protuberances of *Pelecypora aselliformis*, called *podaires*, are different from those of some *Echinopsids*, hence called *cýrtomes*, and both are equivalent to Salm-Dyck's *tubercules* (tubercles).

Lemaire proposed these new botanical terms because he was dissatisfied with those in use at the time: *tubercle* (sg.) / *tubercles* (pl.) [ENGELMANN, 1856; HOOKER, 1839a] and *mammilla* (sg.) / *mammillae* (pl.) in English [HOOKER, 1839b]; *tuberculum* (sg.) / *tuberculis* (pl.) [DE CANDOLLE, 1829; HOOKER, 1839a] and *mammilla* (sg.) / *mammillas* (pl.) in Latin [HAWORTH, 1819; HOOKER, 1839b; WALPERS, 1845-46]; *tubercule* (sg.) / *tubercules* (pl.) [LEMAIRE, 1841-1847], *mamelon* (sg.) / *mamelons* (pl.) [LEMAIRE, 1857b, 1858c], *dents* (pl.) [LEMAIRE, 1857a] and *gibbosité* (sg.) / *gibbosités* (pl.) [LABOURET, 1853; LEMAIRES, 1857a, b, 1858d] in French.

In the same article Lemaire promises to demonstrate that the *mamilla* (v. *tuberculus*) represents a true petiole, and the term(s) which is / are not proper must be replaced by something else suitable: "...verbo isti non apto aliud omnino congruens erat substituendum – podarium (ποδάριον, parvus pes)" / for this unsuitable word, another completely suitable word was to be substituted – podarium.

In the following years Lemaire constantly uses the term *podaire* in the description of the species presented in the journal coordinated by Verschaffelt, including in the Latin diagnosis: *podariis* [LEMAIRE, 1860a], *cyrtomis* [LEMAIRE, 1859, 1860b] respectively. Probably the consecration of the term *podaire* and the Latinized form *podarium* are due to the botanist Pierre Edmond BOISSIER (1862) who uses the term proposed by the horticulturist Lemaire in the volume dedicated to the Euphorbiaceae family in De Candolle's Prodrromus.

In the same year LEMAIRES (1862) reviews Boissier's work and notes with satisfaction the use of the term proposed four years ago. Thus Lemaire believes that BOISSIER (1862, 1866) adopted the term because it is "convenient for the describer/descriptor"; in addition, it was "missing from the nomenclature and expresses well what needs to be pointed out". He also describes the term *podaire* (*podarium*) as "the extension in the form of gibbosity which, in fleshy euphorbias, carries the leaf, its stipule (thorn) and the flowers in the axil or a secondary branch that constantly aborts". Lemaire likens it to the protuberances of *Mammillaria*, *Echinocactus*, *Echinocereus* within the Cactaceae family.

In 1868 LEMAIRES publishes a comprehensive paper on cacti, on which occasion he brings numerous clarifications on the subject, as he had promised in 1858. He points out once more the analogy of the organs designated by *podarium* in succulent euphorbias and cacti. He also highlights the fact that in the species of cacti with areoles, this "curious and strange" organ is actually the metamorphosed petiole and even states that *podarium* is "synonymous with petiole".

We can speculate that Lemaire's proposal to replace the terms may have also been influenced by the peculiarities of the French language. Specifically, the protuberances specific to cacti are referred to in English as *tubercles*, different from the *tuber* which generally refers to the thickened parts of the modified stems. This differentiation is not found in the French language, where the term *tubercule* designates both types of structures.

Here is the definition of the term in the DICTIONARY of the FRENCH ACADEMY, ed. 6, in the year 1835: "Tubercule (terme de jardinage). Excroissance en forme de bosse qui survient à une feuille, à une racine, à une plante. Il se dit plus particulièrement de celles qui se forment à la racine de certaines plantes alimentaires. *Les pommes de terre, les topinambours sont des tubercules*" / Tuber (garden term). Bump-shaped growth that occurs on a leaf, a root, a plant. It is said more particularly of those which are formed at the root of certain food plants. Potatoes, Jerusalem artichokes are tubers.

To better understand Lemaire's proposal we will quote some definitions from the specialized dictionaries of the time. These seem restrictive and do not refer to the interesting structures specific to cacti and fleshy euphorbias:

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Tubercle, tuberculum (lat. a pimple): a small wart-like excrescence. Synonym: a form of Apothecium [HENSLOW, 1840]; succulent expansion of certain roots [COOKE, 1862]. *Tuber*. An annual thickened subterranean stem (...). When very small it is called *tubercle* [HOBLYN, 1850].

Mamilla (a little teat). Little granular prominences on the surface of certain pollen [HENSLOW, 1840]; granular prominences on pollen-grain [COOKE, 1862]; a term applied to a surface which is studded over with prominences which are smooth, thick, and rounded, like a teat [HOBLYN, 1850].

JOURDAN'S polyglot dictionary (1837) is not of much help either:

Tubercule (fr.), *tuberculum* (lat.), *Hockerchen* (germ.), the definition of this term is very extensive, but we only note that it is applied to lichens, algae, or the thickened, starchy parts of plants.

Mamelon (fr.), *mamilla* (lat.), *warze* (germ.), *nipple* (engl.). Protuberance arrondie, qui fait saillie au milieu d' une surface quelconque. / Rounded protrusion, which protrudes from the middle of any surface. In the botanical field, the author exemplifies this term only for “the top of some mushrooms that have a conical hat”.

Only in the case of the adjective “*mamillaire* (*mamillaris, mamilla, mamelle*) = which resembles a nipple”, we learn that we encounter this aspect in *Euphorbia mamillaris* “which bears tubercles in the shape of nipples”.

It is also worth mentioning that the term *Warze* (Germ.) is equivalent to *verru* (Fr.) / *verruca* (Lat.) and *papille* (Fr.) / *papilla* (Lat.).

Lemaire was trying to propose a term to replace the phrases used by the authors to express as correctly as possible the appearance of the protuberances specific to cacti or fleshy euphorbias: „tubercules mammiformes” [LABOURET, 1853], “plantae mamillato-tuberculatae” [ENGELMANN, 1857], „costis mammillosis” [PFEIFFER, 1845], “tuberculis mamilliformibus elongates” [LEMAIRE, 1855].

We pointed out that Lemaire actually proposed two terms which he states are necessary in treating the genera of the family Cactaceae. The free protuberances, true petioles, characteristic of the genus *Mammillaria* are called *podaire* (podarium), while the confluent protuberances with the adjacent tissue, present in genera such as *Cereus*, *Pilocereus*, *Echinocereus*, *Aporocactus* represent *cyrtôme*.

As early as 1829 DE CANDOLLE argues that a distinction must be made between *tubercles* and *mammillas*, as he considers the long protuberances from species of the genus *Mammillaria* to be true leaves. This differentiation is specified by other authors, but it is very obvious in the bilingual article published by PFEIFFER & OTTO (1843). The equivalent terms in Latin, German and French are different, depending on the genus to which the plants belong:

Echinocactus: *tuberculis* (Latin) – *Höckern* (German) – *tubercules* (French).

Mammillaria: *mammillis* (Latin) – *Warzen* (German) – *mamelons* (French).

HAWORTH (1819) and ENGELMANN (1856) prefer the term *tubercle/tuberculis* to describe most cacti known at the time.

The term *podarium* – a chronological perspective

In the period following the publication of De Candolle's work, leading biologists of the time took up the term in their works to describe spiny species of *Euphorbia*, especially in the Latin diagnosis [HOOKER, 1865; GROENLAND, 1866; SCHWEINFURTH, 1866; BAYLEY, 1888; NORTON, 1900; ENGLER, 1902; BERGER, 1899, 1902], including in works published in Japan [HAYATA, 1904].

In a few years the term is adopted in German – *podarium* (sg.) / *podarien* (pl.). It is used in papers to designate important formations in the differentiation of species or as a diagnostic character in the keys to determine the species of *Euphorbia* analyzed [PAX, 1895, 1905a,b; BERGER, 1905a; VIERHAPPER, 1907]. After the 1930s, the term is used more and more frequently in German-language specialist journals [NEL, 1933, 1935-1936; WERDERMANN & MANSFELD, 1935; STEPHAN, 1937].

BERGER is an author with numerous works in German who adopted the term proposed by Lemaire in the description of the analyzed species, most often synonymous with leaf base. In the valuable work in which he analyzes succulent euphorbias, he uses several terms to describe the same characteristic formation: *podarium* / *podarien*, synonymous alternately with *Blattbasen* but also *Blattkissen*, as well as *Höcker*, and in 1905 also with *Warzen*. It is worth recalling his clarification regarding the fact that “Die Blattbasen (*Podarien*) laufen bei den allermeisten dieser *Diacanthium*-Arten in fortlaufende Längsrippen oder Kanten zusammen./ In the vast majority of these *Diacanthium* species, the leaf bases (*podaria*) converge in continuous longitudinal ribs or edges.

From his numerous articles on succulent species, it can be seen that BERGER predominantly uses the term *warzen* (1905c) to describe cacti, only in a work from 1926 does he use the term *podarien* (oder *Blattkissen*) / *podaria* (or cushion).

Berger's proposed classification of the group of succulent Euphorbias is largely taken up by PAX in a collective volume on the vegetation of the earth (1921). Pax also uses the term *podarien* / *podarium*, most likely in Berger's sense (*Podarien* = *Blattbasen*), only in describing species of section *Diacanthium*. About this he states: “perhaps the most difficult group of relatives of the whole genus, as herbarium material is scarce and photographs of the growth conditions are mostly lacking”, and characteristic is the presence of “thorny podaria, which merge into rib-like ledges or edges”.

An exception to the use of the term is in the case of subsect. *Tetracanthae*, where he uses the term *Fußstücke* in the key. In the presentation of the subsection, it states that its species “ausgezeichnet durch vier, paarweise zu-sammengehörige Dornen am Podarium” / are distinguished by four pairs of spines on the podarium.

Croizat is one of the authors who frequently uses the term *podarium*, in different variants (English, French, Latin). From the analysis of his works in French [CROIZAT, 1938a] and English [CROIZAT, 1939] we deduce how Croizat understands the structure of the spiny protuberances of succulent euphorbias: *podaire* couverte des écussons épineux / *podaria* with spine-shields. Probably these works are among the first in which the English term spine-shields appears as the horny part covering the apex of the protuberance.

In 1939 Croizat explains the term *podarium* by *tooth to the wing or angle*, recalling the expression “dents (podaires!)” used by Lemaire, and few years later [CROIZAT, 1942] the author defined podarium as “decurent succulent petioles”. We observe that Croizat emphasizes the constant character of this formation, so that it can be considered a diagnosis character.

BOITEAU (1947) shows that the thornless euphorbias from the Cape region, South Africa (*Euphorbia bupleurifolia*, *E. pubiglans*) show “des mamelons formés par les *podaires* rudimentaires” (*mammilles* formed by rudimentary *podaria*), different from *podaires* specific to the subsection *Diacanthium*. In this case the term *mamelons* probably does not have the same meaning as in Lemaire and is among the few instances when it is used to describe the stems of some species of the genus *Euphorbia*. BAILLON (1858) uses the same term both to describe the portion of the leaf base that persists on the stems of fleshy euphorbias and to designate structural elements in the organization of the gynoeceium in species of this genus.

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From the analysis of the available bibliographic data, it seems that until around the 1940s the term *podarium* with its various forms appears mainly in articles related to the genus *Euphorbia*. That is probably why some authors [WHITE & al. 1941] define the term *podarium* as “A raised foot or stand; the term is used in many writings on the *Euphorbiae*”. On the other hand, about the *tubercle* he states that “... designate the swollen base of a leaf or leaf rudiment, such as is found in many different forms on the stems and branches of most of the highly succulent species of *Euphorbiae*”.

We will further look at issues regarding the use of the term *podarium* in articles about cacti.

BERGER has numerous articles on cacti; only in 1926 does he use the term *Podarium* (pl. *Podarien*) to explain the way some species develop, then in 1929 he prefers the term *warzen*, which he mentions is synonymous with *podarium* (*Hökker*).

It is worth emphasizing that Lemaire's works are cited by authors from Latin America, that is, the homeland of cacti. In the 1937 paper, BRAVO HOLLIS, a renowned Mexican botanist, uses the term *tuberculos* (Spanish) in the species description; she cites Lemaire with a paper from 1853, before he proposed the two terms. Lemaire was previously also cited by OCHOTERENA (1922) with the work “Les Cactées”, but without mentioning the year. It is difficult to say whether the author was aware of the proposed terms, which ARECHAVALETA mentioned as early as 1905, in the volume of the Flora of Uruguay, where he uses *tuberculos* or *mamilas* in the description of the species.

BUXBAUM is the one who has an indisputable contribution in clarifying the aspects related to the morphology, ontogeny and anatomy of cacti. There are many articles in which he refers to the morpho-anatomical features of cacti (1956), and the contribution to the volume edited by Krainz [BUXBAUM, 1956-1960] is defining.

It is very likely that his volume, published in English [BUXBAUM, 1950], facilitated the access to its valuable information to a much larger number of authors and also enhanced the use of the term *podarium*. The work includes very detailed explanations on the formations specific to cacti (areoles, protuberances, cephalium), but also on the term *podarium*. About this term Buxbaum states that it represents an enlargement of leaf base and neighboring regions of the stem, which together take the form of a protuberance (tubercle). In fact, *podarium* designates the juvenile stage of these formations, which either grow alone in an outgrowth (tubercle) or converge among others in a vertical direction forming ribs.

The richly illustrated work allows the understanding of the formation of the protuberance that is present in cacti, but also in other succulent plants (it only exemplifies euphorbias).

The 1940-1955 period is characterized by the appearance of Buxbaum's works [BUXBAUM, 1949], which has extremely valuable contributions in clarifying some cacti-specific terms. In the works that appeared later, in the description of the representatives of the Cactaceae family different terms are used depending on the authors: *tubercle* [TAYLOR, 1979], *tuberculos* [KIESLING, 1984]; *podarium* [DONALD, 1971, 1976; PEUKERT, 1977], *podariis* / *podario* [BRAVO HOLLIS, 1956; MEYRÁN, 1956]; *mamelon* and *gibbosités* [GAY, 1954]; *mamelones* [CASTELLANOS, 1962], *podario* or *tuberculo* [BRAVO HOLLIS, 1978], *tubercles* or *podaria* [BRUHN & HOLMSTEDT, 1973]; *warzen* and *Hökker* [BACKEBERG, 1958].

In order to clarify the relationship between the terms protuberances (tubercles) and ribs, commonly used in the description of cacti, Zimmerman [BUTTERWORTH & al. 2002] recommended in 1985 the use of the term *podarium*, suggesting that in reality the ribs are series

of *podaria* joined together. Protuberances represent free or distinct *podaria*. This terminology allows for intermediation between ribs and protuberances.

GIBSON & NOBEL (1986) proposed a different view of the term. Thus from an anatomical point of view the *podaria* are similar to the parts of the stem which surround the base of the leaf and are simple swellings of the stem over which the leaves and their modified axillary buds (areoles) rise. They show that the *podaria* are “bases in the sense of a pedestal for the leaves, not the basal portion of the leaves themselves”. Extensive cell division in the *podarium* contributes to the formation of tubercles.

After 1990, the term *tubercle* / *tuberculos* is frequently used in texts about cacti [MONTES & al. 1997], most often specifying that it is synonymous with *podarium*.

A unanimous acceptance of the term *podarium* (among other terms) is not to be found even after the year 2000. TAYLOR (2000), in his doctoral thesis highlights the need to clarify some terms used in the text and offers brief explanations/definitions for areoles, glochids, pericarpe, flower-tube and *podaria*.

“*podaria* (sing. *podarium*) are the swellings often subtending areoles that represent the points of attachment of leaves or bracts that have been lost, or almost lost, in the course of evolution of the highly succulent habit”

The comments of DIGHT & LÜTHY (2005), which illustrate the difficulties caused by the lack of terms or their different understanding (depending on the authors), are to be understood in the same context:

“...the areole essentially consists of three different organs: the spiniferous part, the groove, and the axil. In most cactus literature the expression areole is used only for the spine-bearing part. For the whole areole, another word, e.g. *podarium*, should be used. For clarity and consistency with former publications, we describe the three parts of the *podarium* separately as areole (spine-bearing part), groove and axil.”

The term *podarium* in works relating to euphorbias and other succulents

Efforts to clarify terminology specific to cacti have no equivalent in the situation of the genus *Euphorbia* (or other succulents). At least until 1977, when S. CARTER publishes a short note in which she analyzes the advantages of using the term *podarium* to describe succulent euphorbias. Careful analysis of the information in this text in conjunction with data from previous works reveals confusion and diverse interpretations of this aspect.

Although the history of the term *podarium* is already starting to be rich, the statement that until 1962 “no author questioned its validity” seems inexplicable. Because, as we have shown, as early as 1950 Buxbaum clarified aspects of morphology and organogenesis related to the structures called *podarium*, also including references to the genus *Euphorbia*.

The author recognizes (only then) the accuracy of the term “*podarium*” compared to “*scutellum*”, which she specifies already has four uses, and persisting in using it as a synonym for *podarium* can lead to “confusion”. The term *scutellum* is very rarely used in relation to the appearance of fleshy euphorbias, we find it at COSSON (1874) in the Latin diagnosis of the species of the section *Diacanthium*. Three years before he designated however the formations present in *E. resinifera* with the term *podariis* [COSSON, 1871], corresponding in French description with “coussinets” / cushions. The mention of the term *scutellum* highlights a confusion that seems to have very old roots, perhaps even in the works of Boissier.

Podarium for Lemaire means a small foot (parvus pes – Latin), while *scutellum* means shield, which makes us associate it with the term spine-shield. The latter designates the horny pad on which the thorns usually develop in some species of *Euphorbia*.

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If we analyze the works published over time, it becomes obvious that the term *podarium* was used with two different meanings:

1. as a protuberance similar to that of cacti, therefore equivalent to *tubercle*, *mammilla* or *mamelon* [BERGER, 1905a,b; CHEVALIER, 1933; WHITE & al. 1941; URSCH & LEANDRI, 1954],

2. as a horny pad covering the protuberance, in this case designating a formation specific to spiny euphorbias [COSSON, 1871; PAX, 1909; BRUCE & al. 1951; KEAY, 1955; BALLY, 1973; BALLY & CARTER, 1974; VERDUS, 1973; LEACH, 1976a,b] called *spine-shield* (English) or *coussinet foliare* (French).

To understand where this difference in interpretation comes from, we will return to the works of Boissier. Thus in Prodrumus (1862) BOISSIER uses the term *podarium* / *podaria* within the group of succulent euphorbias and shows that for the definition of the section *Diacanthium* “Pulvini foliorum prominentes in tuberculos elevatos (podaria Ch. Lemaire)” is characteristic. Within the subsection *Biaculeatae* *podaria* represents a differentiating character: “Podaria basi distincta” versus “podaria in costas confluentia”.

Various phrases appear in the description of the species:

Euphorbia drupifera: “ramis ob podaria subdissita” / branches divided by podaria; *E. canariensis*: “ramisque ... calloso-tuberculatis tuberculis fuscis” / branches with ... callous-tuberculate brown tubercles; *E. caput medusae*: “ramos ... podariis depressis obtuse carinatis basi decurrentibus” / branches ... with podaria obtusely carinated from the base; *E. scopoliiana*: “costis subverticalibus e podariis mamillaeformibus subdistinctis conicis acutis constantibus” / subvertical ribs from the nipples-shaped podaria subtended by acute cones.

In the case of the thornless species (*E. drupifera*, *E. caput medusae* and *E. scopoliiana*), the term *podarium* (*podariis* – declination in Latin) seems to have the meaning of *tubercle*, while in the spiny species *E. canariensis* the formations are called *tuberculis/tubercles*, and the term *podarium* is missing from the diagnosis.

In the French work *Icones Euphorbiarum* (1866), BOISSIER shows that in the *Diacanthium* section “...les coussinets des feuilles se groupent pour former des tubercules coniques tantôt distincts, tantôt réunis en côtes verticales ou spirales”/ the cushions of the leaves are grouped to form conical tubercles sometimes distinct, sometimes united in vertical ribs or spirals.

Comparing the Latin and French texts it seems that actually for Boissier *podarium* is equivalent to *coussinets des feuilles*, so *spine-shield* in English. This may mean that he took over the term proposed by Lemaire, but with a different meaning.

A similar phrase – “coussinets écarté” (spread cushions) is used by CHEVALIER (1951) to describe the spiny succulent euphorbias of the Congo. It is difficult to say whether the expression is synonymous with *podaria* or *spine-shields*.

Phrases such as “Kegelförmigen *Podarien*” / conical *podaria* [BERGER, 1899], “*Podarien* verlängert, kleine flachkegelige Warzen bildend” / *podaria* elongated, forming small flat-conical warts [BERGER, 1905a] or “Die Warzen (*Podarien*) der Stengel” / the warts (*podaria*) of the stems [BERGER, 1905b] show that Berger used *podarium/podarien* sensu Lemaire. On the other hand, although Pax mostly takes Berger's classification (which he cites) for the *Diacanthium* section, he uses the term *podarium/podariis* sensu Boissier.

The inconsistency of the understanding of the term *podarium* persists and is all the more obvious when we encounter it within the works of the same author. Thus GILBERT (1987) in a paper in which he presents two new geophytic species of *Euphorbia* compares the characteristics of the representatives of the subgenera *Euphorbia* and *Lacanthis*. He shows that

one of the important differences is the way the spines occur (subgen. *Euphorbia*) or not (subgen. *Lacanthis*), on the “horny pad around the insertion of the leaf at the tip of the prominence (podarium)” (spines borne on clearly defined horny spine-shield round leaf insertion at tip of tubercle (podarium)).

He also claims that a subsection should be recognized for euphorbias of the subgenus *Diacanthium* native to Madagascar and gives an example of the unusual characteristic of *E. corniculata* where “the spine-shield are unusually large and almost entirely cover the *podaria* on which they are mounted”.

In the same year, in the description of the species *Euphorbia heterospina* together with SUSAN C., GILBERT [CARTER & GILBERT, 1987] uses the term *podaria/podariis* with the meaning of *spine-shields*.

The analysis of later published works shows that very frequently the term *podaria* (Latin or English) is translated by *spine-shield* (English) [CARTER, 1987; BUDDENSIEK & al. 2005; KILIAN & al. 2006; MALPURE & al. 2016]. WEBER & al. (2020) prefer the term *podaria* to name the formations present in *Euphorbia poisonii*, called *tubercles* by BROWN (1911).

The terms *podaria/podarium* also appear sporadically in works (predominantly of taxonomy) on succulent species from other genera and families: Apocynaceae [MEVE, 1997; MÜLLER & ALBERS, 2004], *Beiselia* (Burseraceae) [FORMAN & al. 1989], Burseraceae [EGGLI, 2002], Didiereaceae [RAUH & DINKLAGE 1979], Fouquieriaceae [ROWLEY, 2002a], *Cotyledon* [POELLNITZ, 1942], *Othonna* (Asteraceae) [ROWLEY, 2002b], *Peperomia* (Piperaceae) [NYFFELER & ROWLEY, 2002].

Rauh shows that the organization of the species of Didiereaceae is similar to that of primitive cacti, specifying that *podaria* are present in the genus *Didierea*, similar to the genus *Leuchtenbergia* [RAUH, 1983]. They also consider brachyblasts homologous to areoles. If we extend this homology to the *Euphorbia* species of the *Diacanthium* section, the *podarium* is homologous with long-shoots and protuberances, and the spine-shield with brachyblasts and areoles. FRANCK (2016) talks about the difference between long-shoots and short-shoots in *Harrisia* species where he shows that “the green photosynthetic stems have indeterminate long-shoots which contain numerous short-shoots. A cactus short-shoot is referred to as an areole”. A summary of these analogies is shown in Table 1.

Table 1. Homologous structures in *Euphorbia*, *Didierea* and *Leuchtenbergia* genus

Homologous structures	Genus		
	<i>Euphorbia</i> (<i>Diacanthium</i>)	<i>Didierea</i>	<i>Leuchtenbergia</i>
	podarium	long-shoots	protuberance
spine-shield	brachyblasts	areole	

The difficulty of naming formations specific to succulent plants with a single phrase is obvious: RAUH (1979b) uses the formulation “Mamillenartige bildengen” / nipple-like formations, while a decade before FRIEDRICH (1968) used the phrases “höckerig-warzigen oder kurz stiftförmigen Auswüchsen” / bumpy-warty or short pin-shaped outgrowths with the meaning *podarien / podaria* in the description of the genus *Cotyledon*. In the same context, we mention Chevalier's 1933 work, which uses four different terms to describe African succulent species: *protuberances* (*E. sudanica*), *tubercule* (*E. unispina*, *E. tellieri*, *E. sapini*), *ecusson* (*E. darbandensis*) and *mamelons* (in the determination key – section *Diacanthium*).

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JACOBSEN (1954) uses the terms *Basen der Blätter*, *Blattpolster*, *Blattkissen*, *Warzen* and *podarien* to describe the same formation in different species of the genus *Euphorbia*. Only in the description of group 19 (section *Florispinae* Haw.) does it indicate the synonymy between *Warzen* and *Podarien*. It is difficult to say whether either term is synonymous with spine-shield.

In the case of the genera *Ocimum* (Lamiaceae) [VOGEL, 1998] and *Polypodium* (Pteridophyta!) [HAGEMANN, 1969] the use of the term *podarium* is disconcerting and requires much wider discussion. In the same context is the statement of HEADS (1994): “The nature of the leaf-base (= leaf-cushion, podarium, soubassement foliaire, etc.) in *Leonohebe* (Plantaginaceae, formerly Scrophulariaceae) is problematic, and has hardly been studied”.

Synonymy relationships with other terms/expressions

It is noted that over time, the term *podaria* has been synonymous with different botanical terms or expressions, which do not all have the same meaning: tubers, areoles (in their entirety), the base of the leaves (in the sense mentioned by Buxbaum – the thickened portion of the leaf petiole), horned pad (preferred translation for spine-shields), ridged stem teeth (in the case of *Euphorbia* species), collective term for the protuberances on the surface of cacti (areoles, tubercles).

In a limited number of works, the term *pulvinus*, *cushion* (English), *coussinet* (French) [CHEVALIER, 1951; URSCH & LEANDRI, 1954] appears used in connection with the special formations present in cacti and other succulents.

For an easier understanding of the amplitude of the variation of the terms or expressions used to designate the specific formations discussed so far, the information gathered from the analyzed bibliographic sources [KILIAN & al. 2006; KAPLAN, 2001; CROIZAT, 1942; TROLL & WEBER, 1954; LEMAIRE, 1865; LEACH, 1969; MARNIER-LAPOSTOLLE, 1966; NEUWINGER, 1996; BRAVO-HOLIS, 1978; CALVENTE, 2010; LÜTHY, 1996; LÓPEZ & al. 2015; BRUYNS, 2022] is presented in the Table 2.

We notice that terms such as gonflement, teeth, projection mainly refer to appearance, while areoles, tubercles or spine shields designate a well-defined anatomical structure. From a semantic point of view between these terms and podarium there seems to be a relationship which is illustrated in the image below:

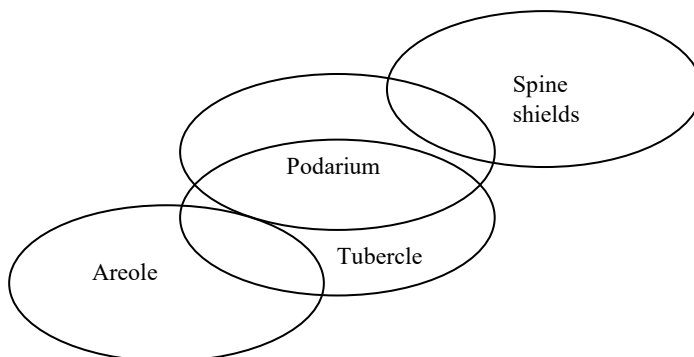


Figure 1. A hypothetical semantic relations between *podarium* and related terms used by various authors.

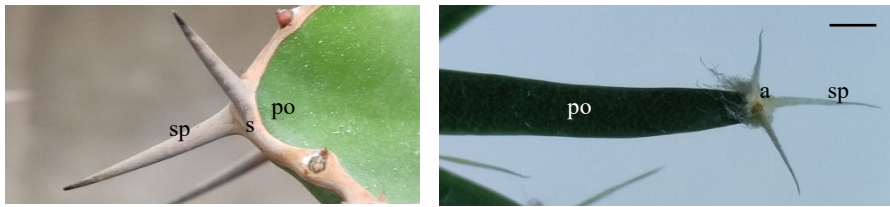


Figure 2. A. *Euphorbia grandicornis*, podarium (po) with spine-shield (s) and spines (sp).
B. *Leuchtenbergia principis*, podarium (po) with areole (a) and spines (sp). (Scale 1 cm)

Table 2. Terms and expression synonymous with *podarium* used in botanical references.

Term/expression synonymous with <i>podarium</i>	Author/Authors	Language	Publication year	Botanical Family / Genus
Ampliacao da base foliar	Calvente	Spanish	2010	Cactaceae
Areole (whole)	Dicht & Lüthy	English	2005	Cactaceae
Basen von Blättern/ Blattbasen	Troll & Weber	Deutsch	1954	Cactaceae
	Berger	Deutsch	1907	Cactaceae
Blattpolster	Rauh	Deutsch	1979	<i>Euphorbia</i> , Asclepiadaceae (Stapeliaceae), <i>Allauadia</i>
Coussinet (foliaires)	Cosson	French	1871	<i>Euphorbia</i>
	Verdus	French	1973	<i>Euphorbia</i>
	Ursch & Leandri	French	1954	<i>Euphorbia</i>
Cushion	Kaplan	English	2001	Cactaceae
Decurrent succulent petioles	Croizat	English	1942	<i>Euphorbia</i>
Dents	Lemaire	French	1858	<i>Euphorbia</i>
Ecusson epinier	Marnier-Lapostolle	French	1966	<i>Euphorbia</i>
Enlarged leaf pedicel	Rosas-Reinhold & al.	English	2021	Cactaceae
Gaine	Boiteau	French	1947	<i>Euphorbia</i>
Gonflement	Groenland	French	1866	<i>Euphorbia</i>
Leaf base	Barthlott & Hunt	English	1993	Cactaceae
	Endress & al.	English	2018	Cactaceae
	Kaplan	English	2001	Cactaceae
Mamelons	Kiesling	French	1999	Cactaceae
	Chevalier	French	1933	<i>Euphorbia</i>
L'organe pétioliforme	Lemaire	French	1865	<i>Euphorbia</i>
Peculiari escrescenze del fusto	Mosti & al.	Italian	2001	Cactaceae
Protuberancia tuberculada	Rivas Rossi	Spanish	1998	Cactaceae
Spine shields	Kilian & al.	English	2006	<i>Euphorbia</i>
	Dyer	English	1937	<i>Euphorbia</i>
	Keay	English	1955	<i>Euphorbia</i>
	Leach	English	1969	<i>Euphorbia</i>

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Teeth of stems	Croizat	English	1939	<i>Euphorbia</i>
Tubercle	Gilbert	English	1987	<i>Euphorbia</i>
	Neuwinger	English	1996	<i>Euphorbia</i>
	Bruyns	English	2022	<i>Euphorbia</i>
Tubercule	Chevalier	French	1933	<i>Euphorbia</i>
Tubérculo	Bravo-Holis	Spanish	1978	Cactaceae
	López & al.	Spanish	2015	Cactaceae
Warzen	Berger	Deutsch	1905, 1926	<i>Euphorbia</i>
	Lüthy	Deutsch	1996	Cactaceae

When analyzing the data of the Table 2, Figure 1 and Figure 2 it becomes obvious the terms *podarium*, *tubercle*, *areola* and *spine shield* are not synonymous, much less the term *scutellum*.

POC (Plant Ontology Consortium) ruling on the term *podarium*

The POC analysis from November 2011 established the synonymy of the term *podarium* with *tubercle*, which it defined as: “An enlarged leaf base that is fused with adjacent shoot axis tissue”.

However, this ruling does not resolve the semantic chaos surrounding the term *podarium*. In the case of the family *Didiereaceae*, the equivalent term is not specified and *tubercle* is not usual, and for the genus *Euphorbia* the relationship with spine-shield is not clarified.

Even in the case of cacti, things are not so simple. The question of the relationship of the terms *tubercle-mammilla* needs to be clarified. If we analyze over time how the two terms have been used we often find confusing aspects.

Thus in the general description of the botanical characters of cacti GUILLAUMIN (1933) uses the term *mamelons*, which he shows are fleshy and probably represent branches. However, in the description of most of the genera, he uses the term *tubercule*, the same term used to describe the ornaments present on the seeds. A few decades later (1984) KIESLING uses the term *tuberculos* to describe cacti, then in 1996 he uses *mamelones* and *podarios* [KIESLING, 1996].

There are several examples of works in Spanish that highlight the confusion caused by the loose use of terms.

Thus FLORES (2005) seems to use the terms *mamillas* and *tubérculos* (Spanish) sensu DeCandolle, but the fact that both appear in the description of different species of the genus *Coryphantha* contradicts this assumption. In addition, the term *protuberancias/protuberances* present in the description of some species of *Ancistrocactus* and *Astrophytum* makes it even more difficult to understand how to select the terms. Expressions which create confusion are:

... pequeñas *protuberancias* como *tubérculos* / small tubercle-like bumps – *Ferocactus histrix*, *Gymnocactus aguirreanus*

... *tubérculos* como pequeñas *protuberancias* espaciadas/ tubercles as small, spaced bumps – *Glandulicactus wrightii*

Returning to the use of the term *tubercle* brings again into discussion the confusion determined by the polysemantic character of this term (*tubercle* / *warze*).

A first example is found in an old work (1907) by BERGER who uses the term *warze* (equivalent to *tubercle*) with three different meanings: structure of spiny euphorbias, growths on seeds, warts (or other skin growths in humans). A few decades later, *tubercle* [MCCLEARY,

1968] is used in the sense of a formation typical of spiny euphorbias, but also as a sensitive organ in snakes and amphibians.

RIVAS ROSSI (1998) describes *podario* as „protuberancia tuberculada”/tuberculated protuberance, present in genera such as *Epiphyllum*, *Disocactus*, while in globose species (*Melocactus tuberculos*) are present. Earlier [RIVAS ROSSI, 1996] defined these terms in a glossary in a way that excluded the relation of synonymy:

Podario, en las cactaceas, protuberancia que queda en el tallo, remanente de la base de las hojas,

Tuberculo, tallo modificado en un organo de reserva, que generalmente esta bajo tierra.

A singular / isolated situation is found by REPPENHAGEN (1984) who in the Latin diagnosis of a new species of *Mammillaria* (*M. hubertmulleri*) uses the term *verrucae* (Latin) as a synonym/homologue for *Warzen* (Germ.), with the meaning of a protuberance bearing thorns.

Despite the recommendation made by the POC after 2011, enough papers appear in which the controversial term appears in the description of taxa [BARTHLOTT & HUNT, 2013; HOUSE & al. 2013; HOLMES, 2016; NAIDU, 2017; PRAT & FRANCK, 2017; ROLIM, 2017; SAROJINIDEVI & VENKATARAJU, 2017; ENDRESS & al. 2018; ROSAS-REINHOLD & al. 2021].

It seems obvious that the recognition or non-recognition of the usefulness of the term *podarium* depends on each individual author. Thus, in the vast work coordinated by Kubitzki, the term *podaria* is used in the description of the family Cactaceae [BARTHLOTT & HUNT, 2013] and Apocynaceae – Subtribe Stapeliinae [ENDRESS & al. 2018], but not in that of the family Euphorbiaceae [WEBSTER, 2014]. SCHRÖDER (2018) prefers the term *podaria* with the meaning “mit der Sprossachse verschmolzene Blattbasen” / leaf bases fused with the stem axis to characterize the species *Ceropegia simoneae*, and with the term *Warzen / tubercle* he designates the formations that are present in a specimen named as Form “green bizarre”.

It should be noted that the works in Spanish in which the term *podario(s)* appears are relatively numerous [de OLIVEIRA N., 2014; SCHEINVAR & al. 2015; TAPIA & al. 2017; VÁZQUEZ-SÁNCHEZ & al. 2017; AGUIRRE, 2018; ARANDA-PINEDA & al. 2019; ARIAS & AQUINO, 2019; BARRIOS & al. 2019; CAMPOS DÍAZ & al. 2020]. We cannot help but wonder if it is of any significance that the term *tuberculos* is most commonly associated with thickened subterranean formations of some edible plants. GALLEGOS (2014) in the Spanish diagnosis uses the term *podarios*, which in the short English commentary is translated as *tubercles*.

The fact that CASTILLON and RAJAOVELONA in the French paper of 2019 prefer to describe a new species of *Euphorbia* using the term *protubérances (protuberances)* is further evidence that there is no unanimously accepted term to designate a unanimously recognized formation.

Terminology aspects

The term *podarium* and its various forms of declension (*podaria* – English, *podariis* – Latin) appear frequently in diagnoses, of course predominantly in Latin. If in the case of cacti it corresponds to tubercles (*mammilla*, *tuberculos*, *tubercule*), in the case of the genus *Euphorbia* it most often corresponds to spine-shield [BRUCE & al. 1951; DYER & al. 1958; RAYNAL 1967; CARTER & al. 1981; MALPURE & al. 2016], horny margin, but sometimes also to teeth of the branches (“dentibus”) [CROIZAT, 1938b].

It seems that the history of the evolution of this term is little known. The renowned cacti expert RAUH (1979a) notes with amazement that “sukkulente Basalabschnitt der Blätter

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wird von Berger (1926)! auch als *Podarium* bezeichnet / succulent basal section of the leaves is described by Berger (1926)! also known as a *podarium*.” It is difficult to interpret the meaning of Rauh’s surprise, but it seems hard to believe that he did not know that Berger was analyzing a term that was already 70 years old. In the same context, the designation of the term *podarium* as “unique structure (!) for the Cactaceae family” [KOROTKOVA, 2011] or “exclusive character of the Cactaceae family” [TOVAR ROMERO, 2005] is included.

Hence the need to understand the meaning of the term, to use it with as much accuracy as possible, but above all to define it unambiguously. From this perspective, consulting dictionaries or glossaries is not very useful.

As early as 1977, CARTER pointed out that up to the date the term *podarium* had most likely not been included in a Latin dictionary [STEARNS, 1966] or a glossary of botanical terms, and he hoped that this would be remedied.

A German dictionary of biology [EICHHORN, 1998] is among the first works in the field containing the definition of the term:

“*Podarium* n *podarium*: mit Sproß verschmolzene Blattbasis bei Cactaceae, eine Struktur bei sukkulenten Euphorbiaarten” / leaf base fused with stem in Cactaceae, a structure in succulent species of Euphorbia.

In 2000, HICKEY & KING set out to produce a glossary “...that includes all the terms most commonly used in describing vascular plants, as well as some that are found in more specialized works.” The term *podarium* is missing from their work. The same situation is in the case of the dictionary edited by ALLABY (2006) which was presented as “the most comprehensive and up-to-date dictionary of botany”.

Only in 2010, the terms *podarium* and tubercle appear in a glossary published under the auspices of RBG Kew [BEENTJE, 2010], but not as synonymous:

“*podarium*, (in cacti or other succulents) a modified leaf base functioning as the photosynthesising organ;

tubercle, 3. (in ball – or barrel-shaped cacti), cone-shaped protuberances that are enlarged modified leaf bases fused with adjacent stem tissue”.

Other definitions present in works dedicated to the Cactaceae family are:

podarium. Collective term for stem-surface protuberances in cacti (pl., *podaria*) [POWELL & WEEDIN, 2004].

podaria: are the swellings often subtending areoles that represent the points of attachment of leaves or bracts that have been lost, or almost lost, in the course of evolution of the highly succulent habit [TAYLOR & ZAPPI, 2004].

podario: “Como podio, pie, sustentáculo; es decir, el internodio que sirve de pie a una rama axilar que brota de su nudo apical. En las cactáceas dícese de la base foliar, dilatada y expandida en forma de un pequeño tubérculo, que sirve de pie a la aréola vegetative” (engl. that is, the internodium that serves as a foot for an axillary branch that sprouts from its apical node. In cacti, it is said to have a leaf base, dilated and expanded in the form of a small tubercle, which serves as a foot for the vegetative areola [VÉLIZ, 2008]; se refere aos espessamentos encontrados no caule, na porção que subtende as aréolas /refers to the thickenings found on the stem, in the portion that subtends the areolas [SOLLER & al. 2014]; base foliar dilatada en forma de pequeño tubérculo, que sustenta a la aréola / leaf base dilated in the form of a small tubercle, which supports the areola [ARIAS & AQUINO, 2019].

According to the specifications in the theories of terminology, Lemaire highlighted a concept for which he proposed an appropriate term to designate it. It is still not clear whether this term is mono or plurisemantic. If it is considered monosemantic, then it should be preferred

in favor of tubercles because “we should not tolerate, in scientific language, a plurality of meanings for one term” [RICKETT, 1954].

Compared to *podarium*, tubercle seems to be an ambiguous term; in Bentjee's work it is mentioned with 3 different meanings:

tubercle, 1. a small tuber, used for any small growth (hypothetically) associated with symbiotic organisms; 2. a small protuberance; 3. (in ball- or barrel-shaped cacti), cone-shaped protuberances that are enlarged modified leaf bases fused with adjacent stem tissue [BEENTJE, 2010].

In addition, in the Oxford Dictionary we also find these two definitions:

1. (anatomy, biology) a small round part, especially on a bone or the surface of an animal or plants;

2. (medical) a small swollen (= larger than normal) area in the lung caused by tuberculosis.

CARTER (1977) said that *scutellum* had too many definitions thus motivating the preference for the term *podarium*; it looks like the term *tubercle* finds itself in a similar situation.

The analysis of the use of the term *podarium* did not aim to exhaust the subject, but to emphasize its lack of clarity. After more than 160 years since Lemaire's proposal, there are still many question marks, but also the possibility that *podarium* will become a forgotten term, as well as “cyrtomê” proposed by the same author.

Conclusion

Changing the meaning of botanical terms with the accumulation of new knowledge is natural, but sometimes they can become obscure. *Podarium* is in such a situation; we cannot say whether it defines a strictly cauline, strictly foliar structure or a concretion of the two, if it designates a unique structure or is actually a collective term. We consider that the term *podarium* sensu Lemaire can be very useful, because it designates a formation specific to succulents and implicitly indicates its heterogeneous, both caulinar and foliar origin.

With the evolution of modern language translation technologies, in the matter of understanding and explaining some terms translations could have a significant contribution to the reduction of linguistic borders or barriers. With the elimination of word-for-word translations and the optimization of finding the right translation, the sources of misunderstandings and errors that are common today will be eliminated.

The translation must observe certain constraints and rules, and faithful observance of the essence of the term in question is a priority. The terminology in question, words without equivalent or misunderstood, can raise real problems. The correct translation is the one adapted to the local language, but also to the exact knowledge of the botanical terminologies, verified and re-verified not by whomever, but by translators with real botanical knowledge, experienced in the targeted field of activity.

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