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Staminodes: Their Morphological and Evolutionary Significance

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I. Abstract

Different approaches to circumscribe staminodial structures in the angiosperms are reviewed. The need for a morphological distinction between "true staminodes" (derived from stamens or homologous to stamens) and "pseudostaminodes" (nonhomologous to stamens) is emphasized. In phylogenetic studies the term "staminode" is often used uncritically, without

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knowledge of the true homology of these structures. Staminodes are either whole organs (outer tiers or whorls, namely petals, intermediate tiers, or organs within a tier), or partial organs.

This article aims to discuss the shortcomings of the past and current approach of staminodes and proposes definitions of staminode types for use as characters in phylogenetic analyses. Staminodial structures should be classified according to their position and function in the flower. Both aspects are intricately linked and make the identification of staminodes sometimes problematic. Shifts in time (heterochrony) and space (heterotopy or homeosis) make that a regressing organ either aborts completely or becomes remodeled into something new. Petals are included in the definition of staminodes as they combine function and heterotopy. A hierarchical ordering of staminodial types is given and discussed. Three interdependent but possibly complementary functions are attached to the occurrence of staminodes: an attractive, nutritional, and structural function. The importance of staminodes for the evolution of the androecium and flower is demonstrated. The difficulty in unmasking pseudostaminodes, comprising receptacular disks, is demonstrated. The value and shortcomings of molecular-based interpretations of staminodes are discussed. It is shown that the decision to recognize a staminode from receptacular emergences often relies on unstable grounds and remains largely dependent on the acceptance of a given phylogenetic background.

II. Introduction

For the majority of the angiosperms the functional stamen is differentiated into a basal supportive part, namely the filament, and upper microsporangia-bearing tissue, namely the anther (see, e.g., D'Arcy, 1996; Endress, 1994; Endress & Stumpf, 1990, 1991; Hufford & Endress, 1989; Weberling, 1989). Each anther consists of two equivalent halves, the thecae, joined together and with the filament by a connective. Each theca is built up of two pollen sacs (microsporangia), dehiscing in various ways. When stamens fail to develop into the above-mentioned sporogenous structures but retain the same characteristics of microsporophylls, they are usually referred to as sterile stamens or staminodes (e.g., Eames, 1961; Weberling, 1989).

Different definitions can be applied for staminodes. For Watson and Dallwitz (1992–), a staminode is a sterile stamen, or a modified structure identifiable as such, borne in the androecial region of the flower. It may be merely imperfect, vestigial, or specialized (e.g., petaloid or nectariferous). For Mione and Bogle (1990: 78), studying Hamamelidaceae, staminodes are "sterile floral appendages which are most certainly derived from stamens, i.e., appendages which are morphologically similar to stamens but are sterile."

The identification and description of a staminode often remains vague and arbitrary, and may overlap a whole range of different structures: It is an abstraction of something that is neither a stamen (except for those cases with clearly abortive anthers), nor a petal proper, nor any other clearly distinguishable organ. It is clear that, when a stamen aborts, the resulting structure should obviously be called a staminode. This is important for recognizing evolutionary trends in flowers, as the staminode represents a transitional phase from one category of organs to a totally different structure. Difficulties arise when there is absolutely no resemblance between the sterile structure and the fertile stamen. To interpret staminodes in an unequivocal way—like any other floral organ—necessitates a clear-cut approach of homology. For this purpose positional homology should be of major importance in the study of the morphology of staminodes. Staminodes may occur in the same whorl as fertile stamens, as a result of nutritional limitations (e.g., Baillon, 1862b; Fukuoka et al., 1986) or as the result of a zygomorphic development of the flower (e.g., in many Scrophulariaceae: Endress, 1998, 1999; Reeves & Olmstead, 1998; Table II). An organ that shows no resemblance whatsoever to a stamen may be homotopic; that is, it takes the space in the flower usually reserved for members of the androecium but lacks all resemblance with stamens on a structural ground, even being restricted to vascular bundles, or is totally different in physionomy. The question is whether that organ can always be considered homologous with the stamen. This question cannot be answered positively in all cases, as the homology criteria of Remane (1952, in Sattler, 1994) remain arbitrary. The similarity criterion proposed by Patterson (1982), referring to a combination of topographic, ontogenetic, and compositional homology, was partly taken over by Albert et al. (1998), who distinguished between historical (having a single origin on a phylogenetic tree), positional (originating from the same organs), and process homology (having arisen by the same genetic process). The three definitions of homology used by Albert et al. 1998 (also called "orthology") apply to separate organismic levels (organisms, organ primordia, and genes) and may have different applications when discussed for the different levels separately. Ontogenetic homology, referring to a similar ontogeny of stamen and potential staminode (e.g., Kluge, 1988; Nelson, 1978) is another approach combining the historical, positional and process homology, where the staminode is a specialization appearing at one stage in the ontogeny of an organism. According to Sattler (1994) a 1:1 correspondence between structures that is the theoretical (static) criterion for homology is untenable and oversimplified, because of transformations of structures during development ("developmental hybridization") and the occurrence of homeosis, which may be partial or complete. Characters must be compared at all stages of development, and because they eventually become transformed, partial correspondences and multiple relations must be taken into account. This leads to conflicts of homological interpretation, which are only resolved by a dynamic approach of morphology.

The definition of staminodes also implies the presence of heterotopic structures. A typical example of heterotopic staminodes are petals, if petals are considered a category different from the androecium. There is a broad literature covering the homologous nature of petals with stamens, as the subject has fascinated botanists since Goethe (see Weberling, 1989, for an overview). It is undeniable that petals often represent structures reminiscent of stamens and that there is a strong vascular and ontogenetic correlation between the petals and the stamens (see also Albert et al., 1998; Eames, 1931; Endress, 1994; Weberling, 1989). Staminodes can be seen as partially homeotic mutations. They develop from normal stamen primordia but have undergone altered developmental processes and patterns (Li & Johnston, 2000). The development of petals has gone a step farther by the onset of a novel developmental pathway. We could term this transformation from stamen to staminode, and to petal, "serial homeosis," but not in the sense of Takahashi (1994). Takahashi (1994) proposed this term for the homeotic process occurring in the apetalous flower of *Trillium apetalon* (Trilliaceae), where there is a serial replacement of organ whorls from the center of the flower to the periphery.

Structures in flowers have often been described as staminodes either because of their superficial resemblance to stamens or because of their spatial association with the stamens. Indeed, it is sometimes very difficult to distinguish between structures that look like staminodes but are not homologous with stamens and those that are derived from stamens. As those structures have often been described as staminodes in the literature, the resulting misinterpretations can have far-reaching consequences for the definition of character states used in data matrices, and they can mislead hypothetical semophyleses of the androecium. It is clear that the interpretation of staminodial structures meets the same difficulties as the definition of the nature of nectaries and demands a clear-cut characterization (e.g., Ronse Decraene & Smets, 1991c; Smets, 1986, 1988a, 1988b; Smets & Cresens, 1988).

Walker-Larsen and Harder (2000) recently presented a handsome survey of staminodial structures in the angiosperms. They discussed the possible origins of staminodial structures as the result of reductive processes in the androecium using the phylogenetic framework of angiosperm evolution presented by Chase et al. (1993). Patterns of staminode formation are intricately linked to patterns of evolution of whole floral structures. Therefore, staminodes will have different positions and functions in acyclic magnoliids, polysymmetric rosids, or zygomorphic asterids. The authors point to the functional integration of staminodes in the flower of many groups, as we will also discuss below. Shortcomings of their approach are caused by their reliance on literature citations about staminodes and also on certain shortcomings of the phylogenetic hypotheses they use to discuss staminode evolution.

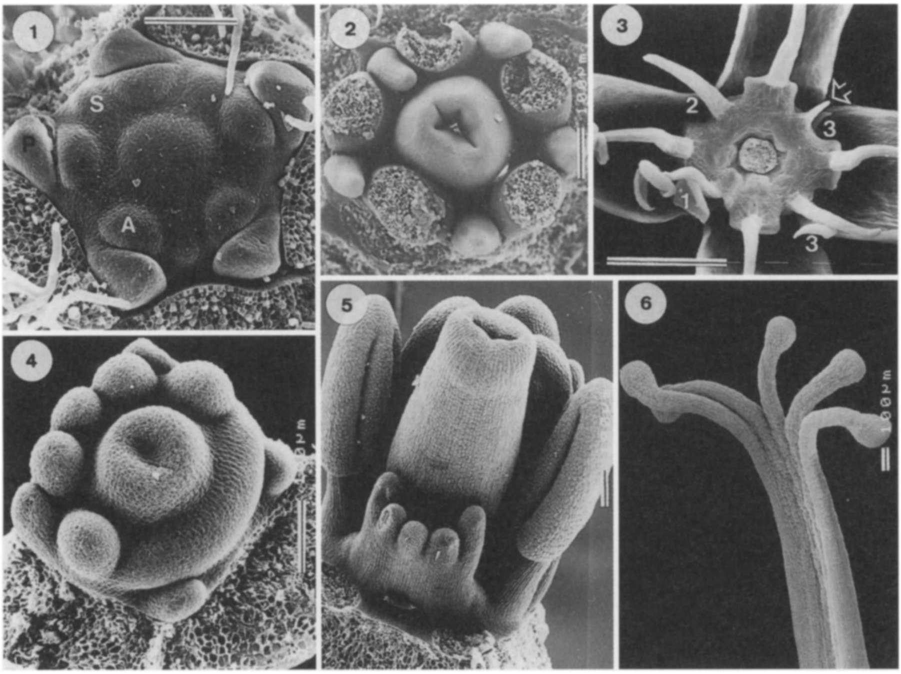
In this article we present a survey of the occurrence of staminodial structures and their functionality in the flower and give an overview of possible misinterpretations of staminodes and their relevance in morphological studies. The difficulty of definition of a staminode may rest on uncertainty in interpreting the wide array of emergences on the floral receptacle. Therefore, a global morphological study, relying on floral anatomy, ontogeny, and external morphology, is needed to clarify this question. We consider staminodes only in hermaphroditic flowers, for the same reasons as given by Walker-Larsen and Harder (2000), because the origin and scope of these staminodes is different for unisexual flowers.

III. Possible Origins for Staminodes

Staminodes appear relatively early in the fossil record, and the same variations as in modern angiosperms seem to have been present since the Turonian. Apart from magnoliid fossils having inner and outer staminodes, there is an abundance of eudicots having one whorl of sterile stamens. They occur in Hamamelidae as a whorl alternating with antesepalous stamens, suggesting their homology with petals and as "a transitional stage between apetalous and petalous flowers" (Crepet & Nixon, 1996: 37). Also in Capparales-like fossils, such as *Dressiantha,* five setiform staminodes alternate with five stamens (Gandolfo et al., 1998). Crepet & Nixon (1996) report the presence of antepetalous staminodial nectaries in flowers of Ericalean/Ebenalean affinity. They also suggest that staminodes are responsible for the derivation of nectaries and petals within the rosid-hamamelid complex by a "division of labor" in the stamens. In the ranunculids, staminodes and petals have been derived several times from stamens in separate lineages (see Drinnan et al., 1994).

Several functional explanations have been given for the origin of staminodial structures in flowers linked to evolutionary modifications of flowers (see Walker-Larsen & Harder, 2000). Staminodes may result from nutrient limitations, alterations in the construction of flowers, or adaptations to pollinators. However, different factors may contribute en masse to the elaboration of staminodes.

For obvious nutritional limitations, an entire whorl of stamens may become reduced or may completely disappear. This is illustrated by Rodríguez-Riaño et al. (1999) in southwest European Fabaceae, where the incidence of reduced diadelphous androecia is correlated with an autogamous syndrome. In several taxa an inner stamen whorl (usually the antepetalous whorl) may be present, vestigial, or even absent within a single species or between different species of the same genus (Table I). Very often the upper flowers of a racemose inflorescence will not attain full development, leading to a partial sterilization of whorls. This process of reduction, once settled genetically, has affected several lineages of the angiosperms and has arisen several times independently (see Walker-Larsen & Harder, 2000). The process is consistent with the fossil record with the profusion of taxa that have apparent staminodial nectar-



Figs. 1–6. Homotopic and heterotopic staminodes (A = fertile stamen; P = petal; S = staminode). **1–2.** *Moringa oleifera* Lam. (Moringaceae): reduction of antesepalous whorl into staminodes. **1.** Early stage, showing retarded initiation of the antesepalous whorl. **2.** An older bud with nearly mature staminodes; stamens removed. **3.** *Sagina procumbens* L. (Caryophyllaceae): example of homotypic and heterotypic staminodes; the antepetalous whorl bears a single staminode (arrow), and the petals are either developed (1), lost (2), or staminodial (3). **4–6.** *Euadenia trifoliata* (Schum. & Thonn.) Oliv. (Capparaceae): example of a partly staminodial whorl. **4.** Early androecial initiation, the staminodes visible as a continuous girdle. **5.** An older bud with the perianth removed, showing the connected staminodes facing the fertile stamens. **6.** Detail of the tip of a mature staminodial phalange. (bars = 100 μm, except in Fig. 3 bar = 500 μm)

ies (Crepet & Nixon, 1996). The shape of these staminodes is characteristically stublike or sometimes not exceeding the stage of primordium (e.g., Figs. 2–3, 17–19, *Myrsine africana, Samolus valerandi, Moringa, Linum*). Walker-Larsen and Harder (2000) consider such nonfunctional staminodes temporary and doomed to be lost quickly. However, such structures may have a function in the flower that we do not grasp at this moment.

The trends in the reductive process of stamens (staminode origin) are understood as a semophyletic sequence that can still be traced in certain groups of plants. A reduction in size of stamens, correlated with a retardation of initiation of primordia, can be seen as a first obvious step in the process (Fig. 54). That one of two whorls is often retarded developmentally in diplostemonous flowers has been illustrated (see Ronse Decraene, 1992; Ronse Decraene & Smets, 1995a, 1998; Walker-Larsen & Harder, 2000). The occurrence of obdiplostemony with positional shifts of stamens is one of the mechanisms bringing about the reduction of one whorl in correlation with limitations in time and space for development (Ronse Decraene &

Table I

The occurrence of complete staminodial whorls in the Magnoliatae as derived from (ob)diplostemonous or dicyclic androecia[a]

Family	Tribe, genus, or species	Position of staminodial whorl	Authority
Alliaceae	*Allium, Trichlora, Gilliesia*	Opposite inner tepals	Rahn, 1998
Anacardiaceae	*Pentaspadon*	Antepetalous	Eichler, 1878
Bombacaceae	*Chorisia*	Antesepalous	Eichler, 1878
Bonnetiaceae	*Ploiarium, Archytaea*	Antepetalous	Dickison & Weitzman, 1998
Brexiaceae	*Brexia, Ixerba*	Antepetalous	Bensel & Palser, 1975a
Burseraceae	*Santiria*	Antepetalous	Engler, 1931d
Caesalpiniaceae	*Dimorphandra*	Antesepalous	Eichler, 1878
Caryophyllaceae	*Paronychia, Herniaria, Habrosia, Schiedea*, etc.	Antepetalous	Ronse Decraene et al., 1998b; Wagner & Harris, 2000; Figs. 17–18
Celastraceae (Lophopyxidaceae)	*Lophopyxis*	Antepetalous	Cronquist, 1981
Combretaceae	*Thiloa*	Antepetalous	Eichler, 1878
Commelinaceae	*Murdania, Anthericopsis* (1), *Palisota* (2)	Opposite inner (1) or outer tepals (2)	Faden, 1998
Connaraceae	*Connarus*	Antepetalous	Saunders, 1939
Corynocarpaceae	*Corynocarpus*	Antesepalous	Narayana et al., 1986; Philipson, 1987; Figs. 7–8
Crassulaceae	*Sempervivum*	Antepetalous	Berger, 1930
Diapensiaceae	All	Antepetalous	Palser, 1962
Dioscoreaceae	*Dioscorea sects. Macrocarpaea, Asterotricha*	Opposite inner tepals	Huber, 1998
Dipterocarpaceae	*Dipterocarpus oblongifolius*	Antesepalous	Woon & Keng, 1979
Fabaceae	*Teramnus, Biserrula sp., Vicia sp.*, etc.	Antepetalous	Eichler, 1878; Rodríguez-Riaño et al., 1999
Geraniaceae	*Erodium*	Antepetalous	Kumar, 1976; Payer, 1857; Figs. 12–13
Hamamelidaceae[b]	*Hamamelis, Corylopsis, Loropetalum,*	Antepetalous	Endress, 1967; Mione & Bogle, 1990; Figs. 15–16
Hyacinthaceae	*Albuca*	Opposite outer tepals	Speta, 1998
Hydnoraceae	*Prosopanche*	Alternitepalous	Cocucci, 1975
Hydrocharitaceae	*Lagarosiphon*	Opposite outer tepals	Cook, 1998
Johnsoniaceae	*Hodgsoniola*	Opposite outer tepals	Clifford & Conran, 1998
Lepuropetalaceae	*Lepuropetalon*	Antepetalous	Engler, 1930b
Loasaceae	*Mentzelia* sect. *Bartonia*	Antesepalous	Urban, 1892
Lomandraceae	*Sowerbaea*	Opposite outer tepals	Conran, 1998
Linaceae	*Linum, Reinwardtia,* etc.	Antepetalous	Kumar, 1976; Narayana, 1964; Narayana & Rao 1971, 1976a, 1976b, 1977a, 1977b
Medusandraceae	*Medusandra*	Antesepalous	Cronquist, 1981
Melastomataceae	*Poteranthera, Anplectrum*	Antepetalous	Eichler, 1878
Meliaceae	*Toona, Cedrela*	Antepetalous	Harms, 1960, Sheela Lal, 1994
Mimosaceae	*Pentaclethra*	Antepetalous	Eichler, 1878

Table I *(continued)*

Family	Tribe, genus, or species	Position of staminodial whorl	Authority
Moringaceae	*Moringa*	Antesepalous	Ronse Decraene et al., 1998a; Figs. 1–2
Myrsinaceae	*Myrsine*	Antesepalous	Caris, 1998
Myrtaceae	*Darwinia, Chamaelaucium*	Antepetalous	Baillon, 1873; Ronse Decraene & Smets, 1991b
Ochnaceae	*Sauvagesia, Leitgebia*	Antepetalous	Eichler, 1878; Goebel, 1933
Olacaceae	*Olax*[c], *Liriosma*	Antepetalous	Agarwal, 1963; Baillon, 1892; Sleumer, 1935
Onagraceae	*Clarkia sp.*	Antepetalous	Eichler, 1878
Oxalidaceae	*Averrhoa, Oxalis corniculata*	Antepetalous	Al-Nowaihi & Khalifa, 1971; Eichler, 1878; Kumar, 1976; Moncur, 1988; Fig. 14
Parnassiaceae	*Parnassia*	Antepetalous	Bensel & Palser, 1975a; Engler, 1930b; Saxena, 1976
Primulaceae	*Samolus*	Antesepalous	Caris, 1998; Ronse Decraene & Smets, 1995a; Sattler, 1962
Pterostemonaceae	*Pterostemon*	Antepetalous	Engler, 1930b
Ranunculaceae	*Clematis* sect. *Atragene*	Alternitepalous	Eichler, 1878
Rutaceae	*Diosmeae, Flindersia*	Antepetalous	Engler, 1931b; Sheela Lal & Narayana, 1994
Sapotaceae	*Magodendron, Mimusops, Synsepalum, Achras,* etc.	Antesepalous	Ayensu, 1972; Eichler, 1878; Hartog, 1878, Moncur, 1988; Pennington, 1991; Vink, 1995
Simaroubaceae	*Alvaradoa*	Antepetalous	Engler, 1931c
Sterculiaceae	*Buettneria, Theobroma, Abroma*, etc.	Antesepalous,	Venkata Rao, 1952; Heel, 1966; Fig. 38
Suriancaceae	*Suriana*	Antepetalous	Tschunko & Nickerson, 1976
Themidaceae	*Brodiaea, Dichelostemma*	Opposite outer tepals	Rahn, 1998
Theophrastaceae	All	Antesepalous	Cronquist, 1981; Eichler, 1878
Thymelaeaceae	*Gnidia, Craspedostoma*	Antesepalous	Domke, 1934; Gilg, 1894
Tiliaceae	*Brownlowia, Pentace*	Antepetalous	Bocquillon, 1866; Eichler, 1878; Heel, 1966
Triuridaceae	*Seychellaria*	Opposite inner tepals	Maas-van de Kamer & Weustenfeld, 1998
Xyridaceae	*Xyris*	Opposite outer tepals	Kral, 1998
Zygophyllaceae	*Tribulus* (occasionally)	Antesepalous	Engler, 1931a

[a] No information is available for *Centroplacus* (Pandaceae), Daphniphyllaceae.

[b] The nectaries of *Hamamelis* represent an inner staminodial whorl, whereas in *Corylopsis* one or two whorls of supplementary staminodial nectaries are said to arise next to the staminodial whorl (Endress, 1967). We observed that an antepetalous staminodial whorl is initiated following antesepalous stamen initiation before gynoecium initiation. Two inner protuberances bearing stomata are initiated much later and represent—we believe—receptacular nectaries (Figs. 15–16).

[c] Not exactly antepetalous in *Olax* due to reductions of stamen number.

Smets, 1995a). These reductive trends have phylogenetic implications as they are correlated with the configuration of the androecium in the eudicots: Diplostemony predominates, but there is a global trend to haplostemony or obhaplostemony. In some genera, species with staminodes coexist with species that have lost staminodes altogether (e.g., *Linum, Hesperolinon:* Narayana & Rao, 1976a, *Samolus:* Caris, 1998; Sattler, 1962).

In the monocots similar reductive trends are operating. The Zingiberales are a classic example of the semophyletic sequence in stamen reduction from an original dicyclic androecium running in a continuous sequence (the reductive process is represented with symbols used for floral formulas; *A* refers to the androecium, the numbers refer to the number of stamens in a whorl, and the raised circle refers to staminodes): Musaceae [A3+3 or A3+2(1°)] / Heliconiaceae [A2(1°)+3] – Lowiaceae / Strelitziaceae (A3+2) – Zingiberaceae [A2°+1(2°)] / Marantaceae [A1°/2°/0+1(2°)] – Costaceae [A3°+ 1(2°)] – Cannaceae [A2°+1(2°)] (see, e.g., Kirchoff, 1991; Kress, 1990). These reductions are correlated with a trend from small vestigial organs to specialized pollination mechanisms (pollinator attraction, trigger mechanisms, pollinator guidance: Endress, 1994, Walker-Larsen & Harder, 2000). The process of staminode formation must be seen as the ongoing interaction of heterochrony and heterotopy. Heterochrony changes the developmental timing and rate of development of the organ, without changing the developmental direction; heterotopy changes the nature of the organs formed, not the timing and rate of morphogenesis (Li & Johnston, 2000).

In a first evolutionary step staminodes are incidental and must be seen as a response of the flower to a changing external or internal condition. For example, a trend to zygomorphy induces one side of the flower to become retarded in its development relative to the opposite side (e.g., Leguminosae: Tucker, 1984, 1996; Moringaceae: Ronse Decraene et al., 1998a). This leads to a retardation versus stagnation in inception of part of the androecium and finally to its sterilization or abortion. This shift to sterility can run from the adaxial side to the abaxial side; *Emblingia* has four adaxial stamens opposite the petals and four abaxial staminodes (Erdtman et al., 1969). The opposite occurs in *Dactylaena* and *Euadenia* (Capparaceae), in which four adaxial staminodes fuse into a stalked appendage facing the single abaxial stamen (Figs. 4–5; Karrer, 1991). Different reductive trends may be correlated in one flower, as in *Moringa* (Ronse Decraene et al., 1998a). A generalized feature in the genus is that the antepetalous stamen whorl is reduced to stublike staminodes with no obvious function. The flower also develops a strong oblique zygomorphy. As a result, one of the staminodes is much smaller than the others and is sometimes absent (Figs. 1–2; see Ronse Decraene et al., 1998a). The duality between two groups of stamens (heteranthery) is a frequently recurring pattern related to pollination and is one probable origin of staminodes in zygomorphic flowers. Pollen flowers with some feeding stamens and only a small number of larger pollinating stamens are characteristically arranged in two opposing groups in a monosymmetric pattern (see Endress, 1999; Vogel, 1978). The feeding stamens either produce either nonviable pollen or ultimately become completely sterile.

In a second step (probably simultaneously with the loss of pollen-producing activities), these retarded organs can become transformed (by a reversal of the original strictly reductive trend) and may gain another function in the flower. Statements of functionality versus nonfunctionality are sometimes dubious, as very little is known of the floral biology of flowers. Such alternations of trends are clearly very dynamic and are related to several internal (e.g., the degree of sterilization, occurrence of homeosis) or external factors (e.g., pollinator–flower relationships). It is essential that a genetic basis exist for a reprogramming of a moribund staminodial structure; otherwise, the staminode is doomed to disappear quickly. However, one can argue whether a stublike structure should still be present in flowers when it has no obvious function. At the same time it is an indication of an ongoing evolutionary process (Heß, 1983). In the zygomorphic Scrophulariaceae the adaxial staminode can be variously developed, may vanish completely, or be sometimes conspicuous (see Endress, 1998, 1999; Reeves & Olmstead, 1998; Walker-Larsen & Harder, 2000).

Table II illustrates the strong link between zygomorphy and the occurrence of adaxial staminodes spread over different genera. Notable exceptions with anterior staminodes are *Emblingia* (Erdtman et al., 1969), *Lopezia* (Eyde & Morgan, 1973), and *Pelargonium* (Kumar, 1976; Sattler, 1973). The siting of staminode formation is linked to such factors as the orientation of the flower on the inflorescence and the type of visiting pollinator. The development of staminodes in zygomorphic flowers is independent of the number of stamen whorls, reflecting a different gene expression.

IV. A Redefinition of Staminodial Structures

A. SURVEY OF THE PROBLEM: SOME CASE STUDIES

Character research implies that characters are selected for their systematic value and their consistency (absence of homoplasy) in phylogenetic analyses. As staminodes are integral part of the androecium, they are involved in definitions related to topologies of the androecium (see, e.g., Ronse Decraene & Smets, 1993, 1995a, 1998). Predominating ideas or theories of floral evolution have influenced the approach of the androecium and staminodes in particular. As staminodes are by definition vestigial structures, they have been linked to a reductive process in flowers, along the lines of the ranalean theory. This has repercussions on descriptions of "vascular stubs" that occur on the receptacle and that are related with preexisting staminal whorls. Also, reports on the presence versus absence of vascularization in staminodes are often contradictory. In this article we demonstrate that staminodes can be confounded with all sorts of structures. Therefore, a careful study of their nature is required, involving anatomical, ontogenetic, and—if possible—genetic investigations. It should be stressed here that the circumscription of floral characters in a hierarchical ordering of characters and character-states remains a necessity for all phylogenetic analyses and that staminodes must also be approached in this way (Table I). The difficulty in interpreting staminodial structures can be illustrated by following examples:

1. The flower of the monotypic genus *Corynocarpus* J. R. & G. Forst. (Corynocarpaceae) has a perianth differentiated as five sepals and petals and an androecium of five antepetalous stamens, alternating with antesepalous scales bearing a ventral nectary (Figs. 7–8). In the past, different interpretations have been given for the petaloid antesepalous scales. Krause (1960), among others, considered the scales staminodes and the nectaries opposite these scales a disk (namely, receptacular outgrowth). Narayana et al. (1986) interpreted the scale and nectary as part of a single staminodial structure; the nectary represents the modified anther part and the petal-like scale equals the transformed connective. Another interpretation, formulated by Philipson (1987), represented the petaloid scales as equivalent to petals and the nectaries as staminodes, not as a disk. However, he admitted that the common vasculature of scale and nectary could be an indication of a strong relation between "petal" and scale. Nonetheless, scarce ontogenetic evidence seemed to suggest that "it is not possible to distinguish between the primordia of petals and scales, nor between those of stamens and nectaries" (Philipson, 1987: 13). In the absence of any clear evidence, Philipson opted for avoiding the use of the term "staminode" and preferred terms such as "petaloid scale" and "nectary" instead. The interpretation of Krause (1960) is supported by the fact that the nectary is inserted

(Text continues on p. 363)

Table II

Presence of staminodes within a whorl of fertile stamens

Key: 1 = antesepalous whorl; 2 = antepetalous whorl (alternisepalous whorl); 3 = antesepalous and antepetalous whorl; 4 = position of staminodes; 5 = number of staminodes; 6 = presence of zygomorphy in the flower

Family	Genus	1	2	3	4	5	6	Authority
Anacardiaceae (Figs. 20–21)	*Mangifera*, *Anacardium*	–	–	+	One antesepalous fertile	9	+	Copeland, 1961; Sharma, 1954
Amaranthaceae	*Lithosperma*	+	–	–	?	3	–	Eliasson, 1988
Bignoniaceae	*Catalpa*, *Kigelia*	+	–	–	Adaxial upper, or three adaxial	1, 3	+	Eichler, 1875; Neubauer, 1959
Caesalpiniaceae	*Tamarindus*, *Bauhinia*, *Cassia*, *Amherstia*, etc.	+	+	–	S2, 5/P post, Spost+P	1–2, 6	+	Eichler, 1878; Tucker, 1988b, 1988c, 1996, 1997, 1998
Cannaceae	*Canna*	–	–	+	Only Ppost fertile	1–4 (–5)	+	Kress, 1990
Capparaceae (Figs. 4–6)	*Euadenia*, *Dactylaena*	+	–	–	Slat & Spost	3	+	Karrer, 1991; Pax & Hoffmann, 1936; Ronse Decraene, unpubl.
Caryophyllaceae	*Microphyes* (1), *Ortegia* (2)	+	–	–	S1, S2 (1), S4, S5 (2)	2	–	Ronse Decraene et al., 1998b
Chrysobalanaceae	*Hirtella*, *Parinarium*	–	–	+	Spost, Ppost	?	+	Eichler, 1878
Combretaceae	*Lumnitzera*	–	+	–	Antepetalous (variable number of stamens)	1	+	Fukuoka et al., 1998
Commelinaceae	*Cochliostema* (1) *Palisota* (2), *Murdannia* (3), *Polyspatha* etc. (4)	+	+	+	Pant+Sant–lat (1), Plat–post (2), Spost (3), Plat–post+Spost (4)	1, 2–3	+	Faden, 1998
Costaceae	All	–	–	+	S, Plat–post?	5, fused into labellum	+	Larsen, 1998
Dichapetalaceae	*Tapura*	+	–	–	S2,S4	2	+	Baillon, 1874
Gentianaceae	*Hoppea*	+	–	–	?	2–3	?	Kshetrapal, 1973
Geraniaceae	*Pelargonium*	–	+	–	Pant	3	+	Kumar, 1976; Sattler, 1973
Gesneriaceae	*Sanango*	+	–	–	Spost	1 or absent	+	Dickison, 1994
Globulariaceae (incl. Selaginaceae)	*Globularia*	+	–	–	Spost (vascular bundle)	1	+	Saunders, 1937
Haemodoraceae	*Schiekia* (1), *Pyrrorhiza* (2)	+	+	–	Slat–ant (1) or Plat–post (2)	2	+	Simpson, 1998

Heliconiaceae	*Heliconia*	+	–	–	Sant	1	+	Andersson, 1998
Hydrocharitaceae	*Nechamandra, Maidenia, Vallisneria*	–	+	+	Alternitepalous (and antetepalous if petal considered as staminode)	1–2? (if petal considered as staminode)	+	Cook, 1998; McConchie & Kadereit, 1987
Krameriaceae	*Krameria*	+	–	–	Sant (S1)	1	+	Cronquist, 1981
Lamiaceae[a]	*Lavendula, Bystropogon, Salvia*	+	–	–	Spost, S4 and S5 (Slat–post)	1–2	+	Eichler, 1875; Payer, 1857
Linnaeaceae	*Linnaea, Abelia*	+	–	–	S2	1	+	Eichler, 1875
Loasaceae	*Petalonyx crenatus*	1	–	–	Spost and Slat–post	3	–	Urban, 1892
Loganiaceae	*Usteria guineensis*	+	–	–	Spost (fertile or absent)	1	+	Hakki, 1998
Malpighiaceae	*Stigmaphyllon, Gaudichaudia, Camarea*	+	–	–	S1, 5	2–3	+	Eichler, 1878
Marantaceae	All	–	–	+	Plat–ant or 0, Slat–post (only Ppost fertile)	1–2 (0)+2	+	Andersson, 1998; Eichler, 1878; Kress, 1990
Mimosaceae	*Neptunia* (staminate flowers)	–	–	+	Abaxial stamens	3	+	Tucker, 1988a
Morinaceae	*Morina*	+	–	–	Slat–ant (S1,S3?)	2	+	Hofmann & Göttmann, 1990
Musaceae	*Musa*	–	+	–	Ppost	1	+	Kress, 1990
Myoporaceae	*Oftia*, etc.	+	–	–	Spost	1 or absent	+	Bocquillon, 1861a; Cronquist, 1981
Olacaceae	*Ptychopetalum*	+	–	–	Alternipetalous	3	–	Sleumer, 1935: fig. 1H
Onagraceae	*Lopezia*	+	–	–	Sant	1	+	Eyde & Morgan, 1973
Orchidaceae	All	+	+	–	Spost, Plat–post	1, 2	+	Endress, 1994
Pedaliaceae (incl. Martyniaceae, Trapellaceae)	*Martynia, Sesamen*	+	–	–	Spost, Slat–ant	1, 2	+	Baillon, 1861, 1862c; Cronquist, 1981
Podostemonaceae	*Podostemon*	–	–	–	Incomplete inner whorl	1	–	Baillon, 1886; Rutishauser, 1997
Pontederiaceae	*Hydrothrix*	+	–	–	?	2	–	Cook, 1998
Proteaceae	*Conospermum, Protea* (1), *Synaphea* (2), *Placospermum* (3)	+	–	–	Sab (1), Sad (2), Slat and Sab (3)	1	+	Haber, 1959, 1966; Douglas, 1997 (1, 2); Douglas & Tucker, 1996 (3)
Rutaceae	*Cusparieae*	+	–	+	S2, 3, 5(4), Ppost	3–5	+	Baillon, 1872; Eichler, 1878; Kallunki, 1998

Table II *(continued)*

Key: 1 = antesepalous whorl; 2 = antepetalous whorl (alternisepalous whorl); 3 = antesepalous and antepetalous whorl; 4 = position of staminodes; 5 = number of staminodes; 6 = presence of zygomorphy in the flower

Family	Genus	1	2	3	4	5	6	Authority
Sabiaceae	*Meliosma*	–	+	–	Opp. Pant and Ppost	3	–	Beusekom, 1971
Solanaceae	*Salpiglossis, Schizanthus, Anthocercis*	+	–	–	Sant (opp. sepal 1), S1,2,5	1, 3	+	Eichler, 1875; Mair, 1977; Murray, 1945
Scrophulariaceae	*Bonnaya, Gratiola* (1), *Ixianthus* (2), *Digitalis* (3), etc.	+	–	–	Slat–ant (1), Slat–post (2), Spost (3)	1, 2	+	Chatin, 1873a; Eichler, 1875; Payer, 1857; Singh, 1979; Walker-Larsen & Harder, 2000
Surianaceae	*Suriana*	–	+	–	Antepetalous,variable (combination of fertile and sterile stamens	1–5	–	Gutzwiller, 1961; Tschunko & Nickerson, 1976
Tecophyllaeaceae	*Tecophilaea* (1), *Zephyra* (2)	+	–	+	Ppost+Slat–post (1), Slat–post (2)	2–3	+	Simpson & Rudall, 1998
Trigoniaceae	*Trigonia* (1), *Lightia* (2)	+	–	+	In adaxial part of flower (1), S3 (2), partly transformed as staminodes	2–6 (1), 1 (2)	+	Eichler, 1878; Kopka & Weberling, 1983; Smets, 1988a
Verbenaceae	*Duranta, Stachytarpheta, Lantana*, etc.	+	–	–	Sab, Slat–ant	1, 2, 3	+	Bocquillon, 1861b; Eichler, 1875; Payer, 1857; Sattler, 1973
Vochysiaceae	*Salvertia, Vochysia, Qualea*	–	+	–	Plat & ant	2, 4	+	Eichler, 1878; Kopka & Weberling, 1983; Litt, 1997
Zingiberaceae	All	–	–	+	Plat–ant, Slat–post	2+2	+	Larsen et al., 1998

[a] Payer (1857) described the initiation and later abortion of the posterior staminode in the Lamiaceae. This is rejected by Chatin (1873a), who states that no trace of a fifth stamen exists in the Labiates, unlike the Scrophulariaceae. Eichler (1875) mentions the presence of a rudimentary stamen in *Bystropogon*.

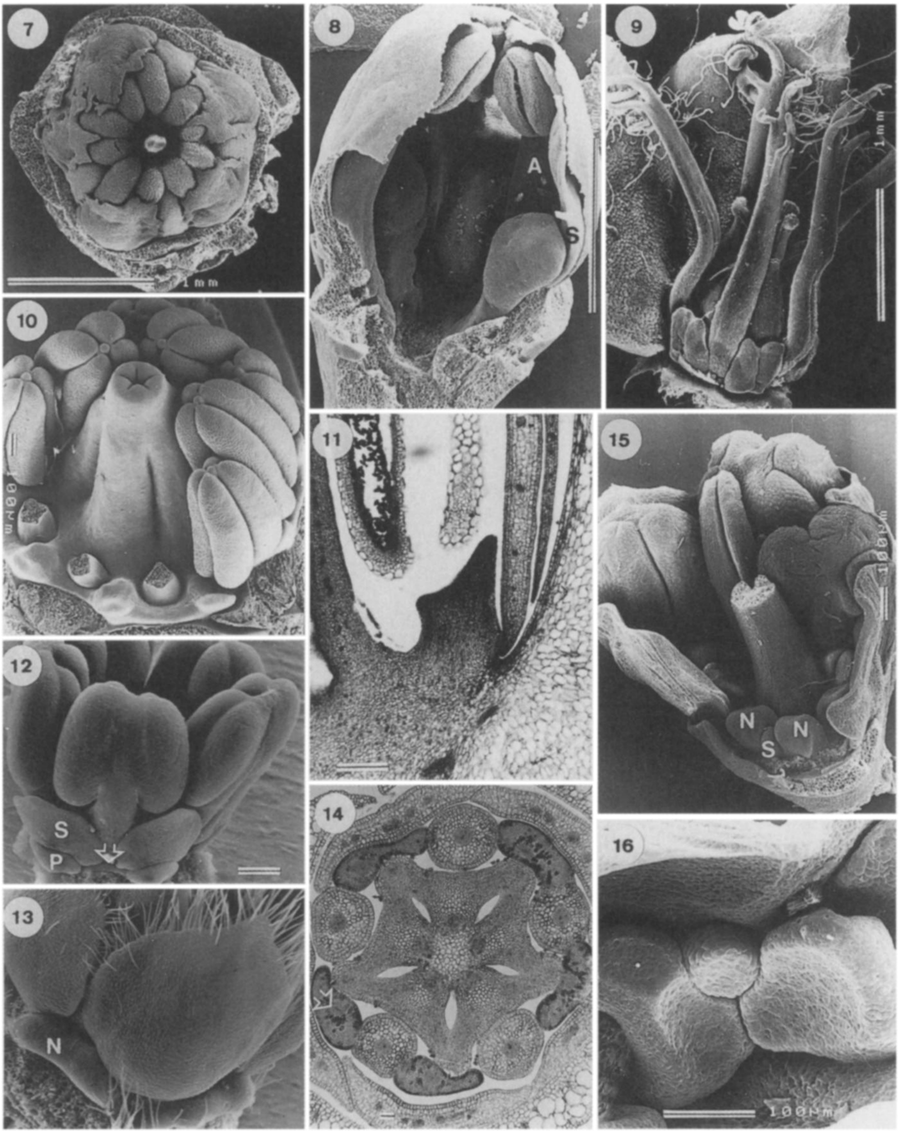
lower on the hypanthial slope and has no vascular connection (Ronse Decraene, unpubl. obs.). A thorough ontogenetic study should give more evidence of the nature of staminode and nectary, as the morphological evidence is still uncertain.

2. *Harungana madagascariensis* (Clusiaceae) and several other Clusiaceae possess antepetalous stamen fascicles alternating with five indented nectary scales (Fig. 9). Although the scales arise relatively late in ontogeny and have occasionally been interpreted as receptacular emergences (e.g., Leins, 1964), they are supplied by massive bundles alternating with the stamen traces and look superficially like anthers (Fig. 9). On this evidence Ronse Decraene & Smets (1991a) concluded that the nectaries represent a second staminodial whorl. In other taxa in which the presence of staminodes is beyond discussion (e.g., *Samolus* in Primulaceae) the staminodes also arise at a very late stage of development but are without vascular tissue (Caris, 1998; Ronse Decraene & Smets, 1995a).

3. Greyiaceae and Francoaceae have been shown to be closely related on the basis of *rbc*L data (e.g., Chase et al., 1993; Morgan & Soltis, 1993) and ontogenetic evidence (e.g., Ronse Decraene & Smets, 1999). Both families have interstaminal emergences that resemble staminodes and have been described repeatedly as such in the literature (e.g., Bensel & Palser, 1975b; Cronquist, 1981; Dahlgren & van Wyk, 1988; Morgan & Soltis, 1993; Takhtajan, 1997). Ontogenetic and anatomical studies have shown that these emergences represent nectaries with a receptacular origin and without vascular connection, and that they are not homologous with the stamens (Figs. 10–11; e.g., Klopfer, 1972; Payer, 1857; Ronse Decraene & Smets, 1999).

4. Staminodes in a similar antepetalous position either are vascularized (e.g., *Erodium*) or are not vascularized (e.g., *Linum*). For some taxa, reports are contradictory (e.g., *Erodium:* Figs. 12–13, *Averrhoa:* Fig. 14; Al-Nowaihi & Khalifa, 1971; Kumar, 1976; Narayana, 1966). For example, Al-Nowaihi & Khalifa (1973) consider the antepetalous "teeth" of Linaceae ligular appendages, not staminodes, because they lack vascularization. Indeed, other studies in Linaceae (e.g., Narayana, 1964; Narayana & Rao, 1976a, 1976b, 1977a, 1977c) report the absence of vascularization, except for Kumar (1976), mentioning short vascular stubs leading to the staminodes in *Linum*. The presence of antepetalous staminodes, together with antesepalous nectaries against the stamens in *Erodium* (Figs. 12–14), led to even more imaginative interpretations. Dawson (1936) and Kumar (1976) interpreted the androecium of Geraniales as originally triplostemonous with a progressive reduction series, leading to the transformation of outer antesepalous stamens into glands and antepetalous stamens into scale-like staminodes. However, the staminodial nature of the nectary was put in doubt by Al-Nowaihi & Khalifa (1971) because of the absence of any vascularization. It is clear that the nectaries in *Erodium* have nothing to do with the staminodes and arise independently (Figs. 12–13). In *Averrhoa,* nectaries and staminodes occur as undistinguishable structures that are vascularized (Fig. 14). The presence of an intrastaminal disk, together with a whorl of vascularized staminodes (as in *Toona, Cedrela* of Meliaceae and *Flindersia* of Rutaceae: Sheela Lal, 1994; Sheela Lal & Narayana, 1994), makes the interpretation of staminodes more concordant among authors. In *Cedrela* the antepetalous stamens are suppressed, but their traces persist within the receptacle. The related genus *Toona* has persistent staminodes (Baillon, 1895; Harms, 1960).

5. In the Hamamelidaceae it is difficult to distinguish among sterile phyllomes or appendages, staminodes, and nectaries. In *Hamamelis,* Mione and Bogle (1990) describe an antepetalous whorl as nectary primordia, while they describe the homotopic antepetalous whorl of *Loropetalum* as sterile phyllomes. In both taxa the sterile structures occasionally develop as staminodes, suggesting a staminodial origin (Baillon, 1871; Mione & Bogle, 1990). Sterile



Figs. 7–16. Variable delimitations of staminodial structures (A = fertile stamen; P = petal; S = staminode; N = nectary). **7–8.** *Corynocarpus laevigatus* J. R. & G. Forst. (Corynocarpaceae). **7.** Apical view of a flower: the staminodes form an outer whorl, partly wrapping the stamens. **8.** Longisection of flowers, gynoecium removed: staminodes are connected to a ventral nectariferous protuberance. **9.** *Harungana madagascariensis* (Choisy) Poir. (Clusiaceae): lateral view of mature flowers, corolla partly removed, staminodial nectaries alternating with the stamen fascicles. **10–11.** *Greyia sutherlandii* Hook. & Harv. (Greyiaceae). **10.** Apical view of a nearly mature flower, showing an extrastaminal disc with staminodium-like appendages. **11.** Longisection of a nectariferous appendage. **12.** *Erodium sp.* (Geraniaceae): lateral view of a nearly mature flower; note the obdiplostemonous arrangement with small petals and

(Caption continues on p. 365)

phyllomes similar to those of *Loropetalum* occur in other genera of Hamamelidaceae (*Rhodoleia, Corylopsis:* see Bogle, 1989; Endress, 1967; Figs. 15–16). Mione and Bogle (1990) argue that the sterile phyllomes of *Loropetalum,* nectaries of *Hamamelis,* and staminodes of *Corylopsis* are not derived from the same whorl of organs, because they do not arise at similar times in the development of the flower, because they have a different vascular connection, and because the least specialized genera, *Maingaya* and *Dicoryphe,* bear two whorls of both staminodes and sterile phyllomes with a different vascular supply. These facts indicate that progenitors of subfamily Hamamelidoideae of Hamamelidaceae probably possessed an androecium with at least three whorls with a functional divergence of nectariferous staminodes and sterile structures (cf. Bogle, 1989; Mione & Bogle, 1990).

From these examples it is clear that a topological definition for a staminode is sometimes sufficient but that in other cases it is not. In the example of *Harungana,* the topological criterion is supported by the vasculature and by the shape of the nectary. In *Greyia* and *Francoa* the stublike structures are associated with the androecium and alternate with the stamens, but they have nothing in common with staminodes. Indeed, the acceptance of the nectarial stubs as staminodes involves the acceptance of ancestral polyandry in Greyiaceae and Francoaceae, where the related rosid families are all basically diplostemonous.

The characterization of sterile stamens (i.e., staminodial structures) should be based on a combination of function and position in the flower rather than on their external morphology, as they are derived from a nonfunctioning stamen that must have preceded them in evolution (Figs. 52–54). Contrary to fertile stamens that are more or less restricted in their external morphology by their limited pollen-providing function, staminodes have evolved in a great variety of shapes, because of their varied functions, obscuring patterns of homology. The presence of vascular connections and the development of primordia are helpful tools for differentiating a staminodial structure. Therefore, we propose to characterize staminodes in two ways: a functional definition, with a major distinction between vestigial staminodes and functional staminodes (Fig. 52); and a topological definition, in which staminodes are approached on the basis of their relationship with the other organs in the flower (Fig. 53). The functional approach and topological definition can be combined in a time-related model, in which the evolution of the staminodes over time is stressed (Fig. 54).

Staminode evolution should be read as a progressive transformation series running from a fertile stamen into highly specialized forms. It runs from an imperfect, sterile stamen into a regressing or vestigial organ. Further evolution is biased between total loss and a conversion into a novel structure. Topology-based and function-based definitions are essentially hierarchical, in that a staminode either is homologous with a whole stamen or is part of an organ. As the androecium arises in a sequence in the flower, which may be spiral or whorled, a more detailed definition implies that the outer sphere (toward the perianth) has a staminodial nature (petalostaminodia) or that intervening (inner or middle) sterile whorls (antepetalous or antesepalous) are described as staminodial. Staminodes may also exist within a whorl or in a closed series. Staminodes as partial organs imply that they arise by the division of a common primordium.

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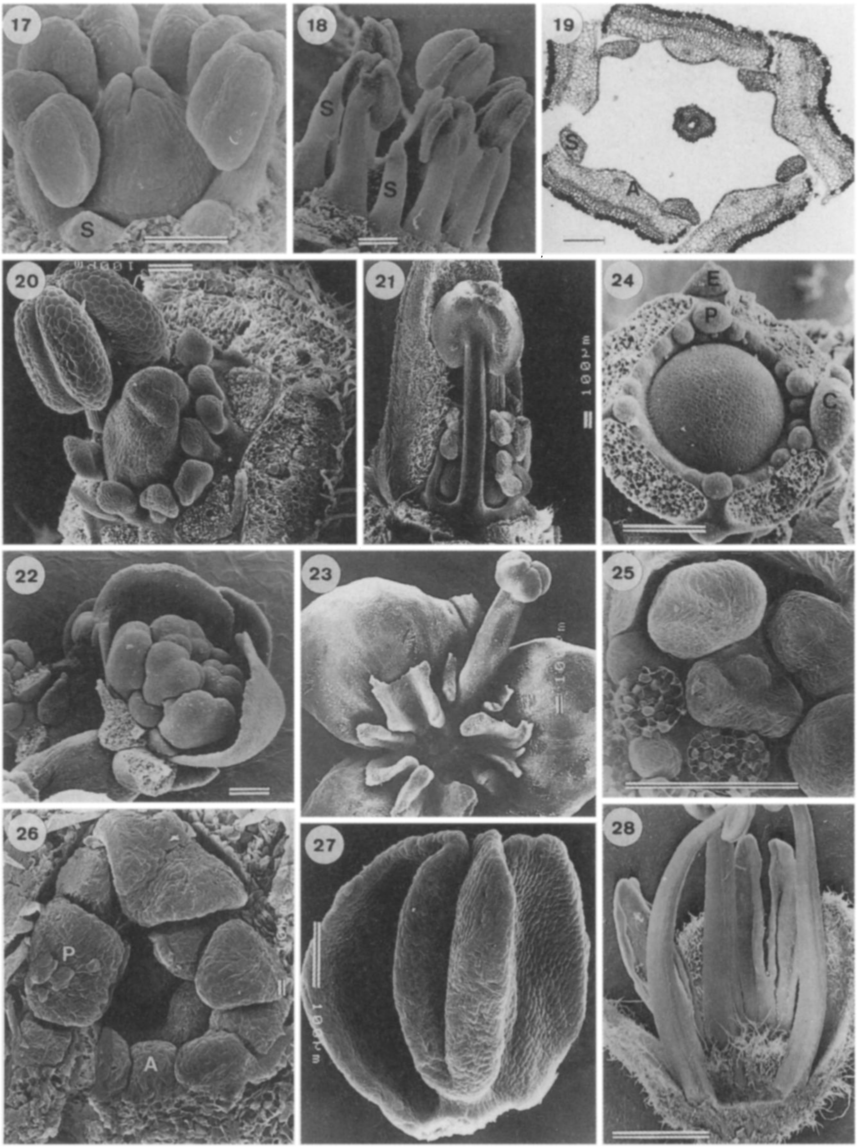
and scale-like staminodes; the arrow points to the nectary being initiated. **13.** An older bud, showing broad staminodial scales and external nectaries. **14.** *Averrhoa carambola* L. (Averrhoaceae): transverse section of a flower bud; note the nectariferous staminodial scales and their vasculature (arrow). **15–16.** *Corylopsis spicata* Sieb. & Zucc. (Hamamelidaceae). **15.** Lateral view of a nearly mature flower with three stamens removed. **16.** Detail of an antepetalous staminode with nectariferous inner scales. (bars = 100 μm, except in Figs. 7, 9, and 11 bars = 1 mm)



Figs. 17–28. Vestigial staminodes and petalostaminodes (A = fertile stamen; P = petal; S = staminode; E = epicalyx; C = calyx). **17–19.** ***Paronychia decandra*** (Forsk.) Rohweder & Urmi-König. **17.** A young flower bud with one stamen removed; note the late initiation of the staminodial whorl. **18.** A mature pistillate flower; note the filament-like staminodes alternating with the sterile stamens. **19.** Transverse section of a flower; note the absence of vascularization to the staminodes. **20–21.** ***Anacardium occidentale*** L. (Anacardiaceae). **20.** A young flower bud; note nine staminodes of unequal size lagging behind the fertile stamen. **21.** A nearly mature bud; the fertile stamen towers above the staminodial whorl. **22–23.** ***Cocculus laurifolius*** DC (Menispermaceae). **22.** Lateral view of a partly dissected flower bud; note two stamen whorls and two outer small "petal" whorls. **23.** A mature flower with all but one of

(Caption continues on p. 367)

B. EVOLUTION OF STAMINODIAL STRUCTURES: FUNCTION-BASED DEFINITION

1. Vestigial Staminodes

In its simplest form and as a primary step in stamen reduction, staminodes can persist as regressing or vestigial organs in the flower. Staminodes are an indication of a changing process, namely a reductive trend, either by the loss of a whole whorl of stamens in the transition from diplostemony to (ob)haplostemony (e.g., in Sterculiaceae, Geraniaceae, Primulaceae, Myrtaceae; Ronse Decraene & Smets, 1995a; Figs. 12, 15; Table I) or by the partial reduction of stamens within a whorl (in relation to zygomorphy: e.g., in Scrophulariaceae, Verbenaceae: see Endress, 1999; Ronse Decraene & Smets, 1994, 1995a; Walker-Larsen & Harder, 2000; Figs. 20–21; Table II). Such structures can be defined as "vestigial staminodes." Although the extent of reduction differs, they are fundamentally little altered morphologically in comparison to fertile stamens. Such staminodes may possibly retain their vasculature (helping in their identification as staminodes), or the vasculature may fade out before reaching the organ or be lost completely (e.g., *Euadenia:* Arber, 1933; Raghavan, 1939). These staminodes may have a function in the flower, but this is not always clear.

Vestigial staminodes may be found at different stages of reduction, namely as a whorl of sterile stamens with small apical anthers (which are occasionally fertile) (e.g., *Manilkara:* Pennington, 1991; *Anacardium:* Figs. 20–21), as filaments without anthers (*Paronychia:* Figs. 17–19), as more or less small stubs (e.g., *Anthirrhinum, Sagina, Moringa:* Figs. 1–3), or as minute organs that appear in the early ontogeny of the flower but are no longer visible at maturity (e.g., *Digitalis:* Chatin, 1873a; Singh, 1979). Such staminodes may be initiated as a regular whorl of stamen primordia but abort at a certain stage of their development (e.g., *Cedrela* [*Toona*]: Baillon, 1895). However, the regular alternation of whorls may often become disturbed when the sterile structures arise after the fertile whorl, as is the case for centrifugal obdiplostemony (e.g., *Theobroma* in Sterculiaceae: Ronse Decraene & Smets, 1995a).

In other cases, staminode initiation is delayed until well after the initiation of the carpels (e.g., *Paronychia decandra:* Fig. 17; *Samolus valerandi, Magodendron:* Ronse Decraene & Smets, 1995a; Vink, 1995). Theophrastaceae, Sapotaceae, Myrsinaceae, and Primulaceae are examples of the derivation of the obhaplostemonous androecium from diplostemonous ancestors. Although all Theophrastaceae possess colored, attractive staminodes little different from petals, some genera of Myrsinaceae (e.g., *Myrsine*), and Primulaceae (e.g., *Samolus*) possess evidence of antesepalous staminodes: In all cases the staminodes arise after the initiation of the common stamen-petal primordia (Caris, 1998).

It is possible that a stamen or a whole stamen whorl has vanished externally but that evidence of residual traces persists internally. For example, in the Primulaceae the median sepal traces split tangentially and give off five internal traces, which alternate with the common stamen-petal traces. They appear in the petal tube as the fused petal marginals. In *Steronema* these bundles split twice, providing the petal marginal bundles and "staminodium" bundles, which come to lie in a ring with the stamens (Douglas, 1936). This induced certain authors to

the stamens removed; the "petals" are wrapped around the base of the filaments. **24.** *Geum urbanum* L. (Rosaceae): laterocentripetal initiation of the androecium from five "petal" primordia. **25.** *Corrigiola littoralis* L. (Caryophyllaceae): initiation of antesepalous stamens (two removed) and "petals." **26–28.** *Dichapetalum madagascarense* Poir. (Dichapetalaceae). **26.** A young flower bud, showing unidirectional growth of flattened "petal" primordia. **27.** Detail of a young "petal"; note the antherlike folding. **28.** Longisection of a mature bud; note the bisected "petals" alternating with the stamens. (bars = 100 μm, except in Fig. 26 bar = 10 μm and in Fig. 28 bar = 1 mm) consider these marginal petal traces transformed stamen traces (e.g., *Soldanella:* Saunders, 1937–1939; *Primula:* Subramanyam & Narayana, 1976). Although this evidence appears to be a point for those who advocate vascular conservatism, it is absolutely not proof of a staminodial origin (see also Arber, 1933; Schmid, 1972).

In *Mangifera indica* L. or *Anacardium occidentale* L. (Anacardiaceae), reductions have affected the whole antepetalous whorl and four stamens of the antesepalous whorl (Figs. 20–21). The antepetalous whorl may often be wholly suppressed, apart from the occasional presence of short vascular traces (Sharma, 1954); the single fertile antesepalous stamen receives a larger trace than do the sterile antesepalous stamens.

The abortion of stamens within a whorl can affect different halves of the flower, with intermediate half-fertile anthers in the genera *Conospermum* and *Synaphea* (Proteaceae). The configuration of the androecium is mirror imaged between the genera, with an adaxial (*Synaphea*) or abaxial (*Conospermum*) sterile anther and two lateral anthers with one half sterile (Douglas, 1997).

2. Functional Staminodes

In several instances staminodes have become adapted to fulfil novel biological requirements in the flower in response to a specific pollination syndrome. Petals (petalostaminodia or andropetals) also play that role, but most often in a more generalized way.

The different functions of staminodes can be summarized as follows (Fig. 53):

- Production of a food supply (nutrient bodies, sterile pollen, or nectar): nutritional function;
- Development of collecting structures in association with nectaries (as nectar recipients), triggering mechanisms for pollen dispersal, secondary pollen presenters, obstacles for selfing: structural function;
- Attraction of pollinators by display of colors, odors, or heat: attractive function.

Staminodes may fulfill several functions at the same time, namely producing nectar, collecting or holding it, and being optically attractive (e.g., *Parnassia*), or different sets of staminodes may have different functions in the same flower (e.g., inner versus outer staminodes in Himantandraceae: Endress, 1984, 1986). In the magnoliids the staminodes have multiple functions related to pollination, such as attracting and directing pollinators by their color, odor, food supply, and secretions, protecting the ovary against predation, effecting pollination or preventing selfing by their position or by movements, or providing shelter and warmth (Endress, 1984, 1994; Thien et al., 1999; Walker-Larsen & Harder, 2000).

The transition from nonfunctional sterile stamens to nectar-producing structures is apparently relatively easy, depending on a vascular connection, as in *Azara* (Flacourtiaceae), where the short stubs produce nectar through stomata (Figs. 36–37). In Loasaceae (subfamily Loasoideae) the antesepalous stamens have become differentiated into colored nectar recipients (Figs. 29–30; Hufford, 1990; Smets, 1988a, 1988b; Urban, 1892). For example, in *Loasa* (Loasaceae) the staminodes are bright yellow and red, contrasting with the white corolla. In *Harungana madagascariensis* (Choisy) Poir. (Clusiaceae) the antesepalous stamen whorl has become transformed into scale-like nectaries (Ronse Decraene & Smets, 1991a; Fig. 9). In the genera *Ploiarium* and *Archytaea* of Bonnetiaceae, nectaries are discrete, antepetalous structures alternating with the stamen clusters that are supplied by double bundles similar to stamens (Dickison & Weitzman, 1998). In certain families, such as Aizoaceae, part of the centrifugally developing stamens grow into colored staminodes (Hofmann, 1993; Ihlenfeldt, 1960). *Parnassia* (Parnassiaceae) has a whorl of antesepalous stamens alternating with staminodial nectaries and resembling a fascicle of sterile stamens (Heß, 1983). Floral anatomy and ontogeny demonstrate that the nectaries are equivalent to single reduced stamens (see Bensel & Palser, 1975a; Klopfer, 1972; Saxena, 1976).

These examples of staminodes are transformed structures, namely they are basically homologous to stamens, but they have been altered by their functional requirements. Because of their obvious role in the flower, contrary to vestigial staminodes, we prefer to describe this type of sterile structures as "functional staminodes."

C. STRUCTURAL SIGNIFICANCE OF STAMINODIAL STRUCTURES: TYPOLOGY–BASED DEFINITION

1. Acyclic Staminodes

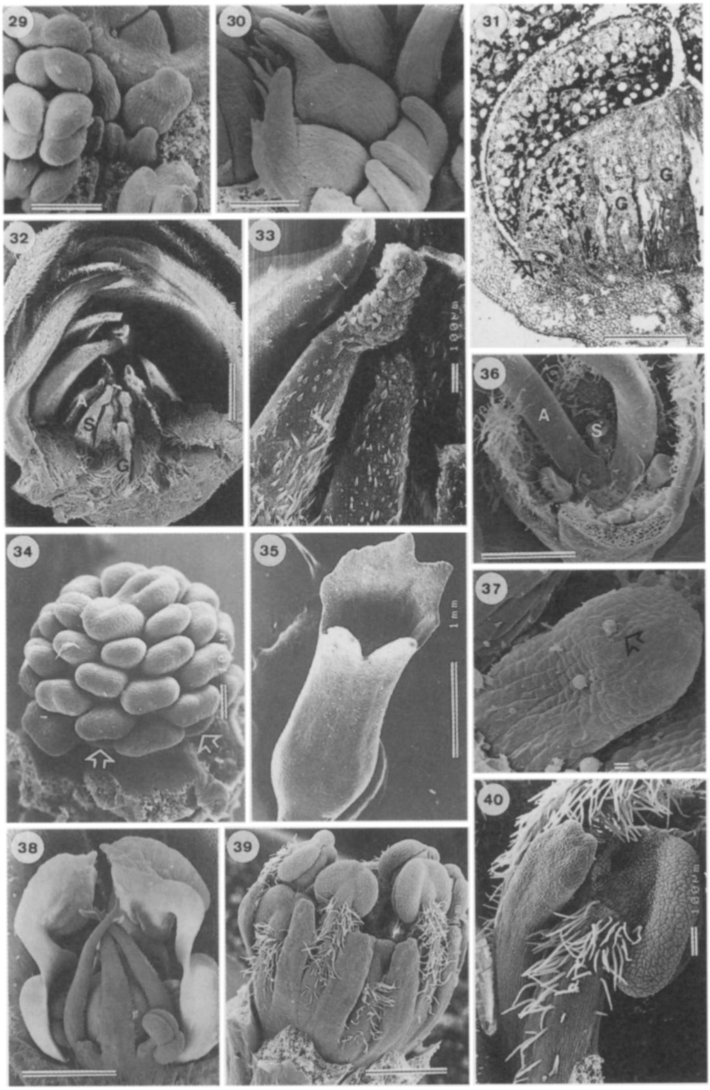
Primitive taxa of the Magnoliidae often possess staminodial structures between stamens and tepals and between carpels and stamens (e.g., Bernhardt, 1996; Endress, 1984, 1986, 1990a, 1990b; Ronse Decraene & Smets, 1993; Walker-Larsen & Harder, 2000). These staminodes are typical of spiral flowers with little or no synorganization. They represent stepping stones between different organs (e.g., tepals–stamens–carpels) and have occasionally attained specific (overlapping) functions in the flower.

For Eames (1961), the first mode of attraction of the angiosperms consisted exclusively of these upper staminodes (Figs. 32–33). However, such cases are isolated and are not linked to the generalized condition with staminodes situated in the periphery of the flower. The initiation of floral organs in a close helical sequence leaves little space for differentiation between distinct groups of floral organs without disturbing the helix considerably. The transition between tepals, sepals, petals, and stamens can only be a gradual process in this case, in which staminodes play an important role as multifunctional transitional structures (e.g., protective structures versus nutrient bodies or showy attractive organs: see Endress, 1984, 1986, 1990a). In the eudicots the different functions often become separated in space and time.

2. Complete Staminodial Whorls

In many cases (see Table I) a whorl of stamens tends to become completely sterilized in the flower. In this way a diplostemonous androecium becomes transformed into an (ob)haplostemonous one. Evidence for a phylogenetic link between the two androecial configurations, running only in one direction, relies essentially on staminodial structures (see Ronse Decraene & Smets, 1995a). Staminodes evolved many times in the rosids (Walker-Larsen & Harder, 2000). In the Malvales and former Theales the occurrence of antesepalous staminodes is correlated with secondary multiplication of the other stamen whorl (Fig. 38). Staminodes tend to be the expression of a no-return reductive process, although they occasionally attain a new function in the flower (e.g., Bonnetiaceae, Clusiaceae, Malvaceae, Sterculiaceae, Parnassiaceae, Lepuropetalaceae: Figs. 2, 7, 9, 12, 15, 36, 38).

Whorls of staminodes related to a reductive trend also occur in the more primitive taxa with a polycyclic androecium. *Monanthotaxis whytei* (Stapf) Verdc. (Annonaceae) has two outer whorls of staminodes (Ronse Decraene & Smets, 1990a, 1993; Fig. 31). The more external whorl of six pairs appears in early development but is hardly visible at maturity; the next whorl of nine staminodes remains relatively large at maturity. Such cases probably represent stages in a stepwise reduction of a polycyclic androecium (see Ronse Decraene & Smets, 1993).



Figs. 29–40. Functional staminodes and developmental staminodes (A = fertile stamen; S = staminode; G = carpel). **29.** *Blumenbachia hieronymi* Urb.(Loasaceae): young stage of staminodial development, alternating with antepetalous stamen groups. **30.** *Cajophora contorta* K. B. Prest (Loasaceae): an older stage of staminodial development; note the difference between the outer nectar sacs and inner appendages. **31.** Longisection of a flower of *Monanthotaxis whytei* (Stapf) Verdc. (Annonaceae): the fertile stamens are surrounded by two series of staminodes, with a degression in size toward the periphery. **32–33.** *Calycanthus fertilis* Andr. (Calycanthaceae). **32.** Longisection of a flower with a transition of tepals, stamens, staminodes, and carpels. **33.** Detail of stamen and staminode, with "food bodies." **34–35.** *Helleborus foetidus* L. (Ranunculaceae). **34.** A young flower bud with spiral initiation of stamens and two carpels; staminodial structures (arrows) arise in alternation with the outermost stamens. **35.** Detail of a mature staminodial nectar recipient; note the two ventral appendages. **36–37.** *Azara microphylla*

(Caption continues on p. 371)

3. Petalostaminodia

The corolla, or petal whorl, represents a special case of a complete staminodial whorl. Staminodes are sometimes petaloid, leaflike appendages that cannot be differentiated from the petals (e.g., in some Theophrastaceae, Corynocarpaceae: Figs. 7–8). They are evidence of a direct link between stamens and petals. As they are not different from petals or it is in some cases not possible to differentiate them (e.g., in some Caryophyllaceae), this kind of petaloid staminodes are best called "Petalostaminodia." Teratological cases of double flowers, as in Rosaceae or Malvaceae (e.g., Innes et al., 1989; MacIntyre & Lacroix, 1996) are a classic example of this transition. In other cases petaloid staminodes may be observed in the position that petals normally occupy (e.g., in Hamamelidaceae: Endress, 1967; Mione & Bogle, 1990, Caryophyllaceae: Ronse Decraene et al., 1998b; Fig. 25). The number of stamens can also be augmented at the cost of petals (Mürbeck, 1918: "staminal pseudapetaly," quoted in Endress, 1967).

Petals represent a problematic case of staminodial origin, as it is generally assumed that the petals of a great many angiosperms have been derived from stamens and are homologous with them (e.g., Cronquist, 1988; Eames, 1961; Endress, 1986, 1994; Hiepko, 1965; Takhtajan, 1980, 1991; Weberling, 1989; Worsdell, 1903). In many cases it is difficult to determine when a petal ceases to be a staminode and when a staminode ceases to be a stamen (Figs. 24–25). At another extreme, petals can sometimes attain all structural and developmental attributes of sepals, concomitant with changing functions (Endress, 1994). Strictly speaking, petals must be seen as showy, flattened, and colored organs occupying the space between the sepals and the androecium. In comparison with staminodes within the androecium, the development of petals from stamens is an evolutionary step that has taken place repeatedly in angiosperm evolution.

Petals have probably arisen several times in the Ranunculales from outer (nectar-producing) staminodes (see, e.g., Drinnan et al., 1994; Endress, 1995; Hiepko, 1965; Kosuge, 1994; Figs. 22–23, 34–35). In Ranunculaceae there are transition series from inconspicuous staminodes to elaborate petaloid nectar leaves occurring among genera (Ronse Decraene & Smets, 1995b). The morphological homology between nectar leaves and stamens has been traced back ontogenetically in a number of species of Ranunculaceae by Erbar et al. (1998). A topological definition of staminodes is also in concordance with the nectary types proposed by Smets (1988a), nectaria nectarophyllomina and nectaria staminodialia. The nectarophyllomina type of nectaries (or *Helleborus* type) correspond with the petalostaminodes characteristic of the Ranunculales (e.g., Ranunculaceae, Berberidaceae, Menispermaceae). The staminodialia type of nectaries (or *Trigonia* type) correspond with staminodes that are more strongly associated with the androecium.

Clear ontogenetic descriptions of homeotic shifts between petals and stamens are *Sanguinaria,* with an extra whorl of petals (Papaveraceae: Lehmann & Sattler, 1993) and *Actaea* (Ranunculaceae: Lehmann & Sattler, 1994), petals transformed into stamens in *Macleaya*

Hook. f. (Flacourtiaceae). **36.** Longisection of a young flower with the gynoecium removed; note the small staminodial (?) appendages alternating with the stamens. **37.** Detail of a nectar-producing appendage; the arrow points to nectarostoma. **38.** *Theobroma cacao* L. (Sterculiaceae): lateral view of a nearly mature flower bud with two spathulate petals removed; note the laciniate antesepalous staminodes alternating with the stamen groups. **39–40.** *Casearia bracteifera* Sagot. (Flacourtiaceae): lateral view of a nearly mature flower bud; the stamens are in two whorls and are flanked by an external whorl of staminodial (?) appendages; detail of fertile stamen and external appendage. (bars = 100 μm, except in Figs. 36 and 38 bars = 500 μm, in Fig. 35 bar = 1 mm, and in Fig. 39 bar = 200 μm)

(Papaveraceae: Ronse Decraene & Smets, 1990b), stamens occupying the position of petals in *Saraca* and *Swartia* of the Leguminosae (Tucker, 1988b), *Dichapetalum* (Dichapetalaceae: Breteler, 1973; Figs. 26–28, but see Table III), or double-flowered *Hibiscus* of Malvaceae (MacIntyre & Lacroix, 1996). Illustrations of *Swartia* in Tucker (1988c: 77) show that there are a single petal and three large stamens in one outer whorl, while the remaining stamens are crowded on a ring primordium. The transition of stamens into staminodes, and further into petals is best described by the term "serial homeosis."

The terms "andropetals" (related to and derived from stamens and similar to staminodes) and "bracteopetals" (related to and derived from bracts and sepals) distinguish between two kinds of petals in the angiosperms, even when shifts have occurred between petals and sepals (see Hiepko, 1965; Kosuge, 1993; Ronse Decraene & Smets, 1993, 1995b; Takhtajan, 1991). Important arguments for the presence of "andropetals" as opposed to "bracteopetals" (Hiepko, 1965; Takhtajan, 1991) are the vascular arrangement (one-trace organs; however, this distinction has little relevance because three-traced stamens may also occur), the ontogeny (similarity to stamen primordia in shape of primordia, retardation of growth of the petals), teratological cases, but most important the spatial relation between stamens and petals (existence of parastichies). Very often petals resemble stamens in having a stalk and a limited insertion area (clawed structures). Staminodes belonging to a staminal whorl may also become secondarily petaloid, as in the Zingiberales (e.g., Kirchoff, 1991; Walker-Larsen & Harder, 2000).

Flowers are occasionally secondarily apetalous but may occasionally become secondarily petaliferous. In that case, outer staminodes may be differentiated as outer petaline structures, which confuses the limits between petals and staminodes as in Scytopetalaceae (Appel, 1996), or there is an outer receptacular corona without clear homology with staminodes (Passifloraceae: Bernhard, 1999a).

The strong link between petals and stamens has a genetic basis that has been extensively studied in the last ten years for the model genera *Antirrhinum* and *Arabidopsis* (e.g., Bowman et al., 1991; Coen & Meyerowitz, 1991: ABC model). At the same time, the petals are intermediate between stamens and sepals. We therefore assume that there are repeated evolutionary origins for petals, either from stamens (in the majority of eudicots) or from sepals.

4. Incomplete Staminodial Whorls

The presence of staminodes within a stamen whorl is often an indication of the monosymmetric development of the flower. A stamen whorl becomes partially sterile, as an adaptation to a "vectorized" pollinator visit. The reduced stamen usually occupies a position crossed by the symmetry line. Staminodial structures may be found within one or two whorls of stamens, depending on the androecial configuration that functions as the starting point.

In the Fabales stamens arise unidirectionally, and the abaxial part of the androecium is often "advanced" compared with the posterior part. Adaxial stamens are often smaller, as they lag in development (e.g., *Chamaecrista:* Tucker, 1996), are staminodial (as in *Petalostylis* with two antesepalous staminodes: Tucker, 1998; or in *Cassia* and *Senna* with three adaxial staminodes and a strong heteranthery: Tucker, 1996), or are missing. An extreme is *Bauhinia divaricata,* with a single stamen, nine staminodes, and a variable number of petals (Tucker, 1988b). Petals and all other stamen primordia are initiated but are arrested at a given stage of their development. Other species of *Bauhinia* have a variable number of staminodes, have sterile stamens, or none at all (Tucker, 1984, 1988b).

In many taxa of the asterids, zygomorphy is correlated with the occurrence of an adaxial staminode. Androecial initiation is unidirectional, with a delayed initiation of the adaxial sta-

(Text continues on p. 383)

Table III

Various misinterpretations of receptacular emergences as staminodes (pseudostaminodes), carpellodes, or structures with unknown or debatable homologies

Family	Genus or species	Protagonist evidence	Description	Protagonist authority	Detractive evidence	Description	Detractive authority
Achariaceae	*Ceratiosicyos, Acharia, Guthriea*	External	"Glieder eines zweiten staminalkreises"; staminodes	Goldberg, 1986; Hooker & Masters, 1871, cited in Harms, 1925b	Ontogenetic, but vascularized	Nectary-like bodies	Bernhard, 1999b
Aextoxicaceae	*Aextoxicon*	External	Fleshy, bilobed glands alternating with the stamens	Ronse Decraene, 1985; Smets, 1988a	External	5 pairs of coalescent glands derived from 10 initial structures	Baillon, 1870
Amaranthaceae	*Achyranthes*, etc.	External	Interstaminal appendages, staminodes	Joshi, 1932; Joshi & Venkata Rao, 1934; Saunders, 1939	No evidence for extra whorl of stamens	"Nebenblätter" (1); pseudostaminodia (interstaminal appendages, part of staminal tube) (2)	Eichler, 1878 (1); Eliasson, 1988; Payer, 1857; Schinz, 1934 (2)
Apocynaceae (Figs. 48–49)	*Vinca, Allamanda,* etc.	Anatomical link with the gynoecium	Nectaries derived from carpellodes	Woodson and Moore, 1938	Anatomical, derivation of disk traces well below ovary	"Proliferation of receptacular tissue between the androecium and the gynoecium"	Rao & Arati Ganguli, 1963: 433
Bataceae	*Batis*	External, no anatomical	Whitish spatulate, slender-stalked, denticulate "appendages" or staminodia; "Petalen die durchaus als staminodien gelten können"	Eckardt, 1959: 416; Johnson, 1935: 23	Lacking; ontogeny needed	No conclusive evidence for staminodes or petals	None

Table III *(continued)*

Family	Genus or species	Protagonist evidence	Description	Protagonist authority	Detractive evidence	Description	Detractive authority
Brassicaceae	None	External	Transformed median stamens	Alexander, 1952; Bernhardi, 1838, cited in Eichler, 1878; Goebel, 1933	Ontogeny, external, anatomical	Receptacular nectaries with variable development and vascular connections	Arber, 1931; Bowman & Smyth, 1998; Eichler, 1878; Norris, 1941, etc.
Burseraceae	*Balsamodendron*	Anatomical	A disk staminal in nature	Shukla, 1955, cited in Narayana, 1960	None	None	None
Capparaceae	*Cadaba, Capparis*	Anatomical, external	Remnant of a former staminal supply, episepalous glands, or unilateral appendage	Stoudt, 1941; Weberling & Uhlarz, 1983	External, ontogenetic	Late appearance in ontogeny, outer morphology	Pax & Hoffmann, 1936; Payer, 1857; Weberling & Uhlarz, 1983
Celastraceae	*Celastrus*	Anatomical	A disk of staminal nature (evidence of small traces)	Berkeley, 1953	None	None	None
Clusiaceae (Fig. 9)	*Hypericum, Harungana,* etc.	Anatomical, ontogenetic	Transformed staminodes	Eichler, 1878; Payer, 1857; Ronse Decraene & Smets, 1991a	Ontogeny	Receptacular emergences	Leins, 1964
Crassulaceae (Figs. 50–51)	None	External, anatomical	Staminodes or carpellodes	Eichler, 1878	External, ontogeny	Receptacular appendages, dorsal appendages of carpels	Eichler, 1878; Payer, 1857; Smets, 1988a
Ctenolophaceae	*Ctenolophon*	Anatomical	Disk as modified stamens	Narayana & Rao, 1971	External, anatomical	Extrastaminal, receptacular	Link, 1992
Dichapetalaceae (Figs. 26–28)	*Dichapetalum*	External	Petals and disk lobes are staminodes	Breteler, 1973	External	Nectary glands, disk lobes	Cronquist, 1981; Leenhouts, 1956, cited in Breteler, 1973

Dipentodontaceae	*Dipentodon*	External	Staminodial(?) nectary glands	Cronquist, 1981	None	None	None
Epacridaceae	None	External	Staminodes represented by a cluster of antepetalous glands (1); or hair bundles on corolla tube (2)	Chatin, 1873b (1); Cronquist, 1981; Eichler, 1875 (2)	Ontogenetic	"Le disque n'est que le gonflement de la partie du réceptacle qui supporte l'ovaire"	Payer, 1857: 578; Smets, 1988a
Euphorbiaceae	*Croton, Cluytia, Mercurialis,* etc.	External	"Écailles ou glandes de nature staminodiale avec loges d'anthères stériles" (1); staminodial origin of inner or outer whorl (3 stamen whorls) (2)	Baillon, 1862b (1); Eichler, 1878; Gandhi & Thomas, 1983; Goebel, 1933; Michaelis, 1924[a] (2)	External, anatomical	Variably episepalous or epipetalous disk lobes with vascular supply from different sources	Baillon, 1874; Beille, 1901; Venkatao Rao & Ramalakshmi, 1968
Fabaceae	Phaseoleae	Anatomical	Disk as sterilized branches of the androecium	Moore, 1936a, 1936b	External, ontogenetic	Very late initiation of disk, diplostemonous flowers	Smets, 1988a
Flacourtiaceae (Figs. 36–37, 39–40)	*Casearia, Azara,* etc.	External	Antepetalous staminode-like disk appendages: "staminodienartigen Diskusforsätzen"	Eichler, 1878; Gilg, 1925; Ronse Decraene, unpubl.	Ontogenetic	Scales are of same number as stamens and appear much later	Bernhard & Endress, 1999
Francoaceae	*Francoa*	External	Staminodes	Bensel & Palser, 1975b; Takhtajan, 1997	Ontogenetic, anatomical	No vascular connection, late initiation, extrastaminal	Ronse Decraene & Smets, 1999
Geraniaceae	*Geranium, Pelargonium*	Anatomical	Original triplostemony with transformation of outer stamen whorl	Dawson, 1936; Kumar, 1976	Ontogenetic, anatomical	Basically diplostemonous, nectaries receptacular	Payer, 1857; Sattler, 1973; Smets, 1988a

Table III *(continued)*

Family	Genus or species	Protagonist evidence	Description	Protagonist authority	Detractive evidence	Description	Detractive authority
Greyiaceae (Figs. 10–11)	*Greyia*	External	10 small staminodes	Cronquist, 1981; Dahlgren & van Wyk, 1988; Steyn et al. 1987	Ontogenetic, anatomical	No vascular connection, late initiation, extrastaminal	Ronse Decraene & Smets, 1999
Humiriaceae	*Sacoglottis, Vantanea, Humiria,* etc.	External	"Des languettes étroites et subulées qui sont des filets dépourvus d'anthères" (1); the disk can be interpreted as the inner sterilized part of the staminal tube (2); inner staminal whorls staminodial (3)	Baillon, 1860a: 208 (1); Narayana & Rao, 1969, 1977b: 150, 1978 (2); Winkler, 1931 (3)	Anatomical; ontogeny lacking	Disk variously supplied by bundles from the stamens, or without vascular connections	Smets, 1988a, this study (based on descriptions in Narayana & Rao, 1977b)
Hydrophyllaceae	*Phacelia glaberrima*	External	"The nectary appears to be the morphologically homologous to an inner whorl of stamens"	Cosa, 1995, cited in Sérsic & Cocucci, 1999: 402	None	None	None
Ixonanthaceae	*Ixonanthes, Ochthocosmus*	Anatomical	Disk of staminal origin	Narayana & Rao, 1966	Ontogeny lacking	None	None
Lauraceae (Fig. 41)	None	Anatomical, external	Splitting of organ in three parts and sterilization of lateral parts (1); result of association of three stamens	Daumann, 1931 (1); Eames, 1961, etc. (2); Rohwer, 1994 (3)	Ontogenetic	De novo emergences, staminal appendages	Endress, 1980; Kasapligil, 1951; Payer, 1857; Singh & Singh, 1985

			and transformation of lateral parts in glands (2); telomic structure (3)				
Lepidobotryaceae	*Lepidobotrys*	Anatomical	Staminodial disk	Narayana & Rao, 1974	External	Receptacular disk	Link, 1991
Melianthaceae	*Melianthus*	External	Posterior stamen as part of abaxial nectary; "dass das hintere mediane Stamen fehlt, . . . und zum Nectarhalter geworden ist"	Eichler, 1878; Wydler, 1863: 149	Ontogenetic, anatomical	No evidence for staminodial nature	Payer, 1857; Ronse Decraene et al., 2001
Nyctaginaceae	*Mirabilis*	External	Interstaminal appendages interpreted as aborted stamens	Buxbaum, 1961; Friedrich, 1956	Ontogenetic	Extensions of the staminal tube	Rohweder & Huber, 1974; Vanvinckenroye et al., 1993
Ochnaceae	*Sauvagesia*	External, anatomical	Staminodial disk, outer staminodes (corona)	Cronquist, 1981; Gilg, 1925; Goebel, 1933; Saunders, 1939	External	Paracorolla as in Passifloraceae (no transition with stamens), next to true antepetalous staminodial whorl	Eichler, 1878; this study
Olacaceae[b]	*Aptandra, Strombosia, Octoknema*, etc.	External	Staminodes	Sleumer, 1935	External	Extrastaminal or intrastaminal disk	Cronquist, 1981; Reed, 1955; Smets, 1988a
Opiliaceae	*Opilia*	External	Scales alternating with the stamens	None	External	"Glandes volumineuses" (1); intrastaminal nectary disk (2); "five broad disk lobes alternate with the stamens" (3)	Baillon, 1892: 412 (1); Cronquist, 1981 (2); Reed, 1955: 41 (3)

Table III *(continued)*

Family	Genus or species	Protagonist evidence	Description	Protagonist authority	Detractive evidence	Description	Detractive authority
Oxalidaceae	*Oxalis*	External, anatomical	Tongue-like structures separated from the back of the alternipetalous stamens	Kumar, 1976	Anatomical, developmental	Extrastaminal appendage or gland, ligular appendage	Al-Nowaihi & Khalifa, 1971; Eichler, 1878
Paeoniaceae	*Paeonia*	Anatomical	"The disk is largely androecial in nature" (1); "the disk represents a sterilised part of the androecium" (2)	Eames, 1953, 1961 (1); Goebel, 1933; Melville, 1984 (2)	Developmental	Receptacular disk	Baillon, 1862a; Eichler, 1878; Hiepko, 1966
Passifloraceae[c]	*Passiflora, Adenia, Crossostema,* etc.	External, anatomical, developmental	Staminodes as "Spitzchen . . . die sich als Staminod. deuten lassen (1); corona partly staminodial (limen) (2); 5 alternating ridges in *Basananthe;* two whorls of 5 protrusions in *Crossostema* interpreted as original triplostemony (3)	Harms, 1925a: 480 (1); Puri, 1948, 1951 (2); De Wilde, 1974 (3)	Developmental	Extrastaminal nectary receptacular in nature; also the 5 antesepalous nectaries of *Adenia* (no positional and time relation with the androecium); 5 alternating ridges dubiously staminodial	Bernhard, 1999a
Peridiscaceae	*Peridiscus*	External	Multilobed disk of staminodial origin	Cronquist, 1981; Hutchinson, 1959	No ontogenetic evidence	None	None

Podostemonaceae	*Polypleurum*, etc.	External	The sepal-like staminodes arise at the base of the filament	Khosla & Mohan Ram, 1993: 257	External	Petaloid, spathulatetepals	Baillon, 1886; Engler, 1930a; Rutishauser, 1997[d]
Polemoniaceae (Fig. 47)	*Cantua*, *Cobaea*, *Phlox*	Anatomical	5 vestigial antepetalous stamen traces split up in numerous small branches and supply disk	Dawson, 1936	None	None	None
Polygonaceae (Figs. 42–43)	*Fagopyrum*, *Polygonum*	External	"Les nectaires isolés sont des étamines réduites"	Emberger, 1939: 591	External, anatomical	Receptacular mamillae	Ronse Decraene & Akeroyd, 1988; Ronse Decraene & Smets, 1991c
Primulaceae	*Primula*, *Soldanella*	Anatomical	A third whorl of vestigial traces (1); as petal marginal traces derived from the dorsal sepal trace and incorporated in the corolla (2)	Dickson, 1936 (1); Saunders, 1939 (2); Subramanyam & Narayana, 1976	Ontogenetic, anatomical (*Coris*)	No external evidence	Payer, 1857; Ronse Decraene et al., 1995
Proteaceae	None	Anatomical, external	Intrastaminal scales[e]	Ronse Decraene, 1985	Developmental	Nectar scales as secondary organs	Brough, 1933; Douglas & Tucker, 1996
Rhamnaceae (Fig. 45)	*Zizyphus*, *Helinus*, etc.	Anatomical	Disk from modified stamens (evidence of obdiplostemony)	Nair & Sarma, 1961; Prichard, 1955	External, developmental	Variable intrastaminal disk, intrastaminal thickening of the receptacle	Bennek, 1958; Payer, 1857; Suessenguth, 1953a
Rhizophoraceae	*Crossostylis*	External	Inner whorl of staminodes alternating with the stamens in 3 of the 10 species[f]	Setoguchi et al., 1996	Developmental	Intrastaminal appendages	Juncosa, 1988; Juncosa & Tomlinson, 1987

Table III *(continued)*

Family	Genus or species	Protagonist evidence	Description	Protagonist authority	Detractive evidence	Description	Detractive authority
Rubiaceae	*Mitchella*	Anatomical	"The disk may represent an expansion of the receptacle, or a second whorl of carpels"	Blaser, 1954: 538	No ontogenetic or anatomical evidence	None	None
Rutaceae	None	Anatomical	Sterilized branches of the androecium, branches from staminal straces (modified stamens)	Tillson & Bamford, 1938	External	Enlargement of the floral axis between the stamens and the base of the ovary	Penzig, 1887, cited in Tillson & Bamford, 1938
Salvadoraceae	*Salvadora, Dobera*	External	Antepetalous "Zähnchen oder Diskus-Drüsen"	Mattfeld, 1960a: 232; Ronse Decraene, 1985	External	Considered as fused stipules of the stamens (1); receptacular nature (no vascular supply) (2)	Glück, 1919, cited in Mattfeld, 1960a (1); Kshetrapal, 1970 (2)
Sapindaceae	*Xanthoceras*	External	5 alternipetalous staminodes	Bonnier, 1879, cited in Smets, 1988a	External	Disk with 5 long, fleshy appendages	Radlkofer, 1896
Sarcolaenaceae	*Xyloolaena*	External	Disk with "cinq écailles alternisépales" (1); nectary disk of probable staminodial origin (2)	Baillon, 1884 (1); Cronquist, 1981 (2)	None	Evidence is lacking to assign a staminodial nature to the disk	Smets, 1988a
Scyphostegiaceae	*Scyphostegia*	External	Three stubs in front of the inner perianth and opposite the stamens (related to petals) (1); or stamens (2)	Baehni, 1937, 1938 (1); Swamy, 1953, all cited in Heel, 1967 (2)	Anatomical	Extrastaminal disk glands	Van Heel, 1967

Simaroubaceae	*Picrasma*, *Brucea* (1); *Samadera* (2); *Picramnia*, *Eurycoma*, etc.	Anatomical, external	Variously receptacular, derived from antesepalous stamens, or mixed antepetalous and carpellary traces; outer whorl of sterile carpels	Eichler, 1878; Engler, 1931c; Nair & Joseph, 1957; Nair & Joshi, 1958	Anatomical	Supply of disk highly variable in the family[g]	Smets, 1988a
Stackhousiaceae	*Stackhousia*, *Tripterococcus*	External	"Die Drüsen selbst entsprechen möglicherweise einem zweiten Staminalkreis"	Mattfeld, 1960b: 243	No ontogenetic or anatomical evidence	None	None
Tamaricaceae	*Tamarix*	Anatomical, External	"The disc is staminal in nature being formed by the staminal bases and their stipules" (1); inner antipetalous staminal whorl (2)	Murty, 1954: 235 (1); Zohary & Baum, 1965 (2)	External, developmental	Stipular appendages ("Stipularzähnchen"), staminal tube with teeth	Eichler, 1878; Payer, 1857
Thymelaeaceae	None	Anatomical, External	Disk is the inner part of androecium	Domke, 1934; Heinig, 1951; Meisner, cited in Gilg, 1894	External	"Receptaculareffigura-tionen" (no evidence of transitions)	Gilg, 1894
Turneraceae	*Turnera*, etc.	External	5 glands or protuberances between the stamens and petals	Cronquist, 1981: 409; Ronse Decraene, 1985	External	Nectar secreted by broadened abaxial parts of filaments (nectarotheca)	Smets, 1988a
Vitaceae (including Leeaceae) (Fig. 44)	*Leea*, *Vitis*	External	Staminodial tube, staminodial scales	Nair & Nambisan, 1957; Ridsdale, 1974; Suessenguth, 1953b	Developmental	Disk arising from the base of the gynoecium	Gerrath et al., 1990

Table III *(continued)*

Family	Genus or species	Protagonist evidence	Description	Protagonist authority	Detractive evidence	Description	Detractive authority
Zygophyllaceae	*Balanites*	Anatomical	Disk of staminodial nature (vascular supply derived from stamen traces)	Nair & Jain, 1956	Developmental	Receptacular emergence	Ronse Decraene, unpubl. obs.

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[a] Michaelis (1924) gives several arguments for a staminodial nature of the nectaries, including the position of the glands and external shape. The late initiation and variable position of the nectaries (e.g., Beille, 1901) are arguments against this.

[b] True staminodes occur occasionally in the Olacaceae (e.g., Agarwal, 1963; Baillon, 1892; Sleumer, 1935: *Olax, Liriosma*). In some genera of tribes Anacoloseae and Aptandreae there are disklike appendages with a possible homology to stamens (Sleumer, 1935: 7: "Es könnte sich bei diesn lappigen Drüsen oder dem gekerbten Drüsenring auch um umgebildete äussere oder inner Stam. handeln").

[c] In *Crossostemma* and *Basananthe* a second series of small protrusions alternates with the stamens (Bernhard, 1999a).

[d] Podostemoideae possess an additional envelope, homologous to prophylls or leaves (spathella), whereas Tristichoideae have a cuplike cover (Cupule) (Rutishauser, 1997).

[e] Haber (1959, 1961, 1966) interprets the scales as a petal whorl, because their vasculature is connected with the sepal lateral bundles, their tetramerous plan, and the alternisepalous position. Joshi (1936) interprets the disk scales of *Stellera* (Thymelaeaceae) in the same way.

[f] The "staminodes" in *Crossostylis* alternate with the stamens and are the same in number. They have no vascular connection and no obvious function. They are situated between the stamens and a nectary disk that is present in all species (Setoguchi et al., 1996). Juncosa (1988: 86) states that the intrastaminal appendages are initiated long after the stamens have developed and are therefore "clearly not staminodes." The common diplostemonous androecium in the family (symplesiomorphy) supports the latter interpretation.

[g] The disk of *Brucea* receives its vascular supply from three sources: branches from the antesepalous staminal traces, a first whorl of disk traces is found alternating with the stamens, followed by a second whorl opposite the stamens, but as part of the carpellary tissue (Nair & Joshi, 1958). Engler (1931c) described *Alvaradoa* as having five sterile antepetalous stamens. In other cases (e.g., *Eurycoma*) the description of antepetalous appendages is more cautious ("wahrscheinlich Staminodien": l.c.: 381).

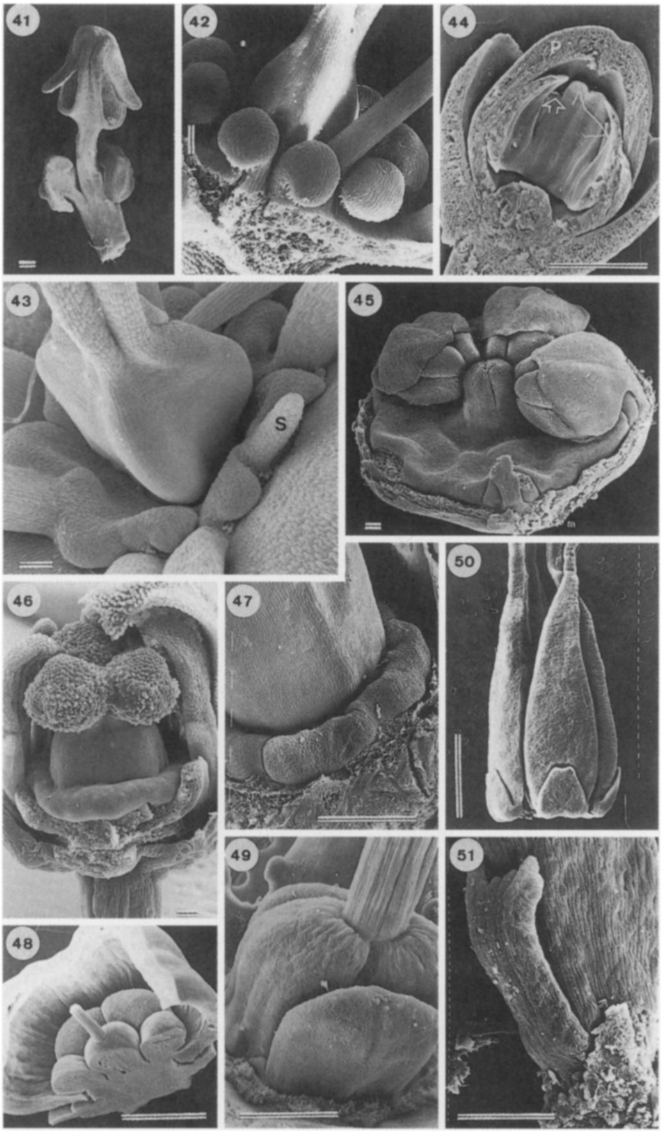
minode, which may not arise at all in some cases (e.g., Baillon, 1860b, 1862c; Bocquillon, 1861b; Chatin, 1873a; Endress, 1998, 1999; Payer, 1857; Singh & Jain, 1978). The posterior staminodes of many asterids either are small and reduced or can be secondarily increased in size, concomitant with a functional diversification (e.g., *Kigelia:* Neubauer, 1959; *Penstemon, Scrophularia:* Endress, 1994). Reductive trends of the posterior stamen in the Verbenaceae can be followed through several intermediates, ranging from the obvious presence of staminodes, to their initiation and consecutive loss and their total absence (Bocquillon, 1861b; Payer, 1857; Sattler, 1973).

The possibility of a reversal of staminodes and the reappearance of fertility has been discussed by Walker-Larsen and Harder (2000) for the Scrophulariales. This reversion is correlated with a transition to radially symmetric flowers. We doubt that this process is possible, because reversals to radially symmetric flowers in asterids operate via the loss of the posterior staminode and the fusion of the posterior petals and the transition to tetramerous flowers (see, e.g., Ronse Decraene & Smets, 1994; Endress, 1999). Loss of stamens seems irreversible, certainly for whole stamen whorls and probably also for reductions within whorls, except for the occasional genetic mutation or monstrosity, unless one considers the event of peloric mutants (e.g., *Antirhinum:* Coen & Meyerowitz, 1991; Coen et al., 1995) as a leading factor in floral evolution. Although insights into molecular evolution of flower development rest mainly on homeotic mutants, their importance to floral evolution remain virtually unknown (cf. Li & Johnston, 2000).

5. Secondary Staminodial Structures

In some families with a multistaminate, centrifugal androecium the outer stamen primordia are not developed beyond the stage of antherless structures (e.g., Dilleniaceae: Baillon, 1865, 1866; Endress, 1997; *Fumana* in Cistaceae: Nandi, 1998; Bixaceae: Ronse Decraene, 1989; Aizoaceae: Hofmann, 1993; Limnocharitaceae: Haynes et al., 1998). The existence of this kind of staminodes is probably linked to the secondary appearance of the centrifugal stamens and is induced by the rapid development of the flower (see Ronse Decraene & Smets, 1992). Centrifugal stamen development lags behind the development of other floral organs, and there is probably not enough time or nutrient allocation to attain a full development of the outermost stamens. Note that the presence of outer staminodes in a polyandrous androecium has often been interpreted as evidence for a reductive trend (see Ronse Decraene & Smets, 1992, 1993). In *Paeonia,* innermost stamens may be staminodial by pressures of the developing internal disk (Hiepko, 1966).

In some cases the outer staminodes of centrifugal androecia have become converted to new functions, linked with pollinator attraction. In Loasaceae subfamily Loasoideae a variable number of antesepalous staminodes develop into colored nectar collectors (Hufford, 1990; Smets, 1988a, 1988b; Figs. 29–30). In Dilleniaceae the outermost stamens may develop into a corona (*Pachynema:* Endress, 1997). The flowers of Scytopetalaceae are basically apetalous but have a showy corona (pseudocorolla) of staminodial origin (Appel, 1996). In the related Lecythidaceae, external staminodes have evolved in colored, complex structures (Endress, 1994). In *Couroupita guianensis* the abaxial part of the androecial ring primordium is detached as a broad flap of tissue with numerous staminodes covering the fertile stamens like a hood. This hood may contain fodder staminodes with pollen, or nectar may be produced at the base of the staminodes. Different pollination mechanisms and references hereto are abundantly discussed in Endress (1994).



Figs. 41–51. Pseudostaminodes and disks (S = staminode). **41.** Fertile stamen of *Laurus nobilis* L. (Lauraceae): staminodium-like glands flank the filament. **42.** *Fagopyrum dibotrys* (D. Don) Hara (Polygonaceae): whorl of glandular mamillae surrounding the gynoecium; all but one of the inner stamens removed. **43.** *Persicaria affinis* (D. Don) Ronse Decr. cv. superior (Polygonaceae): detail of filament bases with confluent inner mamillae; one inner stamen is staminodial. **44.** *Leea coccinea* Planch. (Vitaceae): longisection of a nearly mature flower bud with a pseudostaminodial disk; the arrow points to the insertion of the anther. **45.** *Zizyphus lotus* (L.) Desf. (Rhamnaceae): view of a nearly mature flower bud; note the small petals, incurved stamens, and broad intrastaminal disk. **46.** *Ekebergia capensis* Sparm. (Meliaceae): lateral view of a partly dissected flower; a broad nectariferous disk surrounds the base of the

(Caption continues on p. 385)

Secondary staminodial structures have the same characteristics as secondary stamens arising on common primordia. They may be vestigial or have evolved different functions related to pollination (Fig. 54).

V. Imaginary Staminodes

A. PSEUDOSTAMINODES

The difficulty in interpreting the homology of staminodes has often led to erroneous statements about structures surrounding the androecium. A striking similarity of intrastaminal emergences to filaments, prominent appendages of fused stamen bases, invaginations of the petals, or receptacular emergences, which are sometimes nectariferous, were often taken as evidence of a second aborted stamen whorl. Numerous examples exist in which sterile emergences have been interpreted as staminodes without supporting evidence (see Table III, Figs. 39–40). These appendages commonly arise very late in ontogeny and are not vascularized, or they are vascularized by various means. The following examples illustrate the difficulty in interpreting pseudostaminodial floral appendages:

1. Short-stalked glands occur at the base of the inner staminodes of Gomortegaceae (e.g., Brizicky, 1959) and Hernandiaceae (e.g., Kubitzki, 1969; Sastri, 1965) and on the outer, intermediate, or inner stamens of Lauraceae (e.g., Endress & Hufford, 1989; Kasapligil, 1951; Rohwer, 1994; Sastri, 1965; Vattimo, 1959; Fig. 41) and Monimiaceae (e.g., Endress, 1980; Sampson, 1969). Because the lateral appendages look superficially similar to reduced stamens, most authors have taken the basally inserted nectaries on the stamens of Laurales as evidence of reduced stamen fascicles and have interpreted the nectaries as lateral stamens in a clear state of reduction (e.g., Eames, 1961; Reece, 1939; Rohwer, 1994; Sampson, 1969; Sastri, 1952, 1965). Other evidence, especially a comparison with the lateral androecial lobes of *Chloranthus* (Chloranthaceae), has been used for arguing a derivation of lauralean stamens from primitively branched structures (Rohwer, 1994). Kasapligil (1951: 182), on the other hand, regarded the staminal glands as "emergences produced de novo for a functional purpose." He observed that the staminal glands arise late in ontogeny from lateral meristematic regions of the stamens. Other recent observations of the floral ontogeny of the flower of Lauraceae support Kasapligil's view (Endress, 1980; Singh & Singh, 1985), because no difference is found between the early inception of stamens with nectaries and those without nectaries. Moreover, no fasciculate stamens are known in the Laurales, and the relative (vascular) independence of the nectarial appendages is due to their late appearance in ontogeny (Endress, 1980). However, Crane et al. (1994) interpret fossil evidence of a lauralean flower as having an outer whorl of six staminodes, apparently set in three pairs, each of which appears to be linked to a single stamen. Could the fusion of the staminode with a stamen lead to a tripartite structure? The question of paired staminodes is contradicted by a review study by Eklund (2000) of fossil Lauraceae flowers which demonstrates a basic and constant pattern of four trimerous stamen whorls, the innermost being staminodial and with only the third bear-

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ovary. **47.** *Phlox paniculata* L. (Polemoniaceae): detail of the disk at base of the ovary. **48.** *Allamanda neriifolia* Hook. (Apocynaceae): section of flower; broad nectariferous pseudocarpellodes or pseudostaminodes surround the ovary. **49.** *Vinca minor* L. (Apocynaceae): central part of a flower with two nectariferous appendages alternating with the carpels. **50.** *Bryophyllum sp.* (Crassulaceae): carpels with a basal appendage. **51.** *Sedum spectabile* Bor.: detail of the appendage at the base of the gynoecium. (bars = 100 μm, except in Figs. 41, 44, 47, and 49 bars = 1 mm and in Fig. 51 bar = 500 μm) ing paired glandular appendages. The question is clearly not settled, especially in comparison with the tripartite structure of *Chloranthus* (Chloranthaceae).

2. The intrastaminal appendages between the fused stamen bases of Amaranthaceae have been interpreted either as true staminodes representing a lost stamen whorl (e.g., Goldberg, 1986; Joshi, 1932; Joshi & Venkata Rao, 1934; Saunders, 1937–1939) or as emergences of the staminal tube without clear morphological identity (e.g., Eliasson, 1988; Payer, 1857; Schinz, 1934). Eliasson (1988) observed that broad filaments are correlated with an absence of interstaminal emergences and that small filaments share the presence of pseudostaminodes. The intrastaminal teeth arise late in ontogeny (Payer, 1857) and have no vascular connection (Schinz, 1934).

3. Pseudostaminodes and real staminodes may occur in a same flower, as in *Sauvagesia* (Ochnaceae), with an outer fringe of threadlike appendages and a whorl of five petaloid staminodes in the petal radii (e.g., Amaral, 1991; Eichler, 1875–1878; Goebel, 1933; Saunders, 1937–1939). Outer staminodes may co-occur with the five antepetalous staminodes (*S. erecta*), only the antepetalous staminodes may be found *(S. glandulosa, S. guianensis*), or only small appendages (*Blastemanthus*) may exist (Amaral, 1991). The outer appendages are best interpreted as a corona in colors that contrast with the real staminodes. However, these have also been described as staminodes (e.g., Amaral, 1991). The same interpretation holds for the corona of the Passifloraceae (Table III).

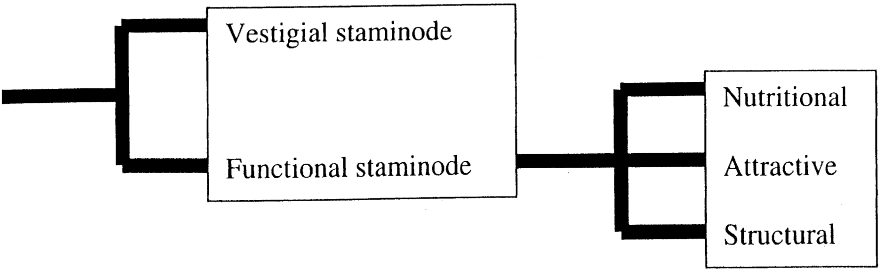
4. In the asterids, several families have "scales" on the corolla alternating with the stamens (e.g., in Apocynaceae, Boraginaceae, Cuscutaceae, Menyanthaceae, Hydrophyllaceae). These have occasionally been interpreted as stipular (e.g., Woodson & Moore, 1938) or staminodial in nature (Lindley, 1853, cited in Lawrence, 1937). However, other floral anatomical studies have shown that the scales are invaginations of the corolla tube, wit no relation to the androecium (e.g., Eichler, 1875–1878; Lawrence, 1937; Rao & Arati Ganguli, 1963).

5. Intrastaminal appendages or lobes functioning as nectary have often been interpreted as evidence of staminodes or even carpellodes in the asterids, especially when the external morphology is reminiscent of these (Figs. 48–51; Eichler, 1875–1878; Sérsic & Cocucci, 1999; Woodson & Moore, 1938). Other examples of incongruent interpretations are given in Table III.

B. RECEPTACULAR DISKS

Disklike nectaries (Figs. 42–47) also belong to the category of imaginary staminodes because they have often been taken for an aborted whorl of stamens (see Table III). This is illustrated by following examples:

1. In the Rhamnaceae there is no external (ontogenetic) evidence of a second staminodial whorl (Fig. 45); nor is there any link between androecium and disk (Bennek, 1958; Suessenguth, 1953a). However, the vascular supply of the disk, which can sometimes be similar to that of the antepetalous stamens, along with the disruption of the "alternance rule" (the stamens are antepetalous), has been used as support for the interpretation of the intrastaminal disk as modified stamens (Nair & Sarma, 1961; Prichard, 1955). Both interpretations—that is, the ontogenetic and the anatomical—can be supported to some extent, as another stamen whorl may have been present in an ancestral state but may be lost in extant Rhamnaceae. This interpretation is also linked to what family is considered the nearest sister group. The development of a disk can have "taken up" the vascular facilities provided for the now-missing antesepalous stamens. This demonstrates that a total rejection of the idea of a "lost" whorl, as well as the recognition of "evidence" of a lost whorl, are not to be considered too strictly. The



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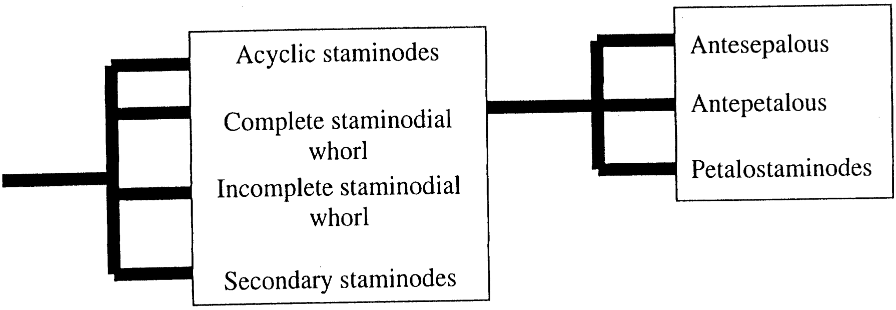

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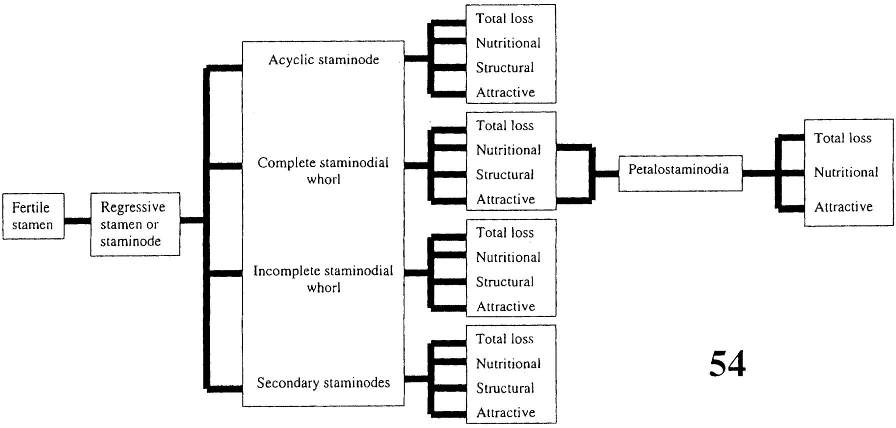

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Figs. 52–54. Different definitions of staminodial structures. **52.** A function-based definition of staminodes. **53.** A topology-based definition of staminodes. **54.** A combination of function-based and topological definitions of staminodes set out over time.

derivation of an (ob)haplostemonous androecium from two stamen whorls could be described as a counterbalancing development within the flower, because the space occupied by stamens is invariably taken over by the developing disk. However, we occasionally observed an antesepalous staminode in *Zizyphus lotus* (Ronse Decraene, unpubl.), which does not support the interpretation of a staminodial disk.

2. In the Polygonaceae the position of lost stamens is often taken over by receptacular nectaries (Figs. 42–43). Emberger (1939) interpreted the nectaries of *Fagopyrum* as staminodes, because of the spatial and numerical correlation between stamens and nectaries. Indeed, there is a high correlation between the number of stamens and the presence of the glands. However, the internal variations of nectarial tissue, as well as anatomical evidence, firmly deny a staminodial nature (cf. Ronse Decraene & Akeroyd, 1988; Ronse Decraene & Smets, 1991c).

More examples of incongruent disks are given in Table III.

C. THE CONTEXT OF IMAGINATIVE THOUGHT

Interpretations of the homology of disk structures have varied according to the methods of investigation used. Floral anatomists attached greater importance to vascular elements and more often favored a phyllomatic (staminodial) nature; therefore, they interpreted floral disks more likely as transformed (reduced) organs. Scholars in floral ontogeny and systematists often ignored the vasculature and favored an interpretation of a receptacular nature for the disk, because of its late inception and the absence of a clear morphological resemblance to other floral organs. This has often resulted in contradictory interpretations in floral morphology. However, it is essential that both methods of investigations be given sufficient weight (see Arber, 1933; Gustafsson & Albert, 1999).

Floral anatomists, especially the American school of Eames (e.g., Berkeley, 1953; Blaser, 1954; Dawson, 1936; Eames, 1931, 1961; Heinig, 1951; Prichard, 1955; Tillson & Bamford, 1938) and the Indian school of Puri (e.g., Nair & Jain, 1956; Nair & Joshi, 1958; Nair & Sarma, 1961; Narayana & Rao, 1971; Puri, 1948) have been obsessive about describing staminodial structures on the basis of the presence of vascular traces and the current belief of primitive polyandry in angiosperms. Indeed, interpretations of staminodial structures (especially for disks) were often related with a hypothetical interpretation of ancestral polyandry and a given direction of evolution (e.g., Humiriaceae: Narayana & Rao, 1978; Geraniaceae: Dawson, 1936). This led to certain highly imaginative reconstructions of "ancestral" flowers.

Evidence of a staminodial nature of the disk was often sought in the presence of vestigial vascular stubs or vascular connections between the supply to the stamens or other organs and the disk (e.g., Nair & Joshi, 1958). There are indefinite possibilities for supplying the disk; the supply of the nectary is opportunistic as it becomes derived from the nearest source of vascular tissue, which is often the androecium. Trying to recognize staminodes or any other structures surrounding the ovary, if no structural evidence of their homology with stamens exists, is senseless. Smets (1986, 1988a, 1988b) restricted the term "disk nectary" to a secondary emergence of the receptacle (nectaria axialia) when there is no homology possible with staminodes and when it is not part of the gynoecium.

VI. Molecular Developmental Genetics and Staminodes

Recently, much emphasis has been laid on the study of expression of developmental genes in order to understand differences of morphological characters from an ontogenetic and phylogenetic perspective. Studies of the molecular controlling mechanisms of organ determination have led to the discovery of MADS box genes (see, e.g., Albert et al., 1998; Theißen et al., 1996; Yanofsky, 1995). These genes are partly responsible for floral organ determination, as demonstrated in the ABC model, with three distinct functions (Coen, 1991; Coen & Meyerowitz, 1991). In its simplest form the ABC model implies that *A* is responsible for sepal expression, *A* + *B* for petals, *B* + *C* for stamens, and *C* for carpels. Beyond the expression of this simple model, the overall expression of flower development is often more complex (see Albert et al., 1998; Kramer & Irish, 2000). Two gene activities have to be recognized, leading to a distinction between whorl identity and organ identity: one that influences the outcome or function of an organ (whether it be sepaloid or petaloid, etc.), or process orthology; and one that influences the position of organs, or positional orthology.

These two processes act independently, as a petaloid organ will occupy the same position as the original organ. For example, in double-flowered *Begonia* (Lehmann & Sattler, 1989; Ronse Decraene & Smets, 1990b), stamens have been replaced by petaloid structures that occupy the same position in the flower. On the other hand, in *Macleaya* stamens occur in the position of the petals in the other Papaveraceae (Ronse Decraene & Smets, 1990b) and in *Calla* (Araceae) in the position of tepals (Lehmann & Sattler, 1992).

Albert et al. (1998) interpreted the nature of organs mainly on the basis of gene activity. In a simple way *AB* gives petals, *BC* stamens, and *ABC* leads to staminodes. Staminodes thus appear as the result of an overlap of the genetic programs of the perianth members and stamens during floral development (cf. Erbar et al. [1998] for the nectar leaves of Ranunculaceae).

Through examples of Lecythidaceae and Clusiaceae, Albert et al. (1998) and Gustafsson (2000) correlated the formation of staminodial structures with the expansion of the *A* function gene activity, which leads to the transference of petaloid characters to stamens.

However, this approach has certain shortcomings. The terminological distinction in zones of influence is not sufficiently detailed to recognize intrinsic variations of expressions of organs (there are different degrees of staminode development), it overlooks external environmental factors and pressures from pollinators, and it denies the historical dimension (what is derived from what), as process homology is equally influenced by time.

The explanation of a shift in gene activity is only a partial explanation for the existence of staminodes, as it is mainly a functional (teleological) explanation of gene activity. In the case of the nectar leaves of Ranunculaceae, Erbar et al. (1998) have demonstrated the homology with stamens in the presence of rudimentary adaxial pollen sacs in early developmental stages. The shift to an increasing *A* function may have been progressive or sudden, but little can be said about that, as the knowledge of the importance of genetic mutations to evolution is virtually nil.

A good case for the oversimplification of the molecular model is the example of sorrel or *Rumex* (Polygonaceae). In *Rumex* the perianth consists of two whorls of three sepaloid tepals. Ainsworth et al. (1995) and Albert et al. (1998) hypothesized that petals were ancestrally present in *Rumex* but that they were lost in evolution. They explain the present sepaloid perianth as the result of the loss of the *B* function and thus as the result of a secondary restriction of the "basal" petaloidy that is considered ancestral in the family. This explanation does not account for the shifts between trimery and pentamery operating in the family, the occurrence of outer stamen pairs, and the improbable distinction between petals and sepals that may not have been present in the ancestors of the Polygonaceae, as no extant Polygonaceae with both sepals and petals exist. The molecular explanation may refer to the process of development, but it is only partial evidence, as the hypothesized assumptions about the evolution of petals have no morphological basis.

To restrict the explanation for stamen, staminode, and petal identity to an alteration in expression or function of *B*-class genes (e.g., Albert et al., 1998; Bowman et al., 1991; Weigel &

Meyerowitz, 1994) is to oversimplify the development and identity of organs. The distinctions made between bracteopetals and andropetals by Hiepko (1965) and Takhtajan (1991), or the terms "homeosis"or "heterotopy," as the total or partial replacement of one part by another of the same organism (e.g., Sattler, 1988, 1994; Li & Johnston, 2000) explain the same as the molecular terminology, but they are based on a different point of view.

VII. Concluding Remarks

It is clear that the decision to recognize a lately arising primordium as a staminodium or merely as a secondary receptacular emergence is often a matter of subjective appreciation and is extremely difficult to assess. Therefore, reliance on indirect evidence can be helpful. For *Harungana* (Clusiaceae), Ronse Decraene and Smets (1991a) hypothesized that the nectaries represent a staminodial whorl, and evidence was given in the vasculature and the external shape. In Proteaceae, Douglas and Tucker (1996) refuted a staminodial nature for the intervening nectary scales, although these are strictly speaking comparable to the nectary scales of the Clusiaceae. Proposed phylogenetic relationships (e.g., Chase et al., 1993; APG, 1998) can help in assigning the true nature of organs, although this evidence could be subject to circular reasoning. The association of Clusiaceae with clades having diplostemonous flowers (e.g., Linales, Ochnaceae, rosids I) supports the acceptance of a staminodial nature of the nectaries in *Harungana*. The association of Proteaceae with the Platanaceae at the base of the eudicots may be evidence against a staminodial nature.

Staminodial structures play an important role in floral evolution (see also Walker-Larsen & Harder, 2000). They are a reflection of the dynamism of the androecium (and flower) in response to changing conditions. Therefore, their importance should not be ignored, and a misinterpretation of structures that resemble staminodes must be recognized. The recognition of types of staminodial structures based on function (i.e., vestigial and functional staminodes) and position is only a partial characterization, but it is a necessary reflection of the complexity of floral forms.

VIII. Acknowledgments

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