The Adaptive and Phylogenetic Significance of Receptacular Bracts in the Compositae

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Summary

Many morphological features of the heads of Compositae are systematically useful. Receptacular bracts (pales or paleae) are of particular significance taxonomically. These structures occur in nine of the 13 recognized tribes (absent in Arctoteae, Calenduleae, Senecioneae and Tageteae), with the greatest concentration in the Anthemideae, Heliantheae, and Inuleae. Because the Heliantheae contain the broadest diversity of pale types, the adaptive significance of these features within this tribe deserves special emphasis. Certain subtribes of the Heliantheae are characterized by distinctive types of pales, such as flattened with orange-brown lines in the Coreopsidinae, pales subtending only the outer series of disc florets in the Madiinae, or their complete absence in the Bahiinae. Of the five principal factors affecting the evolution of features of heads in the family, viz., protection, dispersal, pollination, breeding systems, and seed germination, the former two are most likely the most important selective forces in the evolution of pales. Dispersal functions of pales include attachment or close envelopment of the achene by the pales with removal of the entire unit by wind from the head, conduplicate pales serving as chutes for release of unattached achenes, and brightly colored, fleshy pales being attractive to animals. Protective functions occur against predators and environmental extremes, and occur in bud, anthesis, and mature fruiting stages. Pales function during anthesis to protect ovaries and achenes from apical and lateral insect attack. The particular variations of the pales depend on the associated structures of the heads and breeding systems. In a phylogenetic context, the large and sometimes foliose pales of the Heliantheae seem best interpreted as adaptations for protection of large achenes and not necessarily as reflections of a primitive condition within the family.

Introduction

The Compositae are one of the largest families of flowering plants and have broad geographic distribution (Cronquist, 1981). Within this family many morphological features of the capitulum are known to have high taxonomic value. Despite this acknowledged taxonomic efficacy, the adaptive value of morphological features of the flowering heads of the family is poorly understood. An appreciation of the adaptive value should enhance our understanding of biological significance and homologies of these features and allow for additional taxonomic and phylogenetic insights. This is especially important for the determination of relationships among related families (e.g., Calyceraceae, Dipsacaceae, Rubiaceae, etc.). Some contributions have been made already to the understanding of the adaptive value of reproductive structures in the Compositae (Zohary, 1950; Leppik, 1960, 1970, 1977; Burtt, 1961, 1977, 1978; Burrows, 1973, 1975; Sheldon and Burrows, 1973; Levin and Turner, 1977; Vogel, 1979; Ridley, 1982a, b; Venable and Levin, 1983; Robinson, 1983; Shmida, 1985; Stuessy et al., 1986). The features that have been discussed most in these studies have been style branches, anthers, pappus, and achenes. The receptacular bracts (pales or paleae) which subtend all or at least some of the disc florets of the capitulum have received scant attention. Although they have acknowledged taxonomic significance, their adaptive value has not been considered in detail within the family.

In an evolutionary context, pales have been useful in helping determine relationships between and among taxa. More importantly, they also have been used to suggest primitive status for taxa possessing them, such as for the Heliantheae (Cronquist, 1955, 1977).

[1] Department of Botany, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, U.S.A. Present address of DMS: Department of Horticulture, University of Wisconsin, Madison, WI 53706, U.S.A.

Because pales are associated with inflorescences, it has been reasoned that heads of Compositae still bearing these bracts would represent early evolutionary stages of head condensation from racemose or cymose ancestors, in which each flower is subtended by its own bract. Heads (and taxa) without pales would be considered more derived.

The purposes of this paper are to: (1) describe the occurrence of pales within the family; (2) describe the occurrence and structural variation of pales within the Heliantheae; (3) comment briefly on the taxonomic value of pales in the Heliantheae; (4) describe general factors controlling evolution of the pales in the family and their probable adaptive significance; (5) make predictions as to correlations with other structural features of the heads and environmental conditions; and (6) offer possible insights on the phyletic import of pales within the family.

Materials and Methods

Pale conditions within the Compositae were obtained from a survey of general literature (Bentham, 1873; Stebbins, 1953; Gleason and Cronquist, 1963; Abrams and Ferris, 1960; Munz, 1974) and the systematic reviews in Heywood et al. (1977) and Robinson (1983). Data specific to the Heliantheae were obtained from Carlquist (1959), D'Arcy (1975), Nash and Williams (1976), Stuessy (1977), and Robinson (1981). In addition, numerous original descriptions, taxonomic treatments, and anatomical studies were consulted as well as herbarium material from GH and OS, and more than 300 preparations of head dissections mounted in Hoyer's medium.

A survey of insect damage to heads of various native species in the Compositae was conducted from an examination of randomly collected material on 8 Oct 1983 in an open field just SE of Bethel and Olentangy River Roads, Columbus, Ohio. Heads were collected intact and fixed in FAA for examination in the laboratory.

Results

Pales occur in nine tribes of the family except for Arctoteae, Calenduleae, Senecioneae, and Tageteae (Table 1). It is clear, however, that the most common occurrence of pales in the Compositae is in the Heliantheae (sensu Stuessy, 1977; 85% of genera), a fact which has been recognized for some time (e.g., Bentham, 1873). Most of the pales are deciduous and non-vascularized except in the Mutisieae and the Heliantheae (most common in the latter tribe).

To examine the adaptive value of pales in the family, therefore, it is useful to look at the tribe that contains the most diversity of pale structures; this is clearly the Heliantheae. The distribution of these pale features within the tribe, arranged according to the subtribes in Stuessy (1977), is shown in Table 2. The Bahiinae lack pales altogether, and some genera in some subtribes also lack them (e.g., in the Coreopsidinae, Verbesininae, etc.). Much variation prevails within many pale features, and the different conditions or states of each character (shape, thickness, height, apex, distribution, and attachment) are shown in Table 2.

Discussion

Taxonomic efficacy. —The observed variation in pales of the Heliantheae (Table 2) attests to some difficulties with using these features taxonomically at the subtribal (and other) levels in the tribe. Many studies have shown variation to occur, particularly within individual species or genera, such as pales present or absent in the same genus (e.g., in *Clibadium*, Stuessy, 1975; *Cymophora*, Turner and Powell, 1977; *Geissopappus* and *Calea*, Robinson, 1981; *Hemizonia*, Abrams and Ferris, 1960; *Hymenopappus*, Turner, 1956; and *Layia*, Munz and Keck, 1973), persistent or deciduous in same genus (e.g., in *Galinsoga*, Canne, 1977; *Jaegeria*, Torres, 1968 and Canne, 1975; *Montanoa*, Funk, 1982; *Sanvitalia*, Torres, 1964; and *Tridax*, Powell, 1965), free vs. adnate to the base of the achene (e.g., in *Coreopsis*, Smith, 1975), chartaceous or firm (e.g., in *Helianthella*, Abrams and Ferris,

Table 1.   Distribution of pales within tribes (by number and percent of genera) in the Compositae.

	Total genera in tribe[a]	Genera with pales present[b]	Percent genera with pales present[c]
Asteroideae			
Anthemideae	102	18	17.6
Astereae	135	3	2.2
Calenduleae	7	0[d]	0.0
Eupatorieae	160	9[e]	5.6
Heliantheae	209	177	84.7
Inuleae	180	34[f]	18.9
Senecioneae	100	0[g]	0.0
Tageteae	17	0	0.0
Lactucoideae			
Lactuceae	71	5	7.0
Vernonioideae			
Arctoteae	16	0[h]	0.0
Cardueae	80	11[i]	13.8
Mutisieae	89	5[j]	5.6
Vernonieae	85[k]	7[l]	8.2

[a]   Taken from Heywood et al. (1977).

[b]   Subtending at least some of the disc florets in the head.

[c]   Most of the pales in the family are deciduous and non-vascularized, except in the Mutisieae with some vascularized pales, in the Heliantheae with some persistent and vascularized pales, and in the Vernonieae with some persistent pales.

[d]   Receptacle in *Chrysanthemoides* is hairy, but not paleaceous.

[e]   In *Oaxacana* and *Carterothamnus* the pales are weakly attached to the florets and tend to be deciduous with them.

[f]   Pales primarily in the subtribes Buphthalminae and Filaginae (Bentham, 1873).

[g]   In *Odontocline* and *Scrobicaria* the pit margins of the receptacles have scale-like projections, but these are not regarded as pales.

[h]   *Eremothamnus* is apparently epaleaceous (Robinson and Brettell, 1973).

[i]   Most of the genera of the tribe have setae on the receptacle, but not pales. Pales are known only in the Carlineae (Dittrich, 1977).

[j]   *Stenopadus* and *Stomatochaeta* have vascularized pales (Carlquist, 1958).

[k]   Including the Liabeae.

[l]   The seven genera are: *Bolanosia, Centauropsis, Chronopappus, Dewildemania, Diaphractanthus, Heterocoma,* and *Lepidonia* (Bentham and Hooker, 1873; Blake, 1936; Burtt, 1950).

1960), and shorter vs. longer than the achenes (e.g., in *Parthenice mollis*, Sauck, 1975). This does not mean that they are not useful features taxonomically, but only that they are not necessarily efficaceous *a priori* in any particular context.

The adaptive value of pales: general hypotheses. —Determination of the adaptive value of any morphological feature is a difficult matter. Ideally an hypothesis for the function of the structure must be developed, predictions from the model ascertained, and tests designed and executed to attempt to refute the hypothesis. Such an approach has been done in a few cases (e.g., in ray corollas in *Helianthus*, Stuessy et al., 1986). A further need is to assure the adaptive value of the feature not only in terms of reproductive value for the current generation but also for the population over many generations. The present paper, however, is oriented solely toward developing hypotheses on the adaptive value of pales and not on experimental verification. Such tests await future studies.

Pales, as with all other features of the heads of Compositae, probably relate to changes in the five major components of the reproductive system: (1) defense (or protection); (2)

Table 2. Distribution of conditions of pales in subtribes of the Heliantheae showing predominant (X) and infrequent occurrences (/). Order of subtribes after Stuessy (1977).

Pale condition	MEL	ZIN	ECL	VER	HEL	GAI	COR	FIT	BAH	MAD	GAL	NEU	ENG	AMB	MIL
Shape															
Conduplicate	X	X	X	X	X	/	X	X		X	X	X	X	/	/
Narrow	/										/	/	X	X	
Filiform			/											X	
Partial envelopment				/											
Complete envelopment				/			/								
Thickness															
Scarious	X	X	X	X	/		X			/	X	X	X	X	/
Medium		X	X	X	X		/	X		X	X		/		
Thick, dry			/	/	X	/									
Thick, fleshy					/										
Height															
Shorter than corolla but longer than achene	X	X	X	X	X	/	X	X		X	X	X	X	X	/
Shorter than achene				/										/	
Longer than corolla		X				/									
Apex															
Rounded, acute or acuminate	X	X	X	X	X	/	X	X		X	X	X	X	X	/
Aristate			/		/	/									
Trifid											/	/			
Distribution															
Subtending all florets	X	X	X	X	X	/	X	X		/	X	X	X	X	/
Subtending outer series only										X	/				
Absent			/				X	/	X	/	/	/		/	X
Attachment															
Not attached (other than to receptacle)	X	X	X	X	X		X	X		X	X	X	/	X	/
Among all other pales						/									
Among only outer pales										/					
To ray achenes											/		X		/
To phyllaries										/	/		X		/

[a] Melampodiinae (MEL), Zinniinae (ZIN), Ecliptinae (ECL), Verbesininae (VER), Helianthinae (HEL), Gaillardiinae (GAI), Coreopsidinae (COR), Fitchiinae (FIT), Bahiinae (BAH), Madiinae (MAD), Galinsoginae (GAL), Neurolaeninae (NEU), Engelmanniinae (ENG), Ambrosiinae (AMB), Milleriinae (MIL).

dispersal; (3) pollination; (4) seed germination; and (5) breeding systems. Pales, however, have doubtless not been affected by these factors equally, and their probable importance is as listed seriatim above.

The defense function of pales involves protecting the ovules (and achenes) from predation primarily by insects and to a lesser degree from environmental extremes such as desiccation. Protection occurs during the development of the capitulum, and it is useful to think of stages in head development at which defense is important, viz. bud, anthesis, and mature fruiting conditions. In bud, the apices of the pales often cover the young florets and serve to hinder entry between them and to protect the anthers in the upper part of the corolla. In taxa with aristate pale apices (e.g., *Borrichia, Echinacea, Sanvitalia*) these serve in bud

to deflect larger predatory insects. During anthesis, when the corolla is normally exserted from the pales, protection is clearly for developing ovaries. This protection serves to limit apical and lateral entry by insects (protection from basal entry is provided by the phyllaries and receptacle). Protection from lateral entry into the head is provided also by phyllaries, but if a predator enters apically, pales limit lateral movement to other ovaries/achenes. In addition to the pales, other apically attached structures such as the corollas and/or pappus (if present) limit apical entry. In fact, it may well be that the primary function of the pappus in the Compositae is predator protection, with dispersal being a secondary adaptation. The lateral defenses of ovules vary according to the degree of thickness and enclosure of pales about the ovaries/achenes. In the mature fruiting stage, the corollas usually fall off leaving the achenes exposed. Pales usually enclose the achenes laterally or provide an apical covering to aid in defense. Also at this stage structural and chemical defenses in the achenes come into play, such as in the development of the stony phytomelan layer (Stuessy and Liu, 1983). In some taxa the achenes fall early after fertilization so that long-duration protection on the head is unnecessary. A related important point, however, is that in Heliantheae with large fruits, the time to maturation is relatively long, and therefore sustained protection is needed.

In examining the importance of pales in relation to dispersal, it is important to note that they are occasionally attached to achenes. When attached, pales function as a wind-sail to help disperse the achenes from the head (e.g., *Chrysogonum, Silphium*). However, because pales are only infrequently attached to the achenes and also lack hooks, barbs, mucilage, etc., common features of the achenes themselves (in modifications of the pappus and outer pericarp), it is likely they provide only a modest dispersal aid. In the free condition, adjacent pales sometimes form "chutes" through which the achenes slide out of the head at maturity (e.g., *Balduina*). In rare cases the pales are apically fleshy and brightly orange-colored, which probably serve to attract birds (as in *Wulffia*).

Pales function in pollination in two ways. First, and doubtless most importantly, the apices are often colored to match (usual condition) or contrast with the color of the disc corollas. This affects the total visual appearance (including UV) of the inflorescence to the pollinator (McCrea and Levy, 1983). Second, but of lesser importance, is that the pales, particularly if exserted, will affect the landing surface of the head and will encourage or discourage certain types of insect pollinators.

How and whether pales function in seed germination is uncertain, but if the pale is attached to the achene and deciduous with it (e.g., in *Sclerocarpus*), it could serve to protect the achene from ground predators prior to germination and perhaps keep moisture around the achene, especially in arid climates. It might also regulate the reception of light which is essential for germination in some taxa.

The relationship of pales to changes in breeding systems is poorly understood. However, heads of Compositae occur in many different sexual configurations and the evolution of gender strategies in the family is also worthy of adaptive investigations (Stuessy and Lowrey, in prep.). A frequent change in radiate heads is the complete abortion of disc ovaries, yielding a simple monoecious condition (e.g., *Acanthospermum, Melampodium*). Not unexpectedly, the defense function of pales becomes limited to protection of the anthers while young and for maintaining rudimentary ovaries for support of the pollen presentation apparatus.

The adaptive value of pales: detailed hypotheses and examples from the Heliantheae. — Because the most important factors influencing the evolution of the pales seem to have been adaptations for dispersal and protection, these features are highlighted and discussed here in more detail. With regard to dispersal, there are at least three kinds that are involved with the evolution of pale structure: wind-sail, chute, and birds. With reference to protection, we envision changing selective forces involving normal predation on one hand and structural modifications that might be expected with increased predation on the other.

Table 3. Hypothesized relationships of head and environmental conditions with pale conditions in the Heliantheae.

Pale condition	Small or medium head and achenes	Large head and achenes	Sterile disc achenes	Increased predation	Wind-sail	Chute	Birds
Head and environmental conditions							
Protection					*Dispersal*		
Normal predation							
Fertile disc achenes							
Shape (X-section)							
Conduplicate	X	X					
Narrow			X				
Filiform			X				
Partial envelopment				X	X		
Complete envelopment				X			
Thickness							
Scarious	X		X				
Medium	X						
Thick, dry		X		X			
Thick, fleshy							X
Height							
Shorter than corolla but longer than achene	X						
Shorter than achene			X				
Longer than corolla		X		X			
Apex							
Rounded, acute, or acuminate	X						
Aristate		X		X			
Trifid				X			
Distribution							
Subtending all florets	X	X					
Subtending outer series only			X			X	
Absent			X				
Attachment							
Not attached (other than to receptacle)	X						
Among all other pales				X		X	
Among only outer pales			X			X	
To ray achenes			X		X		
To phyllaries			X		X		

Under normal predation, changes in gender strategy and in size of heads and achenes would clearly cause pale alterations. An especially important shift which has been very common in the Heliantheae is the development of sterile disc achenes yielding simple monoecy. If the disc achenes are fertile, then one can consider pale structure in those small or medium-sized heads (with smaller achenes) versus those with increased or large heads and achenes. These factors are related to the conditions of the pales within the Heliantheae in Table 3.

Conspicuous variations of shape of the pales are: conduplicate, narrow, filiform, partial envelopment, and complete envelopment. Ordinarily, the conduplicate pale provides protection from predators that feed both apically and laterally and therefore it would be expected to be a common condition in the Heliantheae (Table 2). However, in those heads with sterile disc achenes, the adaptive requirement for protection of the disc achenes is removed, and the only need is for protection of abortive ovary tissue to facilitate exsertion of corollas and fertile anthers for pollination. As a result, one would expect to have narrow or filiform pales associated with sterile disc achenes, a condition of the Melampodiinae, Engelmanniinae, and Ambrosiinae, as well as the Milleriinae, although many of these species possess no pales at all. In the Galinsoginae the pales, although described as narrow, are actually trifid at least apically, a feature which provides increased protection towards the margins of the achenes. This augmented defense correlates with the fertility of the disc florets. In the Ecliptinae, it is *Eclipta alba* which possesses a truly filiform pale. Reasons for this structure are difficult to ascertain, but it may have to do with the architecture of the achenes and the head. The fruits of *Eclipta* are fertile, quadrangular and thickened at the apex, and their disposition in the head is in a tight geometrical pattern. It is so tight, in fact, that there is a reduced need for protection by a large conduplicate pale. An area of potential entry into the capitulum is at the corners where the four achenes come together, although often not exactly so, which is precisely where the filiform pales are found. Other filiform pales are found in *Ambrosia, Euphrosyne,* and *Iva* of the Ambrosiinae, which have sterile disc achenes. Nearly complete envelopment of the disc achenes occurs in *Aldama, Montanoa, Rhysolepis, Rojasianthe, Scalesia,* and *Sclerocarpus* of the Verbesininae, and in *Bidens cosmoides* (Gillett and Lim, 1970) of the Coreopsidinae. Such augmented protection suggests increased predation on these achenes. In *Aldama* and *Sclerocarpus* they have more open heads with achenes more subject to apical and lateral predation. In *B. cosmoides,* which has the largest heads of any species of *Bidens* in the Hawaiian Islands, the achenes and heads are perhaps a more likely target as a food resource for insect predation.

The usual situation in the Heliantheae is either scarious or medium bracts. Note that in the subtribes typically with sterile disc achenes, the scarious condition prevails (Melampodiinae, Engelmanniinae, Ambrosiinae, and Milleriinae). The thick and dry condition would be expected under increased predation resulting from larger heads and achenes as well as additional predation independent of increase in achene size. This type of pale is found in *Borrichia* of the Zinniinae, and in *Dimerostemma, Rhysolepis, Scalesia,* and *Sclerocarpus* of the Verbesininae. In the Helianthinae, the genera *Balsamorhiza, Dracopsis, Ratibida, Rudbeckia,* and *Wyethia* share this condition. In the Gaillardiinae, the only genus with this feature is *Balduina.* Clearly with reference to the genera of the Helianthinae, these have quite large heads and the thick and dry pales are probably a response to increased predation, especially considering the longer maturation times of the achenes and hence longer retention on the heads. Thick and fleshy orange-colored pales are found only in *Wulffia baccata,* and the achenes are also fleshy. This is an extremely unusual and striking head condition which may represent an attraction for bird dispersal.

Three conditions of height of pales in the Heliantheae can be considered: those pales that are shorter than the corolla, but longer than the achenes; those that are definitely shorter than the achenes; and those that are clearly longer than the corolla. The first condition is the most common, especially with small or medium-sized heads and achenes. Pales occasionally are shorter than the achene in *Squammopappus* and *Verbesina* of the Verbesininae, and in *Parthenice* of the Ambrosiinae. In *Parthenice,* it is probably a reduction in response to sterility of the disc achenes. With regard to the other two genera in the Verbesininae the significance of this reduction is unclear, but one might speculate on chemical defenses in the achenes to provide protection. In field observations of local populations of *Verbesina alternifolia,* there seems no obvious protection for the mature achenes. They are, however, conspicuously winged and presumably drop from the head to disperse at maturity. As the head increases in size, one would occasionally expect pales to

be longer than the corolla and even exserted conspicuously to provide increased apical protection against predators. The pales that are longer than the corolla are found in the Zinniinae in *Borrichia, Philactis,* and *Sanvitalia.* They are also found in *Echinacea* of the Helianthinae. Of the latter, this head is extremely large and the long pales probably serve for increased apical protection. In the other genera, the heads are not as large, although relative to the size of the plants themselves, they are conspicuous.

The rounded, acute, or acuminate pale apex is the most common condition in the Heliantheae. The aristate condition is known in *Rojasianthe* of the Verbesininae, in *Echinacea* of the Helianthinae, and in *Borrichia, Philactis,* and *Sanvitalia* of the Zinniinae. These genera have been mentioned previously for length of the pales and increased predation selecting for this feature. In *Echinacea* and *Rojasianthe* and to some extent in *Borrichia* and *Philactis* the heads are reasonably large and therefore perhaps subject to greater predation due to greater visibility. Trifid pales are known in the Galinsoginae and Neurolaeninae within the tribe. It is also in these subtribes that the conical or distinctively convex receptacle is found. This has the impact of allowing more achenes to be placed within the same diameter of head by extension upward on a more conical surface. As a result, these heads become a greater food resource for a predator within the same area. Hence, it might not be surprising to have increased protection apically for genera in these subtribes and in particular *Calea,* and some species of *Galinsoga, Schistocarpha, Tridax* and *Zaluzania.*

The common distribution of pales in the Heliantheae is for subtending of all of the florets of the disc. In most of the Madiinae, the pales subtend the outer series of disc florets only. Here a chute dispersal may be indicated. Personal observations on populations of *Madia sativa* indicate that a salt-shaker effect is created by lateral connation of these outer pales in which the loose achenes inside jiggle out at maturity. The absence of pales is a common phenomenon in nine of the 15 subtribes, indicating parallel evolution. Some of these groups (e.g., Ambrosiinae, Milleriinae) do have sterile disc florets. The other groups without pales may represent shifts in overall protective strategy from structural to chemical protection or to a shift in larger numbers of propagules for escaping predation of part of the seed set. Additional structural modifications of the achenes, such as hairs, corkiness, a thicker phytomelan layer, and other adaptations may also occur.

Other than attachment to the receptacle, pales are usually unattached to any other structure. Occasionally, however, fusion does occur among all of the pales as in the genus *Balduina* of the Gaillardiinae. This may represent an increased level of protection required for the achenes in an environment with increased predation. Sesquiterpene lactones are very characteristic secondary metabolites of this subtribe (Hertz, 1977), and these are known as feeding deterrents to insects (Burnett et al., 1974). Chemical defenses in the other genera which do not have such an elaborate bract defense mechanism, therefore, may occur in the subtribe. It is possible to have accumulation of these compounds restricted to the capitulum, such as in *Encelia californica* (Proksch and Rodriguez, 1984). In the Madiinae, the outer pales are often connate to produce a ring. This situation has already been discussed in *Madia sativa* above, in which a dispersal function is suggested. This also might be expected to occur with sterility of the disc florets in which additional protection adjacent to the achene is unnecessary. Attachment to ray achenes and phyllaries would be expected in situations with sterile disc achenes in which increased predation is being placed on the remaining fertile propagules. These also might serve in dispersal as the whole unit would be fused together and leave the head together. The attachment to the phyllaries occurs in all species of *Blepharizonia* (Carlquist, 1959) and *Galinsoga, Parthenice* and *Parthenium.* This fusion also occurs in most of the genera of the Engelmanniinae with sterile disc florets. This is also the case in the Ambrosiinae and Madiinae. This is not the case in the Galinsoginae, however, which has fertile disc florets, but this may represent increased predation on the ray achenes which are known to be heavier, higher in caloric value and contain more proteins and carbohydrates than the disc achenes (Rai and Tripathi, 1982).

Field observations on the protective value of pales. —To assess the success of pales in

Table 4.   Insect damage to heads of Compositae in an old field in Columbus, Ohio.

Taxon	Number of heads examined	Average number of ovaries/ head	Number of heads with insect damage	% damaged ovaries
Epaleaceous species				
Aster ericoides L.	25	68.1	4	1.0
Cirsium vulgare (Savi) Tenore	25	240.0	0	0.0
Solidago graminifolia (L.) Salisb.	25	24.2	0	0.0
Vernonia gigantea L.	25	21.4	2	3.2
Paleaceous species				
Helianthus grosseserratus Martens.	25	49.8	5	1.7
Heliopsis helianthoides (L.) Sweet	16	53.6	1	0.5

providing protection for achenes, levels of predation were examined in several species of the Compositae growing in the same area in a field in Columbus, Ohio. *Aster ericoides, Cirsium vulgare, Solidago graminifolia,* and *Vernonia gigantea,* all of which lack pales, were examined. Two paleaceous species, *Helianthus grosseserratus* and *Heliopsis helianthoides* were also investigated. The average number of ovaries per head (Table 4) varied from 21 (in *Vernonia*) to 240 (in *Cirsium*). It was suspected that higher levels of predation, i.e., more obviously chewed and eaten ovaries and achenes, would occur in those species of the family without pales. However, in these species there is no association between the damage by predators and the presence or absence of pales. The suggestion from this brief survey is that levels of predation are more or less equal in species of the family whether they have pales or not. Apparently pales are only one way of protecting ovaries or achenes from predation. It is possible that the large size and longer maturation of the achenes in the Heliantheae necessitate more conspicuous protection by the conduplicate bracts as opposed to extremely small and numerous flowers in other tribes which develop and disperse rapidly (as in *Solidago*). The strategy for the Cardueae, such as in *Cirsium,* is also for large achenes but with numerous bristles on the receptacle (which possibly serve the function of pales) as well as very thick and spiny phyllaries.

Phyletic insights. — The ecological and adaptive context within which pales have been viewed in this investigation provides opportunities for phyletic insights. Several interesting points arise which bear on the primitive condition of pales within the family. It has been traditional wisdom that because pales are undoubtedly modified involucral bracts, that heads and taxa containing large pales would probably reflect a primitive condition. That is, they are more bract-like and hence more primitive (Cronquist, 1955, 1977). This perspective has been questioned by some (e.g., Stuessy, 1977), and it is worthwhile examining once more in view of the information provided here. It should also be kept in mind that the origin of pales from the receptacle is another alternative, as is their origin from phyllaries as shown in *Isocarpha* (Eupatorieae; Keil and Stuessy, 1981).

The types of inflorescences and bracts in families related to the Compositae are shown in Table 5. The families listed are those which in some fashion have been related at some time or another to the Compositae (e.g., Crepet and Stuessy, 1978). That does not mean that they all were ancestral to the Compositae, nor that anyone has believed them to be so, but only that they have morphological conditions that do place them close to the Compositae. The most important point is that those families that already have large and conspicuous heads, such as the Brunoniaceae, Calyceraceae, and Dipsacaceae, also have mostly long bracts on the receptacle. The other families with more open inflorescences, or only occasionally with heads, have shorter bracts. This suggests that large and conspicuous pales are correlated with the development of conspicuous capitula. If this is so, then one

Table 5. Types of inflorescences and length of bracts relative to other floral features in families related to Compositae.

Family	Type of inflorescence	Relative length of bracts
Brunoniaceae	heads	long
Calyceraceae	heads	long
Campanulaceae	racemes, cymes, heads, solitary	mostly short (some long)
Caprifoliaceae	mostly cymes	short
Dipsacaceae	mostly heads	mostly long
Goodeniaceae	cymes, racemes, heads	short
Rubiaceae	cymes, heads	short
Stylidiaceae	racemes, cymes	short
Valerianaceae	open or compact cymes	short to long

would expect that within the ancestral complex from which the Compositae arose (possibly including some part of the Rubiaceae or Caprifoliaceae (Cronquist, 1977) in which cymose inflorescences are common), heads would have begun to develop from out of this complex as the family acquired other characteristics (such as ovule position, syngenesious anthers, etc.). It is true that heads also exist in both the Rubiaceae and Caprifoliaceae, but the rarity of this condition in these families suggests that they represent evolutionary parallelisms. Further, although the Dipsacaceae and Calyceraceae do resemble the Compositae, these also probably represent evolutionary parallelisms, because they are sufficiently distinct in many other features.

If these above points have merit, then we should be considering the evolution of the Compositae from a cymose ancestor in which head coalescence begins at an early stage in the development of the family. At this time there are small pales associated with this developing inflorescence as is typical in cymose inflorescences. Very early, parallel development into the tribes and subfamilies occurred (Fig. 1). In the Eupatorieae and Astereae many small quickly maturing heads without pales evolved, a reproductive strategy insuring that at least a few propagules survive. In the Lactuceae, we find medium-sized heads without pales but with latex protection as a defensive strategy against predators. The pattern in the Cardueae was toward medium to large heads, with spiny phyllaries and receptacular bristles
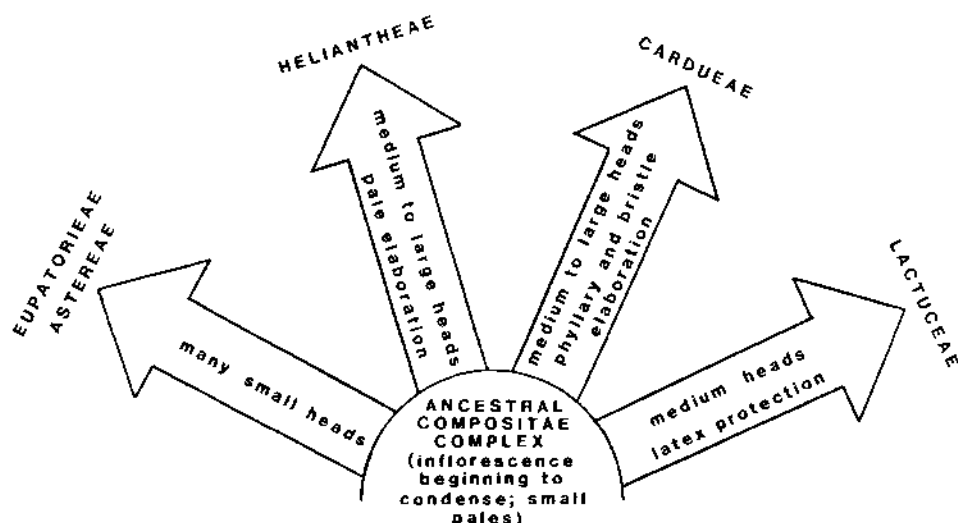

Fig. 1. Examples of parallel trends in protective strategies in the evolution of heads of Compositae.

as efficient defense functions. The Heliantheae, on the other hand, with medium to large heads display pale elaboration, and here occur the most elaborate pale structures of the whole family. The important point is that the very elaborate and bract-like pales in some members of the Heliantheae may reflect the enlargement of pales in response to the increased head size, achene size, and longer fruit maturation times, and not be indicative of a primitive phylogenetic status. These considerations, in addition to the derived condition of gynomonoecious gender strategy in the tribe (Stuessy and Lowrey, in prep.), suggests that the Heliantheae may be a more advanced rather than primitive tribe of the family. The recent cpDNA studies by Jansen and Palmer (1986), in which the Mutisieae are shown to be the most primitive tribe (echoing the conclusions based on morphology by Jeffrey, 1977), do not conflict with the conclusions presented here.

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[Note added in proof]

In a recent paper, unknown to us at the time our manuscript was submitted for publication, Ganders and Nagata (1983, *Lyonia* 2: 23–31) suggest that *Bidens cosmoides* is bird pollinated based upon the copious amounts of nectar produced, which might be an additional, if not perhaps the primary, reason for protection of achenes by the enveloping pales. Such a general correlation of greater protection of ovules in bird pollinated taxa in angiosperms has been documented by Grant (1950, *Evolution* 4: 179–201).