

Types of floral nectaries and the concepts ‘character’ and ‘character-state’—a reconsideration

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SUMMARY

A new approach to the concepts ‘character’ and ‘character-state’, as well as additional observations on the floral nectaries, resulted in more comprehensive insights into the relations among the floral nectary types. Instead of treating the 1986 nectary types (nectaria *caduca*, *n. persistentia*, *n. septalia* and *n. trichomalia*) on a par, a hierarchical ordering is presented. Within the hierarchical system—which comprises types of floral nectaries delineated on the basis of their respective morphological nature—higher and lower level characters and character-states are distinguished. The *n. trichomalia* are not integrated in this character ordination because the presence of nectariferous trichomes is considered to be a feature of a different level. In addition, a proposal is made to replace the term ‘*n. septalia*’ by ‘*n. gynopleurica*’.

Key-words: character, character-state, floral nectary types nectaria *caduca*, nectaria *persistentia*.

INTRODUCTION

On the basis of the localization and the nature of the nectariferous zones, floral nectaries can be typified as nectaria (*n.*) *caduca* (nectaries associated or homologous with the falling floral parts) or *n. persistentia* (nectaries associated or homologous with the non-falling floral parts; see Smets 1986). The presence or absence of floral nectaries as well as these two nectary types are systematically relevant, since their distribution contributes to a better understanding of the relations among the higher taxa of the Magnoliophytina; here it is useful to recall Meeuse’s (1978) caveat: “*sometimes far-reaching conclusions have been drawn on the basis of nectarial topography and although the responsible workers acted in good faith, one should at least from now on pay heed to the saying: Fools rush in . . .*”. The nectary types ‘*caducous*’ and ‘*persistent*’, as well as the feature ‘*floral nectary*’ or ‘*occurrence of a floral nectary*’ are considered as ‘*characters*’. With additional character-research it has also become possible to distinguish between two supplementary types: *n. septalia* and *n. trichomalia* (Smets 1986, 1987).

In our research methodology of character-analysis, Dahlgren’s (1980) two-dimensional classification diagram plays a central role (e.g. Smets 1984, 1986; Ronse Decraene & Smets 1987; Cresens & Smets in press). However, it is also important that the concepts ‘*character*’ and ‘*character-state*’ be defined in an unambiguous way. The aim of the present contribution is (a) to introduce a workable framework for the notions ‘*character*’

and 'character-state' and (b) to clarify the relations between the nectary types mentioned above.

In addition to the observations carried out formerly (Smets 1986), a wide range of species have been observed by SEM at the National Botanical Garden of Belgium at Meise (BR). In this contribution only a few of the resulting photographs are included (Figs 1–6).

APPROACHING THE CONCEPTS 'CHARACTER' AND 'CHARACTER-STATE'

The question whether an attribute's form of expression is to be interpreted as a character or as a character-state has sparked off numerous controversies. For example, Wiley (1980) considers 'red petal' as a character while Dahlgren, Clifford & Yeo (1985) interpret 'red perianth' as a character-state of the character 'perianth colour'. In fact, Wiley (1980) points out: "*While some [most!] biologists term 'red petals' and 'blue petals' character-states of the character 'petal colour', I consider 'red petals' and 'blue petals' to be individual characters*". Dahlgren *et al.* (1985, p. 24) define a character as "*the sum of expressions (states) of a particular kind in a particular respect*". They apply the concept 'character-state' "*when the attribute is shared and [they] have reason to believe it arose in a common ancestor*". In this context, characters are regarded as abstract entities which become concrete in their character-states (cf. Davis & Heywood 1963, p. 113: 'sepal length' is a character, 'sepal length 12 mm' is an expression of that character).

Dahlgren *et al.*'s (1985) definitions lead us to believe that for them the concept 'character-state' (and hence also the notion 'character') carries phylogenetic connotations, as they claim that only homologous parts can be character-states of the same character. If non-homologous parts are taken into consideration, they use the term 'character-condition'.

Though the concepts 'homology', 'morphological nature' and 'synapomorphy' (= homology according to Patterson 1982) are applicable to delineate the notions 'character' and 'character-state', we prefer using the concepts 'qualitative', 'quantitative' and 'gradual' variation for this purpose. Still, we also refer to the homology concept when distinguishing between qualitatively and quantitatively varying forms of expression. Indeed, character-states of different characters vary qualitatively, which means that they are not homologous (different non-homologous parts are referred to). Character-states of the same character are homologous (homologous parts are indicated) but they may vary quantitatively, i.e. "*in den vorhandenen Bauelementen*" (Hagemann 1975). Between forms of expression of the same character there may be 'full' correspondence (cf. Sattler 1986, p. 91: "*absolute sameness does not exist*") or partial homology (cf. Sattler's 1984, 1986 semi-quantitative homology concept). In our view, the '*Prinzip der variablen Proportionen*' advocated by Troll in numerous publications (e.g. 1956) can be related to the gradual variations between the concrete forms of expression of a character-state (for further details on these conceptualizations, see Cresens & Smets in press).

To summarize, the states of a character are variables of a homologous nature, abstracted from reality. The concrete entities we can observe are the gradually varying forms of expression (e.g. every observation of a representative of the Solanaceae leads to the conclusion that the corolla is sympetalous—'sympetaly' being a character-state of the character 'degree of petal fusion'—however, the knowledge that a sympetalous corolla occurs within this family does not allow us to visualize the appearance of the corolla in a particular solanaceous taxon).

Binary characters with 'present' versus 'absent' as their only states are an exception to the rule that only homologizable parts can be designated as states of a character. Although the character 'occurrence of petals' has the states 'presence' and 'absence' of petals, flowers without petals are not necessarily always homologous with petaliferous flowers. Naturally, in these cases other characters will be taken into consideration for deciding on the homologization of the character complexes in which the character in question is present or absent.

TOWARDS A CHARACTER ORDINATION OF THE FLORAL NECTARY TYPES

With regard to the characterization of the floral nectaries, it is important to emphasize that we consider floral nectar secretion as a homologous feature within the Magnoliophytina. This explains why we posit the character 'floral nectaries' or 'occurrence of floral nectaries'; 'presence' and 'absence of floral nectaries' being character-states of this character. However, the above does not imply that all the floral nectariferous zones should be treated on a par, since they are not necessarily homologous (see further).

It is our claim that the state 'presence' is to be termed 'plesiomorphous' with respect to the 'apomorphous' state 'absence' (cf. also Dahlgren & Rasmussen 1983; but see also Vogel 1981). On the other hand, Meeuse (1978) points to the presence of "*primarily non-nectariferous taxa with pollen flowers, e.g. in several dilleniid groups*". Accordingly, one must bear in mind that nectaries can be 'primary' or 'secondary' absent.

In our opinion, the floral nectaries cannot be considered as organs (cf. Magin 1983). Consequently, the nectaries or nectariferous zones do not constitute one additional floral morphome. Still, floral nectaries can be characterized on the basis of their association or homology with the major morphomes of the flower, namely the androecium, the gynoecium, the receptacle and the different perianth-morphomes.

To start with, a distinction can be made between nectaries associated or homologous with caducous floral morphomes (homologous with respect to their caducous nature) and nectaries associated or homologous with persistent floral morphomes (homologous with respect to their persistent nature). Indeed, the presence of floral nectaries does not imply that parts with which the nectariferous zones are associated would necessarily be homologous.

The respective groups of the gradually varying forms of expression of nectariferous caducous parts and nectariferous persistent parts are states of the character 'occurrence of floral nectaries' but also of the character-state 'floral nectaries present'. We prefer to call these 'states' 'lower-level characters' (LLC). Instead of approaching the floral nectaries as one multistate character with the states 'absence', 'caduca', 'persistentia', etc., we advocate a hierarchical system where LLCs are distinguished (namely n. caduca and n. persistentia) within the character-state 'presence of floral nectaries' of the higher-level character 'occurrence of floral nectaries'. Primary and secondary absence of floral nectaries are LLCs of the character-state 'absence of floral nectaries' (Fig. 7).

In our opinion the absence of n. caduca implies the occurrence of n. persistentia, and the absence of n. persistentia the presence of n. caduca. We wish to stress that the presence of n. caduca in a natural taxon does not exclude the presence of n. persistentia and vice versa (e.g. Magnoliaceae, Nymphaeaceae and Illiciaceae with nectar secretion on the tepals and the pistils; Ranunculaceae with typical nectar petals in most genera and secretions on the carpel sides in *Caltha* L.).

Now the question arises how the occurrence of *n. septalia* and *n. trichomalialia*, which were formerly (Smets 1986) treated on a par with the characters '*n. caduca*' and '*n. persistentia*', is to be interpreted.

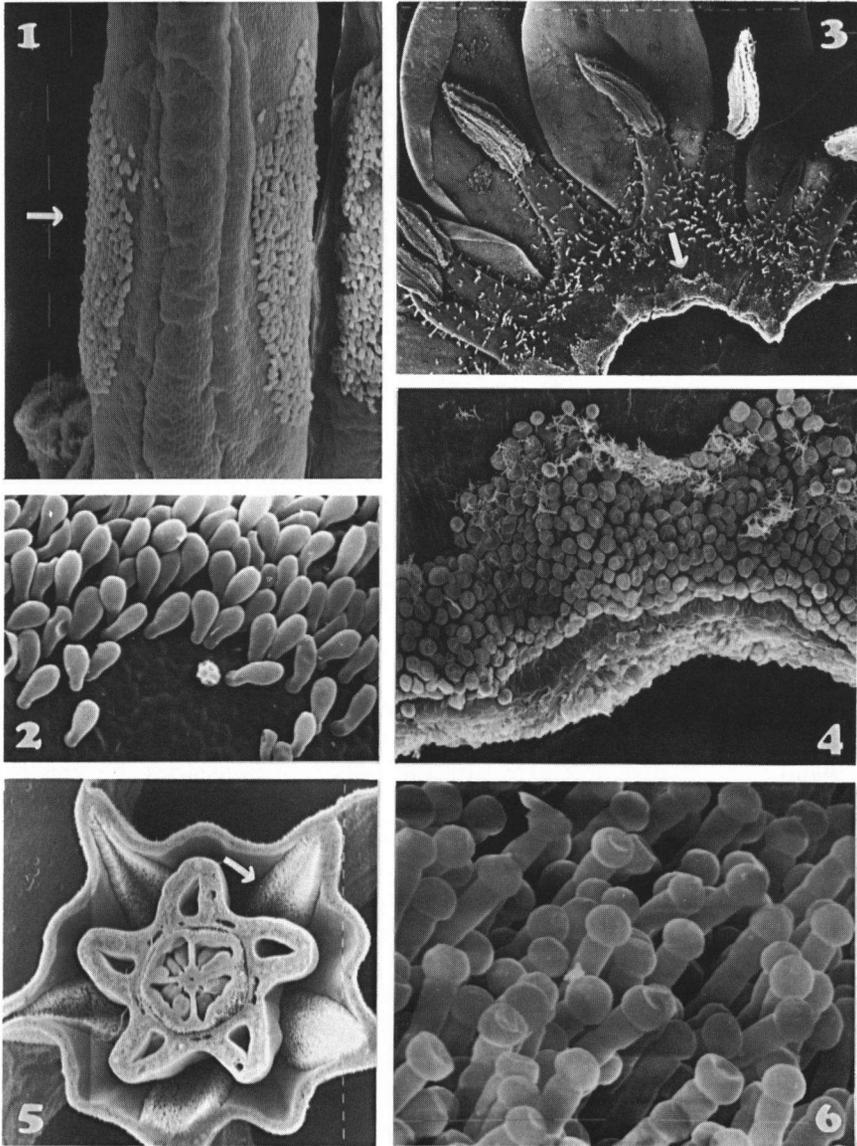
1. On the basis of the new conceptual framework sketched above, and taking into account the nature of the nectaries, we think it is legitimate to interpret the septal nectaries as a separate type of *n. persistentia* along with, for example, the nectaries associated with the floral axis, namely the *n. axialia* (axial nectaries). It should be clear from the preceding that the septal nectaries and the axial nectaries are considered as non-homologous within the *n. persistentia* type (LLC 1) because they are associated with different floral morphemes. Given that the septal nectaries and the axial nectaries are different in quality, we consequently interpret them as second-level LLCs of the first-level LLC. The absence of septal nectaries always implies that another, second-level LLC of the character '*persistent nectaries*' is present.

In Smets (1986) the descriptive term '*discus*' was reserved for the nectaries located on the hypanthium and for the nectariferous zones "*round the base of or on the surface of the gynoecium*". New data, however, suggest that the sense of the term should be limited to axial or receptacular nectaries (including the nectariferous zones on the hypanthium but excluding nectaries that are associated with the gynoecium, namely the *n. gynoecialia* or gynoecial nectaries, see *infra*). Yet, it is our belief that the 'classical' distinction of axial nectaries versus phyllome nectaries leads to artificial groups (cf. Smets 1986).

It is common knowledge that the *n. septalia*, first described in Brongniart (1854), are not always located in the septa of the pluricarpellate pistils (Van Heel 1986; Schmid 1985; Daumann 1970: "*Oberflächennektarien*", "*innere Septalnektarien*" and "*äussere Septalnektarien*"). Though they are obviously homologizable nectariferous zones on the carpel walls, one may have reservations about the term '*septal*'. Moreover, Schmid (1985) states that "*all dicotyledons lack septal nectaries*" and in Smets (1986, 1987) the view that septal nectaries are characteristic and synapomorphic of the Liliatae is advocated (cf. Daumann 1974). This position also needs refining: it is not unwarranted to interpret the nectar secretions on the pistil flanks in the Alismatiflorae, Nymphaeaceae (Emberger 1960), Magnoliaceae and—possibly—Illiciaceae as plesiomorphous gradual variants of the character '*septal nectaries*'.

Although the term '*n. septalia*' is currently used, we propose to replace it by '*n. gynopleurica*' ('*gynopleural nectaries*'). This substitution offers two advantages. First, the term is more appropriate to cover inner, outer and confluent septal nectaries. Schmid's (1985) definition of the septal nectary as "*a nectariferous, that is sugar- or nectar-secreting, cavity resulting from lack of intercarpellary postgenital fusion and lying in a septal radius*" covers a wide range of forms of expression (the author mentions, e.g. the Burmanniaceae, cf. RübSamen 1983) but it conflicts with the literal sense of the term. Since gynopleural nectaries comprise both the 'true' septal nectaries of the Liliatae and the nectaries on the pistil flanks of the Magnoliidae, the second advantage of this term is that it highlights the relations between the nectaries in the two Magnoliophytina classes as well as the natural relationships between Magnoliatae and Liliatae (cf. Dahlgren & Clifford 1982; Dahlgren & Bremer 1985; Ronse Decraene & Smets 1987 on the close link between Magnoliidae, Caryophyllidae—possibly Hamamelidae—on the one hand, and Liliatae on the other).

It should be clear that the term '*gynopleural nectary*' does not subsume the '*gynoecial nectaries*' (non-axial persistent nectaries!) of a few groups in the Rosoid-Dillenoid complex (e.g. Ericales, Cornales, Araliales, Saxifragales, Loasales) and most of Cronquist's (1981) Asteridae (except for instance the Dipsacales). Fahn's (1953) '*Stylar-type*', for



Figs 1–2 *Caltha palustris* L. (Ranunculaceae). Fig. 1: Carpel flanks with trichomatous nectariferous zones (arrow); $\times 22$. Fig. 2: Detail of the glandular trichomes; $\times 170$. **Figs 3–4** *Lysimachia clethroides* Duby (Primulaceae). Fig. 3: Corolla tube opened to show the glandular trichomes (arrow) at the base of the staminal tube; $\times 11$. Fig. 4: Detail of the trichomatous caducous nectary; $\times 88$. **Figs 5–6** *Abutilon megapotamicum* St.-Hil. & Naud. (Malvaceae). Fig. 5: Cross-section of the flower showing the position of the nectariferous trichomes (arrow) on the calyx; $\times 11$. Fig. 6: Detail of the trichomes; $\times 680$.

example, bears no relation to the n. gynopleurica: it might be considered as an additional character-state of the second-level LLC 'n. gynoecialia'. So, n. gynoecialia are a third second-level LLC, the other two being the septal nectaries and the axial nectaries (discs s.s.) (Fig. 7).

2. In the previous typification (Smets 1986), the nectaries on the carpels of *Caltha* L. (Figs 1 and 2) were interpreted as n. trichomalialia, but within the framework created here

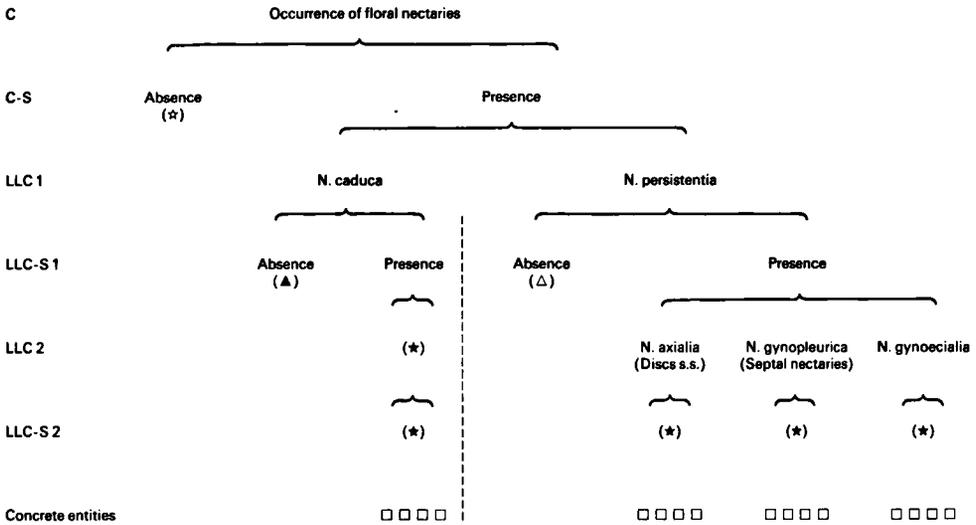


Fig. 7. Hierarchical relations among the nectary types of the Magnoliophytina. C=character; C-S=character-state; LL=lower-level. (☆) will be clarified when a more detailed typification is published; (☆) primary versus secondary absence of floral nectaries are characters of a different level; (▲) implies the occurrence of *n. persistentia*; (Δ) implies the occurrence of *n. caduca*. Note: trichomatous nectaries are not integrated in this scheme (character of different level).

they can be regarded as *n. gynopleurica* (cf. Schaeppi 1972; Vogel 1981). The fact that the nectar in *Caltha L.* is secreted by trichomes (Peterson, *et al.* 1979; our data) points to a qualitative or quantitative difference with the other *n. gynopleurica*, but this is not a sufficient reason to postulate another morphological nature. The presence or absence of trichomes on nectariferous floral parts is considered to be a LLC that should not be confused with the characters delineated on the basis of their morphological nature (which is mainly determined on the basis of the localization of the nectariferous zones). In this context, Fahn (personal communication) correctly pointed out that the occurrence of 'trichomatous nectaries' is a secondary feature. Accordingly, the trichomatous nectaries in Primulales (Figs 3 and 4; see also Vogel 1986), Malvales (Figs 5 and 6; see also Van Heel 1966), (?) Polygonales (the nectariferous zones possess trichomes but there is no certainty as to whether they secrete the nectar) and Dipsacales (figures in Smets 1986; see also Wagenitz & Laing 1984) are to be typified on the basis of the localization centre of the nectariferous zones (e.g. the nectaries in the Primulales and Dipsacales can be characterized as trichomatous caducous nectaries; the malvalean nectaries are usually trichomatous persistent nectaries).

The scheme (Fig. 7) gives a concise outline of the hierarchical relations among the characters that have been delineated formerly (Smets 1986, 1987) and the new types of the *n. persistentia* (the typification of the *n. caduca* will be clarified in another communication). Topics which we cannot discuss in this contribution, are the question of the plesiomorphic or apomorphic relations between the nectary types and the distributional patterns of the characters and character-states on the Dahlgrenogram.

CONCLUDING REMARKS

The quest for a natural ordering of characters and character-states can be of major importance, for it can contribute to the improvement of the predictive value of the

classification system, as it provides a basis for a better understanding of the predictive relations between characters and character-states.

In actual practice, we shall be able to realize only a relative ordering of characters and character-states at different levels. An absolute hierarchy is impossible until all possible characteristics appearing during the plant's life-cycle have been characterized. A hierarchical ordering of types will lead to systematically relevant unit characters, i.e. characters of the lowest level in the sense that their states and their concrete entities are the only recognizable 'subtypes' (cf. Sneath & Sokal 1973).

Numerical and cladistic analyses are in need of character ordination. Therefore, we say that each contribution to an improved characterization of characters will be beneficial to these research methods, because the systematic relevance of a type's occurrence can only be grasped if its relations with other types of the character complex are clarified. Indeed, the present contribution has shown that a characterization in which types of different levels and of different natures are interpreted on a par, can lead to false conclusions.

ACKNOWLEDGEMENTS

We thank Professor Dr E. Petit for critically reading the manuscript. We are indebted to Professor Dr A.D.J. Meeuse for his corrections, suggestions and stimulating remarks. We highly appreciate the financial support of the 'NFWO—Krediet aan navorsers'.

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