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WHAT GOVERNS PROTEIN CONTENT OF POLLEN: POLLINATOR PREFERENCES, POLLEN–PISTIL INTERACTIONS, OR PHYLOGENY?

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Abstract. Pollen ranges from 2.5% to 61% protein content. Most pollen proteins are likely to be enzymes that function during pollen tube growth and subsequent fertilization, but the vast range of protein quantity may not reflect only pollen–pistil interactions. Because numerous vertebrate and invertebrate floral visitors consume pollen for protein, protein content may influence floral host choice. Additionally, many floral visitors pollinate their host plants. If protein content influences pollinator visitation, then pollinators are hypothesized to select for increased protein content of host plants. We analyzed or gleaned from the literature crude pollen protein concentrations of 377 plant species from 93 plant families. Using this database, we compared pollen protein concentration with (1) pollination mode, (2) pollen collection by bees, and (3) distance from stigma to ovule, after accounting for phylogeny through paired phylogenetic comparisons and a nested ANOVA including taxonomic rank. We found that pollen protein concentrations were highly conserved within plant genera, families, and divisions. We found that bees did not collect pollen that was unusually rich in protein, whether they pollinated or merely robbed their host plant. Plant species with vibratile pollination systems, which require visitation by pollen-collecting bees in order to transfer pollen, tended to have very protein-rich pollen, but it was not clear whether this was due to plant enhancement of pollinator rewards or to the possession of very small pollen grains. We found that zoophilous species were not statistically richer in pollen protein than anemophilous species after accounting for phylogeny, although the three most species-rich anemophilous clades surveyed were generally poor in protein. Plant genera hosting specialist pollen-collecting bees did not have particularly protein-rich pollen. Both mass of protein per pollen grain and pollen grain volume were correlated with stigma–ovule distance. We suggest that the need for growing pollen tubes probably plays a more important role in determining pollen protein content than rewarding pollinators.

Key words: anemophilous; pollen protein; pollen volume; pollination; pollinator reward; style length; zoophilous.

INTRODUCTION

Previous analyses of pollen chemistry have shown that pollen ranges from 2.5% to 61% protein by dry mass (Buchmann 1986). This wide variation in protein concentration could greatly influence plant–animal interactions. Pollen provides most of the dietary nitrogen for most bee species and many species of beetles, thrips, and mites, and supplements the diet of facultative consumers, such as bats (Law 1992), birds (Grant 1996), and marsupials (Turner 1984). Increased dietary pollen protein may increase survival (Levin and Haydak 1957), size (Greenberg 1982, Regali and Rasmont 1995), and longevity of bees (Schmidt et al. 1987).

If pollen consumers preferentially collect protein-rich pollen, we hypothesize that they will select for increased pollen protein in potential host plants. Pollen collectors provide more effective pollination than nectar collectors on some host plants (e.g., Bader and Anderson 1962, Free 1966) and may increase the relative importance of pollen reward over nectar reward. Emphasis on pollen reward is most evident in plant species lacking nectar, such as roses (*Rosa* spp.), or species possessing apically dehiscent anthers that only disperse pollen to bees that vibrate the anthers to collect it, as in nightshades and potatoes (*Solanum* spp.). This latter pollination system, called ''vibratile pollination'' (the mode of pollen release) or ''buzz-pollination'' or ''sonication'' (the sound a bee makes while vibrating the anthers), occurs in at least 72 angiosperm plant families and usually involves the secondary loss of floral nectar (Buchmann 1983).

Most pollen consumers seek nectar as well as pollen, and most animal-pollinated plants produce both nectar and pollen. We hypothesize that pollen-only flowers lure and retain pollinators by producing more or higher quality pollen. Simpson and Neff (1983) suggested that pollen-only flowers yield more pollen than related nectar-producing flowers. We know of no careful studies, however, that support this theory. If pollen consumers

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respond mainly to pollen abundance, then they would be expected to visit wind-pollinated species, many of which produce prolific amounts of pollen. Some wind-pollinated (anemophilous) species, such as corn (*Zea mays*) regularly attract pollen collectors, [e.g., bees including honey bees (Mason and Tracewski 1982, Flottum et al. 1983), bumble bees, and *Melissodes* spp. (T. H. Roulston, *personal observation*)] but many, such as pines (*Pinus* spp.) do so rarely. A possible explanation is that pollen collectors favor plant species with protein-rich pollen, and most anemophilous pollens contain little protein, as suggested by Lidforss (1899).

Plants do not produce pollen primarily to feed animals. Pollen transmits male gametes to female reproductive tissue to initiate sexual reproduction. Pollen protein consists mainly of enzymes (Stanley and Linskens 1974) that function during pollen tube growth. Thus, the amount of protein in pollen grains could influence the distance that pollen tubes can grow to reach ovules. This hypothesis parallels the theory that pollen grain volume correlates with style length due to energy storage limitations (e.g., Baker and Baker 1982). Because pollen protein concentration has implications for both pollen–pistil and plant–animal interactions, selection may favor optimizing protein levels for both pollen tube growth and attracting pollinators.

If style length governs pollen protein abundance, what relationships might arise between pollen collectors and pollen protein concentration? Selection may favor pollen consumers recognizing the nutritional content of their host's pollen without favoring mutualistic pollination interactions over pollen predation. Not all pollen consumers are pollinators. For example, thrips and mites frequently enter and exit a flower without effecting pollination. Bees often collect pollen from bird, bat, moth (Baker et al. 1971, Vaughton 1996), or wind-pollinated plants (Adams et al. 1978) without pollinating them. Although such consumers should recognize nutritious pollen, they do not exert selection pressure on their hosts to provide it. Instead, they parasitize (or ''rob'') their pollen hosts and their behavior should select for plant defense mechanisms. Plants may have fewer ways of defending pollen, however, than defending nectar. Plants may hide nectar at the base of tubular corollas that restrict access to animals with long mouthparts (e.g., Nilsson et al. 1987) or not produce any nectar. Plants must produce (or receive) pollen in order to reproduce sexually and must place it in a position to contact pollinators. Selection, therefore, could lead to strong associations between pollen consumption and pollen protein, but not between pollination and pollen protein.

Postulated relationships between pollen collectors and pollen protein concentrations assume that pollen consumers can assess pollen quality, but there is little evidence to support this. Bumble bees preferentially visit the flowers of potato cultivars that produce viable pollen grains instead of cultivars that produce primarily inviable, shrunken pollen grains (Batra 1993). Honey bees, however, sometimes collect toxic pollen and particulate matter of no known nutritional value (Hitchcock 1959, Dietz 1975). Although some bees can distinguish plant species based on the chemical profile of the pollenkitt (Dobson 1987), most pollen nutrients are inside the pollen grain and only released after a slow digestive process (Dobson and Peng 1997). If bees cannot judge pollen quality, they could suffer unpredictable mortality or produce offspring of unpredictable body size if they forage on many different host plants (polylecty). Alternatively, they may limit their foraging to a small number of closely related host plants (oligolecty) and collect a resource of constant quality but variable abundance. Many bee species exhibit such a specialist pollen foraging strategy (reviewed in Wcislo and Cane 1996).

Pollen specialist bees typically forage for pollen on plant species in one or several closely related genera rather than on a single plant species, except when there are no sympatric congeners, as in *Larrea tridentata* (Hurd and Linsley 1975) in the southwestern United States, or no sympatric congeners whose flowering times overlap a specialist bee's foraging times. The only data presently available show that specialists do not require host plant pollen for proper development (Tepedino 1997; N. Williams, *unpublished manuscript*). No hypotheses adequately explain the benefit to bee species of restricting their diet to a single host plant. There are very few examples of pollen that is toxic to bees (but see O'Neal and Waller 1984). Plant species known to have defensive compounds in leaf and floral tissue have reduced amounts in pollen (Detzel and Wink 1993), including plant species pollinated by animals seeking only nectar. Differences in pollen nutrient abundance may be a better predictor of bee performance than presence or absence of defensive compounds. If a specialist bee chooses a novel host plant as a quasi-random process enforced by the undetected quality of the host, we hypothesize that those plants producing nutrient-rich pollen are more likely to maintain specialists than those producing nutrient-poor pollen.

We assembled a database of pollen protein concentrations from 377 plant species to test whether pollen protein concentration better reflects plant–animal or pollen–pistil interactions. To assess correspondence between pollen protein and pollen consumption we first compared protein concentrations of pollens collected or not collected by bees, regardless of their effectiveness at pollination. We focused on bees as pollen consumers because they depend on pollen for survival and reproduction, and because they consume more pollen than any other group of pollinators. Furthermore, bee behavior on host plants, including the plants visited and whether or not they collect pollen, is much better documented than for all other groups of floral visitors. We then compared pollen protein concentration of

plants pollinated by animals with plants pollinated by wind to assess shifts in protein related to pollen being carried externally on animals instead of blown through the air. We compared protein concentration of bee-pollinated species with species pollinated by other animals to assess shifts in pollen protein that seem to reflect pollinator selection for increased pollen quality. Similarly, we compared pollen protein concentrations of plant species possessing vibratile vs. nonvibratile pollination systems to determine if pollination systems requiring intentional pollen collection contained more pollen protein than systems not requiring pollen collection. We compared pollen protein concentrations of plant genera hosting vs. not hosting specialist pollen-collecting bees to determine if protein seemed to play a role either in the selection or the maintenance of specialist bee–host interactions. In order to test for a relationship between pollen protein content and the distance pollen tubes must grow, we converted percentage protein into estimates of protein mass per pollen grain and regressed the protein mass on stigma–ovule distance.

METHODS

Collection of pollen samples

We manually collected pollen from anthers that dehisced in the field or in the laboratory within 24 h of collection. We then dried the pollen immediately, if possible, in a 40°C incubator for at least 48 h or froze it at −15°C for subsequent drying and analysis. Most taxa were collected near Tucson, Arizona; Auburn, Alabama, or Barro Colorado Island, Panama. Pollen reference slides are retained by T. H. Roulston.

Bradford assay: grinding

We manually ground 1-mg dried pollen samples using a mortar and pestle. Each sample was dusted with aluminum powder to facilitate grinding and moistened with two drops of 0.1 mol/L NaOH. After grinding, each sample of pollen was retrieved in 1.5 mL of 0.1 mol/L NaOH, kept refrigerated for at least 24 h, placed in boiling water for 5 min, and centrifuged for 5 min. Most analyses were performed within one week of grinding. Analyses performed without grinding produced much smaller protein estimates.

Bradford assay: choice and preparation of standard

We chose cattail (*Typha latifolia* L.) pollen as a protein standard for all analyses because the plant is widely distributed (circumboreal), common, easily identified, and produces great quantities of easily collected pollen. Because different proteins (e.g., bovine serum albumin or immune globulin) have different binding affinities for Coomassie Brilliant Blue (see *Methods: Bradford assay: analysis*), we reasoned that a pollen standard should be used for comparing pollen proteins. Five mg of dried, hand-collected *Typha* pollen was prepared in the same manner as the samples. The extracted *Typha* pollen was diluted with 0.1 mol/L NaOH to generate five serial dilutions containing 0.002–0.035 mg protein/mL.

Bradford assay: analysis

150 μL aliquots of samples and standards were pipetted into glass vials containing 2000 μL of Bio-Rad Bradford dye reagent augmented with 150 mg of polyvinylpyrollidone (PVP) per 50 mL reagent. Bradford reagent contains Coomassie Brilliant Blue G-250 dye, which binds with protein to form a complex that absorbs visible light of 595 nm (see Bradford 1976, Jones et al. 1989, for details and conditions of the chemical reaction). Extraction of proteins in mildly alkaline solutions both minimizes binding interference from plant phenolics (Jones et al. 1989) and improves the binding equivalence of different proteins (Stoscheck 1990). Absorption readings at 595 nm were recorded on a Beckman Du-62 spectrophotometer (Beckman Coulter Inc., Fullerton, California) 15 min after sample aliquots were mixed with Bradford reagent. A new standard line was generated for each sample run. Percentage protein was calculated using simple linear regression. A pollen sample of known, intermediate protein concentration, usually *Helianthus annuus*, was analyzed during each sample run in order to ensure the accuracy of the regression line. If the calculation of the known sample differed by more than 3% protein from the known value, all estimates during that sample run were discarded. Up to 16 samples were run consecutively, but no more than 5 min elapsed between the analysis of the standard serial dilutions and the individual samples. All samples were run twice, each time on different days, and the two estimates were averaged to produce one sample value.

Analysis of samples: combustion and micro-Kjeldahl methods

When adequate pollen samples were available, we analyzed total nitrogen by combustion using a LECO-600 carbon and nitrogen analyzer (LECO, St. Joseph, Michigan) or by micro-Kjeldahl analysis using a TechniCon AutoAnalyzer II according to the company's industrial methods (see Industrial Method No. 329–74W/B, TechniCon Corporation, Emeryville, California). Mass of samples were 60–150 mg for combustion and 1000 mg for micro-Kjeldahl. Nitrogen values were converted to protein by a multiplier of 6.25, the most commonly used multiplier for plant pollens (e.g., Buchmann 1986). Rabie et al. (1983) reported that there is some variation in actual nitrogen-protein conversion factors among plant products and they recommended using a multiplier of 5.6 rather than 6.25. We used 6.25 to be consistent with previously published literature. We assumed a constant multiplier for all species. Since our calculation of percentage protein based on the Bradford assay depended on our estimate

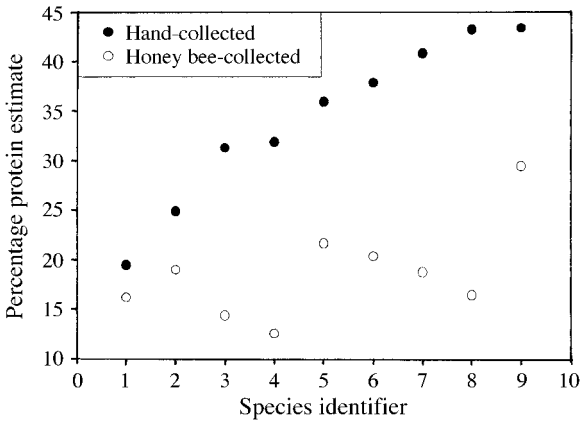

FIG. 1. Comparison of pollen protein estimates for hand-collected and bee-collected pollens from the same plant species. Citations for hand-collected pollens appear in the Appendix. Bee-collected pollen data come from Standifer (1966), Ibrahim (1974), McLellan (1977), and Rabie et al. (1983). Species represented are (1) *Fagus sylvatica,* (2) *Zea mays,* (3) *Salsola kali,* (4) *Brassica napus,* (5) *Brassica campestris,* (6) *Carnegiea gigantea,* (7) *Trifolium pratense,* (8) *Populus fremontii,* and (9) *Phoenix dactylifera.*

for protein concentration of cattail pollen, which in turn was derived from nitrogen analysis, the magnitude of all values presented here is tied to the 6.25 conversion factor. The relative protein concentrations among taxa, however, would remain the same if a lesser multiplication factor were used.

Pollen protein data in the literature

Many studies have determined nitrogen content of pollen stripped from honey bees' corbiculae at hive entrances (e.g., Todd and Bretherick 1942, Standifer 1967, Rabie et al. 1983), but, with one exception, we have summarized data only from pollen that was hand-collected from flowers. We do so because honey bees add nectar to pollen for transport on their legs. Although the liquid portion of added nectar readily evaporates from honey bee-collected pollen, the sugar portion remains and may contribute a large portion of the mass to the pollen being analyzed. Based on comparisons of hand- vs. honey bee-collected pollens (Fig. 1), it appears that half or more of the mass of honey bee-collected pollens can be attributed to the addition of nectar-derived sugars to the pollen. The proportion of sugar added to honey bee-collected pollens appears to vary greatly and does not justify using a constant multiplier to adjust the mass of honey bee-collected pollens to hand-collected pollens. Without accounting for this factor, the concentration of protein and other compounds in the honey bee-collected pollen can be greatly underestimated. Todd and Bretherick (1942) analyzed many honey bee-collected pollen samples. It appears from their data that the presence of reducing sugars in the pollen can be attributed mainly to the addition of nectar by honey bees to the pollen load. Thus, in order to make use of their extensive analyses, we recalculated their values of percentage protein per unit dry mass of pollen after subtracting the mass of water and the mass of reducing sugars. Todd and Bretherick described their techniques as "standard methods," which we assume to be the micro-Kjeldahl acid digestion for determining nitrogen content.

All other summarized data are based on pollen hand-collected from flowers. Data from Lidforss (1899), Buchmann (1986), and Turner (1984) are based on nitrogen estimates through micro-Kjeldahl analysis. Knight et al. (1972) published nitrogen values for many hand-collected pollens as part of their study of cation exchange capacities of pollen. Although they analyzed the nitrogen content by micro-Kjeldahl analysis, they published their results as milliequivalents of N per 100 g of dry matter. We have converted milliequivalents (mequiv) of N to proportional mass of N using:

$$\frac{\text{mg N}}{\text{mg dry matter}} = \frac{\text{mequiv N}}{\text{100 g dry matter}} \times \frac{\text{14 mg N}}{\text{1 mequiv N}} \times \frac{\text{1 g dry matter}}{\text{1000 mg dry matter}}.$$

We converted the proportion of N in the sample to proportion of protein by multiplying by the 6.25 conversion factor and expressed the result as a percentage.

We excluded three published data sets using hand-collected pollen. Howell (1974) published values for several species of Cactaceae and Agavaceae based on micro-Kjeldahl analysis. Her values are consistently much lower than congeneric or conspecific values from other data sets and the range of values given for the genus *Agave* (8–43% protein) is far greater than the range for any genus, including *Agave,* in our overall data set. Rasheed and Harder (1997) published several protein values for their study of bumble bee foraging preferences. They used a novel analytical technique, however, and their estimates fall well below the range of all taxa in our overall database. Gilliam et al. (1980) reported protein values for several *Citrus* species but did not account for moisture in the pollen grains.

Taxonomy

Classification of plants into taxonomic orders and families follows Mabberley (1997), except that family names ending in "-aceae" are given in all cases (e.g., Brassicaceae for Cruciferae, Apiaceae for Umbelliferae). Generic and species classification follows Kartesz (1994) for native North American plants and some naturalized or widely cultivated exotic taxa. For taxa not covered by Kartesz, nomenclature follows Croat (1978) and the publications in which previous protein values were published.

Pollinator assessment

Whenever possible, pollinators of surveyed plant species were determined through published literature.

We attempted to find pollination studies for all plant species in the database that discerned pollinators from visitors. For plant species lacking thorough pollination research, we inferred pollinators based on published reports of appropriate visitation behavior to the target species, summary reports of claimed pollination modes from ecological surveys, or visitation or pollination reports to congeners with very similar flower morphology and color. Additionally, pollinators for several taxa were inferred based on unpublished observations of the authors and other researchers.

Pollen volume estimate

Pollen volume was determined following the methods of da Silveira (1991) and O'Rourke and Buchmann (1991). Pollen grains were mounted in silicon oil and measured at 400× with an ocular micrometer. Polar and equatorial axis measurements were taken for all pollen grains; for pollen grains that were not apparently spherical or elliptical (e.g., *Oenothera*) an estimate of depth was also made. Volumes were calculated using volume equations for spheres ($1/6\pi p^3$), ellipsoids ($1/6\pi e^2 p$), and triangles with consistent depth ($1/2bhd$) where p = polar axis, e = equatorial axis, b = base, h = height, and d = depth. Five to ten noncollapsed, haphazardly encountered grains per slide were measured and these values were averaged for calculating volumes. When pollen was not available for measurement, we used average dimensions taken from published literature.

Estimate of mass of protein per pollen grain

The protein data generated in this and cited studies are based on total protein (or nitrogen) per unit mass of pollen and cannot be translated directly into estimates of protein mass per pollen grain. In order to estimate protein mass per pollen grain, we estimated the dry mass of individual pollen grains for 20 species by weighing 1-mg samples and then counting the grains with a particle counter. One sample was counted per species. We divided the sample mass by the number of pollen grains in the sample to calculate an average dry mass per pollen grain. We regressed pollen grain mass on pollen grain volume to generate a simple linear regression equation that could be used to interpolate pollen grain mass for all species in the database. The 20 species used to generate the regression line included 8 zoophilous and 12 anemophilous species (Fig. 2). Neither the slopes ($t = 0.23$, $P > 0.2$) nor the y-intercepts ($t = 1.55$, $P > 0.1$) differed when separate regression lines for anemophilous and zoophilous species were compared. Thus, estimates of pollen mass based on volume were calculated from the regression line for all species in the database (Fig. 2): $\ln(\text{mass}) = 0.96 \times \ln(\text{volume}) - 12.5$.

Stigma–ovule distance

Using dial calipers calibrated to 0.1 mm, we estimated the maximum linear distance pollen tubes must grow in order to reach the lowest ovule in an ovary. This distance was presumed to be the outer tip of the stigma to the bottom of a compound ovary. For uniovulate ovaries, this distance was measured to the top of the ovary. Estimates were averaged from 1–10 fresh flowers in the laboratory, when possible, or dried flowers from herbaria at Duke University, University of Arizona, or Auburn University. We did not account for shrinkage of floral tissue due to drying of herbarium specimens.

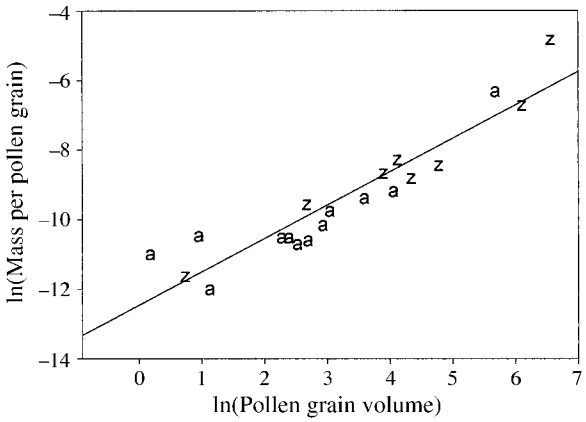

FIG. 2. Regression of pollen grain mass on pollen grain volume for 20 plant species. Key: z = zoophilous pollination, a = anemophilous pollination. Regression equation: ln[mass (mg)] = 0.95 × ln(volume 10–6 cm) − 12.46; $r = 0.87$.

Statistical tests

Testing evolutionary hypotheses based on the present attributes of diverse organisms requires statistical methods that consider the evolutionary relationships of the organisms surveyed. Correlated traits shared among species due to common descent do not present independent evidence for a functional relationship between those traits (Burt 1989, Harvey and Pagel 1991). We used both an analysis of variance approach that incorporated taxonomic rank into a nested variance structure and a cladogram approach that incorporated phylogenetically independent shifts in pollination mode. Herrera et al. (1998) used a similar dual approach. We used the general linear model procedure of the Minitab Statistical Software Package (Version 12) with nesting of the taxonomic ranks of class, order, family and genus (using order, family, and genus as random effects) and the inclusion of pollinator, pollen consumption, and vibratile-pollination as fixed effects. Due to the great imbalance in the number of species surveyed in each taxon and the lack of certain traits in some lineages, we could not use all nested levels simultaneously in all analyses.

We constructed phylogenetically independent comparisons by plotting pollination mode and pollen protein values on recently published cladograms of plant phylogeny. We used the plant phylogeny of Chase et

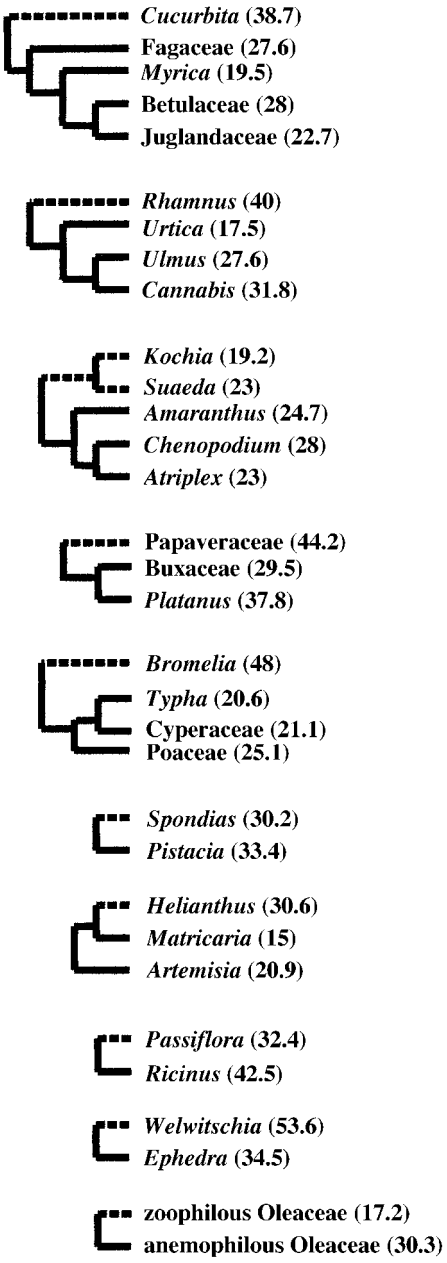

FIG. 3. Paired comparisons of protein concentration between zoophilous and anemophilous taxa that share a common ancestor. Protein concentrations are in parentheses. Key: dashed line = zoophilous, solid line = anemophilous. Overall mean, averaged over lower taxonomic ranks, ±1 SD: zoophilous, 35.6 ± 11.5%; anemophilous, 28.9 ± 7.3%; $n = 10$, $t = 1.6$, $P = 0.15$, paired t test.

al. (1993) as the basis for our analyses, but extended some clades with other, more narrowly focused studies (Asteraceae, Bayer and Starr 1998; Caryophyllales, Downie et al. 1997; Fabaceae, Doyle et al. 1997; Malvales, Judd and Manchester 1997; and Solanaceae, Olmstead and Palmer 1992). Comparisons were made as paired t tests using one value for each replicate pairing on the cladogram and averaging the value of all taxa of lower taxonomic rank than the taxon shown on the cladogram. For example, to test for differences in protein value associated with shifts between wind and animal pollination, we included one replicate that compared the animal-pollinated Cucurbitaceae to the speciose anemophilous clade including Fagaceae, Betulaceae, Myricaceae, and Juglandaceae (Fig. 3). The Cucurbitaceae value represented an average of the two *Cucurbita* species that have been surveyed. For the anemophilous clade, we averaged all species values within their genera and all genera within their families before using an average family value for the whole clade. We proceeded in similar fashion throughout the cladogram, finding 10 independent comparisons of pollen protein concentration of wind vs. animal pollination, five independent comparisons of vibratile vs. nonvibratile pollination, and nine independent comparisons of bee vs. other animal pollination. Although this procedure reduced sample sizes from several hundred to a small handful, it reduced the bias of unequal sampling across plant groups.

We regressed pollen volume and pollen protein mass per pollen grain on stigma–ovule distance in separate tests. Because all three traits are correlated with phylogeny, we attempted to account for some of the effect of phylogeny statistically before analyzing the relationship between the traits themselves. First, we chose only one species per genus in the analysis. We chose the species with the most complete data set, or, if there were several species with complete data sets, then we arbitrarily chose the species with the greatest pollen volume. Next, we performed a nested analysis of variance on the included taxa using taxonomic rank as the nested categorical variable and, in separate trials, the natural logarithm of pollen volume, mass of protein per pollen grain, and stigma–ovule distance as the response variable. We then regressed the residuals of pollen volume and mass of pollen protein per pollen grain on the residuals of stigma–ovule distance for an analysis free of taxonomic covariance. We excluded gymnosperms because of their very different pollen–ovule pathway. In order to find predictor variables for percentage pollen protein, we simply regressed pollen volume and stigma–ovule distance on the arcsine of percentage pollen protein after transforming the dependent variables with their natural logarithm. We did not attempt to account for phylogeny with these predictor variables.

RESULTS

The entire data set is listed in the appendix. It includes data generated during this study and data accumulated from the literature. For taxa analyzed by either micro-Kjeldahl or combustion, which both measure nitrogen, the exact percentage nitrogen value can be retrieved by dividing the given protein value by 6.25, since that was the value used to derive percentage protein from the actual nitrogen value. For taxa ana-

TABLE 1. Comparison of percentage pollen protein estimates ±1 SD for plant species analyzed by Bradford assay and nitrogen analysis by combustion or micro-Kjeldahl.

Taxon	Bradford assay	Combustion
Alnus sp.	33.1 ± 1.6 (3)	30.1 ± 0.5 (4)
Carengiea gigantea	37.8 ± 2.0 (3)	36.8 ± 0.0 (2)
Carya illinoensis	28.6 ± 1.2 (3)	20.0 ± 0.0 (2)
Helianthus annuus	29.8 ± 1.9 (7)	30.6 ± 0.0 (4)
Ochroma pyramidale	49.5 ± 0.7 (3)	41.7 ± 0.6 (6)
Oenocarpus panamensis	24.8 ± 2.7 (8)	23.8 ± 0.2 (3)
Opuntia phaecantha	26.8 ± 0.1 (3)	22.1 ± 0.0 (2)
Pinus taeda	15.9 ± 1.1 (3)	18.1 ± 0.2 (2)
Pseudobombax septanatum	49.3 ± 1.9 (8)	48.1 ± 0.3 (4)
Quercus nigra	41.1 ± 0.5 (3)	41.5 ± 0.3 (3)
Quercus michauxii	40.3 ± 5.4 (3)	38.4 ± 0.8 (2)
	Bradford assay	Micro-Kjeldahl
Agave deserti	43.9 ± 1.4 (3)	45.8
Ephedra trifurca	34.5 ± 1.4 (3)	34.7 ± 1.6 (3)
Juglans regia	25.1 ± 0.7 (3)	24.4 ± 1.1 (3)
Juniperus deppeana	5.1 ± 1.3 (3)	5.7 ± 0.3 (3)

Notes: The number of subsamples analyzed is given in parentheses. Pollen for all analyses was taken from a common sample. Combustion analyses were performed simultaneously with Bradford assay. Micro-Kjeldahl analyses were performed 12–15 years earlier than Bradford assay.

lyzed by Bradford assay, the percentage nitrogen value can be estimated by dividing by 6.25, but it was protein concentration that was actually determined in the analysis.

Analytical techniques

A modified Bradford assay yielded crude protein estimates similar to nitrogen analysis by combustion ($r = 0.93$, Pearson product–moment correlation, 11 samples) and micro-Kjeldahl ($r = 0.99$, Pearson product–moment correlation, four samples) (Table 1). The Bradford assay required 1/100th the amount of pollen needed for nitrogen analysis by combustion and only 1/1000th the amount of pollen typically used in micro-Kjeldahl analysis.

Protein estimates varied little over time for samples frozen between analyses. Subsamples of four species analyzed by Bradford assay in 1998 produced estimates nearly identical to subsamples from the same batch analyzed by micro-Kjeldahl between 1983 and 1985 (Table 1). One subsample analyzed by micro-Kjeldahl in 1985 (17.0% protein) yielded a similar protein estimate (17.1%) when analyzed by combustion in 1998.

Variation in pollen protein content between sites and years has only been measured in simultaneous analyses for *Typha latifolia* (Table 2). Because these analyses were carried out on aggregated samples, variation among individual plants has not yet been determined. Variation due to substrate differences, such as soil fertility, remains unknown.

Phylogenetic consistency

Pollen protein concentration was highly conserved within genera, families, and divisions (Table 3). The average standard deviation for congeners was only 2.9% protein for the 51 genera in which more than one species was sampled. Pollen protein values ranged more widely within plant families, yielding an average standard deviation of 4.7% protein for the 39 families in which multiple genera were surveyed. Floral variability within plant families did not always correspond to variability in protein concentration: The Solanaceae, for instance, uniformly had protein-rich pollen, despite having flowers that range from small, bee-pollinated *Solanum* to enormous moth or bat-pollinated *Solandra, Datura,* and *Brugmansia.* Among plant families surveyed, only the species-rich and morphologically diverse Cactaceae and Fabaceae showed substantial variability in protein concentration. Pollen protein varied considerably more among orders. For instance, the Malvales, which are recognized as a taxonomic unit by

TABLE 2. Comparison of percentage dry mass of protein (±1 SD) of cattail (*Typha latifolia*) pollen collected at different sites and different times.

Site and year	Protein (%)
Auburn, Alabama 1998	19.3 ± 0.1
Auburn, Alabama 1997	19.5 ± 0.2
Auburn, Alabama 1996	20.5 ± 0.7
Tucson, Arizona 1985	17.1 ± 0.1
Chatsworth, New Jersey 1994	16.8 ± 1.1

Note: All samples were stored frozen at −15°C since collection and were analyzed simultaneously by combustion in October 1998.

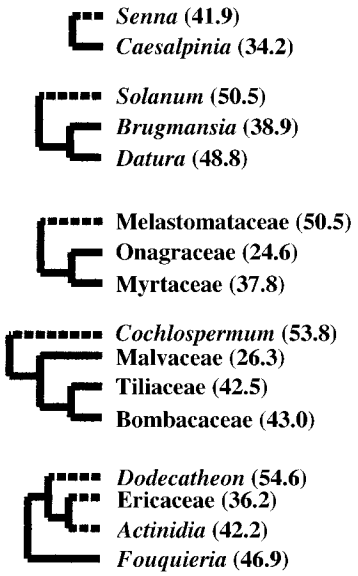

FIG. 4. Paired comparisons of protein concentration between vibratile-pollinated and nonvibratile-pollinated taxa that share a common ancestor. Protein concentrations are in parentheses. Key: dashed line = vibratile-pollinated, solid line = nonvibratile-pollinated. Overall mean, averaged over lower taxonomic ranks, ± 1 SD: vibratile-pollinated, 47.8 ± 5.4%; nonvibratile-pollinated, 38.8 ± 6.7%; $n = 5$, $t = 2.1$, $P = 0.10$, paired t test.

TABLE 3. Nested ANOVA comparing the effect of taxonomic rank on pollen protein concentration.

Source	df	Sequential SS	Adjusted SS	Adjusted MS	*F*	*P*†
Division	3	11 783.41	3663.29	1221.10	5.15	0.004
Order (division)	44	19 381.76	12 106.57	275.15	1.23	0.242
Family (division, order)	43	11 301.82	10 246.41	238.29	5.02	0.000
Genus (division, order, family)	138	6978.08	6978.08	50.57	2.27	0.000
Error	145	3230.41	3230.41	22.28		
Total	372	52 263.85				

Note: All taxonomic ranks except division were considered random effects.
† Not an exact *F* test.

most authors and share several synapomorphies, contain both the protein-poor Malvaceae and the protein-rich Bombacaceae. Among taxonomic divisions, the conifers were protein-poor, but cycads and gnetophytes contained protein-rich pollen; angiosperm pollen ranged from 12–61% protein, overlapping the whole range of gymnosperm species except for the lowest values of the conifers.

Pollen protein and collection by bees

Pollen collected by bees, regardless of whether they were pollinators or only pollen consumers, did not contain more protein than pollen not reported to be collected by bees (Table 4). Bees collected pollen ranging from 12–61% protein, including the pollens of many anemophilous species. We identified five independent derivations of vibratile pollination in our data set. In four of five cases, the vibratile-pollinated clade contained pollen that was richer in protein than the non-vibratile-pollinated clade (Fig. 4). Vibratile-pollinated taxa as a whole contained the pollen richest in protein (47.8%), but there were too few evolutionarily independent derivations to carry out a powerful statistical test. Vibratile-pollinated taxa also had unusually small pollen grains, which were generally associated with protein-rich pollen.

Among plant genera hosting pollen-collecting bees, genera hosting pollen specialist bees did not produce pollen richer in protein than those genera not hosting pollen specialists (Table 5). Among plant genera hosting multiple oligolectic bee genera, the pollen of *Oenothera* and *Opuntia* were poor in protein, while *Helianthus* and *Larrea* were close to the center of distribution (Table 6).

Pollen protein and pollination mode

Animal-pollinated (zoophilous) plants did not contain pollen richer in protein than anemophilous plants when phylogeny was factored into the analysis (Table 4, Fig. 3). The majority of anemophilous species sampled came from three protein-poor clades, the conifers, the ''higher'' hamamelids (sensu Manos and Steele 1997) and the grasses. This gives the impression that anemophilous pollens are generally protein poor. This may be true in terms of total number of species or genera and total amount of pollen produced, but it was not statistically supported among independent evolutionary shifts between zoophilous and anemophilous lineages. Of the ten phylogenetically paired groups that differed in pollination mode, six zoophilous groups contained pollen richer in protein and four anemophilous groups contained pollen richer in protein. The most protein-rich anemophilous pollens were *Ricinus*, *Quercus*, and *Platanus* with 42%, 39%, and 38% pollen protein respectively.

Zoophilous plants pollinated by bees did not contain pollen richer in protein than zoophilous plants pollinated by other animals (Fig. 5). Pollen of bee-pollinated species ranged from ~12–14% protein for some Asteraceae and Malvaceae to >60% protein for *Do-*

TABLE 4. Comparison of pollination modes and pollen utilization by bees within a nested ANOVA.

Source	df	Sequential SS	Adjusted SS	Adjusted MS	*F*	*P*
Order	44	13 186.10	6859.20	155.89	0.91	0.616†
Family (order)	37	7594.99	7120.27	192.44	4.81	0.000
Bees collect	1	3.25	4.18	4.18	0.10	0.747
Zoo/anem/mix	2	22.41	22.41	11.20	0.28	0.756
Error	105	4199.38	4199.38	39.99		
Total	189	25 006.12				

Notes: Pollen protein concentration is the dependent variable. Taxonomic categories were considered random effects, and ''bees collect'' (yes/no) and ''pollen vector'' (zoophilous/anemophilous/mixed) were considered as fixed effects.
† Not an exact *F* test.

TABLE 5. Comparison of protein concentrations of plant genera that host oligolectic bees with plant genera that host only non-oligolectic pollen-collecting bees.

Source	df	Sequential SS	Adjusted SS	Adjusted MS	*F*	*P*
Order	28	4044.17	2537.80	90.64	0.36	0.992†
Family(order)	18	3834.67	3898.55	216.59	5.44	0.000
Oligoleg host	1	84.57	84.57	84.57	2.13	0.153
Error	41	1631.53	1631.53	39.79		
Total	88	9594.94				

Note: Taxonomic categories were considered random effects, and hosts of oligoleges (yes/no) was considered a fixed effect.
† Not an exact *F* test.

decatheon and *Rhexia.* Bird- and bat-pollinated species spanned a similar range of protein concentration.

Association of pollen protein and pollen volume with stigma–ovule distance

Mass of protein per pollen grain and pollen grain volume were positively associated with distance from the stigma to the lowermost ovule for single species estimates in 83 genera (Figs. 6, 7). A similar, positive relationship was found by plotting the actual species values, and thus ignoring the taxonomic distribution of the species sampled, rather than the residuals (pollen volume, $r = 0.24$, protein mass, $r = 0.34$). Pollen grain volume was positively correlated with mass of protein per pollen grain ($r = 0.97$), but it was negatively correlated with percentage of protein in pollen grains ($r = -0.45$). The combination of pollen volume and stigma–ovule distance was a strong predictor of percentage protein for the 83 angiosperm genera for which both traits had been measured [$r^2 = 0.49$, multiple linear regression, equation: pollen protein(%) = 69.5 + (4.75 × ln [stigma–ovule distance]) − (4.53 × ln [pollen volume])].

TABLE 6. List of average percentage protein for plant genera that host at least one species of oligolectic bee.

Plant genus	Average percentage protein	Reference for oligolecty
Acer	41.8	Batra (1980)
Argemone	45.3	
Ceanothus	40.4	Krombein et al. (1979)
Cucurbita	38.6	Hurd and Linsley (1964)
Echinocereus	33.7	
Helianthus	29.8	Neff and Simpson (1990)
Ipomoea	28.5	Austin (1978)
Larrea	45.4	Hurd and Linsley (1975)
Mentzelia	39.7	Griswold and Parker (1988)
Oenothera	24.6	Linsley et al. (1964)
Opuntia	23.0	Simpson and Neff (1987)
Passiflora	34.6	Neff and Rozen (1995)
Petunia	41.1	Wittmann et al. (1990)
Phacelia	58.9	Torchio et al. (1967)
Quercus	38.8	Velthuis (1992)
Salix	41.4	Westrich (1989)
Solanum	46.1	Cane and Buchmann (1989)
Sphaeralcea	29.4	Linsley and MacSwain (1958)
Vaccinium	42.9	Cane and Payne (1988)

DISCUSSION

The wide range in pollen protein concentration among plant taxa has implications for both plant–animal interactions and pollen–pistil interactions. For the

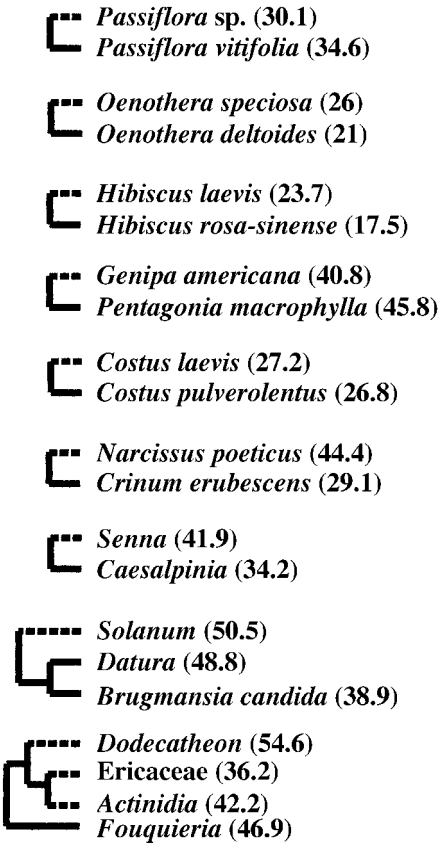

FIG. 5. Paired comparisons of protein concentration between bee-pollinated plant taxa and plant taxa pollinated by other animals. Protein concentrations are in parentheses. Key: dashed line = bee-pollinated, solid line = other animal. Overall mean, averaged over lower taxonomic ranks, ± 1 SD: bee-pollinated, 36.9 ± 10.2%; other animal, 32.9 ± 10.2%; $n = 10$, $t = 1.9$, $P = 0.10$, paired t test.

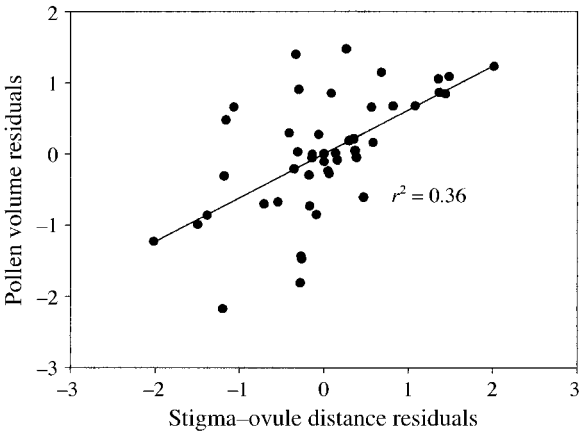

FIG. 6. Simple linear regression of residuals of ln(pollen volume) on residuals of ln(stigma–ovule distance) after removing nested taxonomic covariance.

numerous animals that depend exclusively or facultatively on pollen as a protein source, host plant selection presumably influences the ease with which minimum protein requirements may be met. Pollen abundance and availability, mediated by floral morphology, undoubtedly influence the foraging decisions of pollen-seeking animals. The relative dearth of visitors, however, to some plant species that produce abundant and accessible pollen (e.g., many anemophilous species), indicates that other factors play a role in host plant selection.

For all pollen-collecting animals, net nutritional gain will be the product of pollen harvested at a plant and the proportion of nutrients in that pollen minus the nutrients and energy expended in reaching and manipulating the host plant. Different animal life histories, however, put different foraging constraints on the utilization of plant hosts for meeting protein requirements. Some animals employ progressive feeding strategies, such as adult bats consuming pollen for their own nutrition; adult birds feeding pollen to their offspring, or some social bees feeding pollen or pollen-derived secretions to their offspring at various times during development. For these species, pollen foraging will receive direct, post-digestive feedback in the form of hunger of individual foragers, the food begging of hungry offspring (Grant 1996), or the colony-wide assessment of continual pollen needs in some social species (Dietz 1975). This direct feedback should result in a relatively simple cost–benefit ratio for foraging decisions.

For animals that provide their offspring with all of the food required for development in a single provision, however, additional factors may constrain host plant choice or complicate cost–benefit ratios. Most solitary and some social bees prepare separate, hollow cells in soil, plant stems, or wood to rear each offspring. Adult females place pollen and nectar (or oil) in a series of cells, lay an egg inside each cell, and seal the cell. The offspring receives no additional food during development. Offspring size can be correlated with provision size (e.g., Plateaux-Quènu 1983, Johnson 1990), presumably through the mass of nutrients in the provision rather than simply through the size of the provision. Thus, in order for a mass-provisioning bee to rear offspring of equal size on pollens that differ markedly in protein, the bee would have to compensate for protein-poor pollen by making more foraging trips to collect it (Neff and Simpson 1997) and constructing a larger cell to hold it. No direct tests have been made, however, to determine if bees compensate for nutrient content of pollen sources by adjusting their foraging effort. Increased bee body size has been associated with increased mating opportunity among some male bees (Alcock 1995), increased dominance and likelihood of reproduction among females within the nest of social species (Buckle 1982), increased likelihood of surviving diapause (Tepedino and Torchio 1982), and increased fecundity (Kim 1997).

Despite the apparent importance of pollen protein concentration to pollen consumers, there is no indication in our data that pollen protein concentration has responded evolutionarily to the dietary demands of pollinators. The independent shifts between zoophilous and anemophilous pollination did not inevitably lead to increased pollen protein in zoophilous pollen. Among zoophilous pollens, shifts between bee pollination and other animal pollination did not result in changes in pollen protein that reflected its use as a pollen reward. Furthermore, despite the importance of dietary protein content to bees, bee species collect pollens that differ widely in protein content and do not show an apparent association with protein-rich species. We base this conclusion, however, on an overall pattern of use and nonuse of host plants, irrespective of habitat and local foraging decisions. Such a hypothesis could be tested more directly through choice tests with captive bees or by an analysis of foraging patterns within

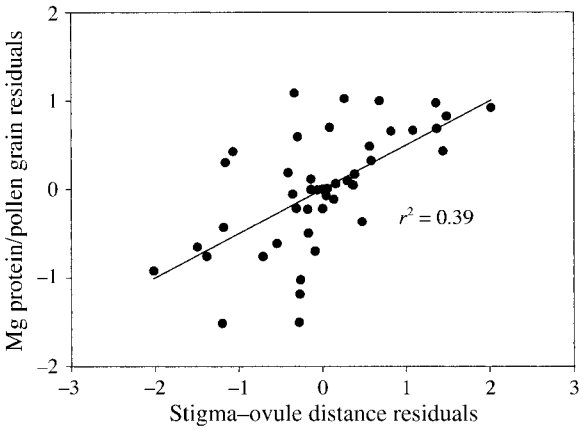

FIG. 7. Simple linear regression of residuals of ln(pollen mass) on residuals of ln(stigma–ovule distance) after removing nested taxonomic covariance.

a single habitat (as done by Rasheed and Harder [1997], but using a validated pollen protein analytical technique).

Plant genera that host oligolectic bees do not provide more protein-rich pollen than other plant genera that are routinely visited by pollen-collecting bees. Although some of the genera included in our survey and scored as hosting oligolectic bees were represented by species that do not host oligolectic bees, primarily because they are not sympatric with the oligolectic bee species, we justify our analysis in two ways: (1) Oligolectic bees typically restrict foraging to a plant genus, several closely related genera, or a plant family, rather than to an individual plant species. (2) The pollen protein content of plant species in the same genus is very similar.

Because oligolectic bee species collect pollen from hosts with very different protein concentrations, we can make one set of alternative predictions: oligoleges on more protein-rich species will either make smaller provisions or rear larger offspring from equally sized provisions than oligoleges on protein-poor pollens. This prediction follows from known correspondence between offspring size and provision size and between protein content and offspring size. It also makes the untested assumption that the nitrogen assimilation efficiency of bees, which is among the highest of all animals studied (Wightman and Rogers 1978, Schmidt and Buchmann 1985), does not vary between pollens or bee species.

Our conclusion that pollen protein content does not differ between zoophilous and anemophilous pollens refers only to statistical evidence for changes in protein content reflecting evolutionary shifts in pollination modes. The majority of anemophilous species in our data set are protein-poor, and a statistical analysis treating genera (or species) as independent data points would reveal that anemophilous pollens contain significantly less protein (25.8%) than zoophilous pollens (39.3%). This discrepancy arises from a sampling bias in our data set that is attributable partly to limitations in analytical methods and partly to the proliferation or ecological dominance of species within three anemophilous clades. The analytical limitation reflects the amount of pollen required for protein analysis (100–1000 mg by combustion or micro-Kjeldahl, 1 mg by Bradford assay). The relative ease of collecting pollen from conifers, angiosperm trees such as oaks, birches, and hickories, and some grasses, makes those species more likely to be sampled if encountered. Because those species form a prominent part of many floras, they are likely to be encountered by both researchers and pollen-consuming animals. Within many habitats, anemophilous species are likely to contain less pollen protein than zoophilous species. Thus, determining the difference between anemophilous and zoophilous pollens requires a statistical technique to match the scope of the question being asked (i.e., whether anemophilous and zoophilous species within a habitat differ or whether evolutionary shifts in pollination mode result in a predictable shift in protein concentration).

Vibratile- or ''buzz-''pollinated taxa contain pollen particularly rich in protein. Buchmann (1986) made a similar observation and explained it as pollen reward enhancement by plants that depend on pollen-collecting bees for pollination. When vibratile-pollinated species do not provide nectar, pollen functions as the sole reward and must lure pollinators away from species that produce both nectar and pollen. The present data set offers ambiguous support for this hypothesis. Although bees collect pollen from vibratile-pollinated taxa, and vibratile-pollinated taxa contain protein-rich pollen, bees do not show a general trend toward collecting protein-rich pollen. Vibratile-pollinated taxa also have unusually small pollen grains, which is probably an adaptation to facilitate their release from narrow, tubular anthers. Small pollen grains were generally protein-rich in our data set, and the functional significance of protein-rich pollen in vibratile-pollinated taxa could reflect selection to favor small grain size rather than to reward pollinators.

Our finding that pollen grain size relates to stigma–ovule distance affirms previous findings that pollen grain diameter correlates with style length (Lee 1978, Baker and Baker 1982, Plitmann and Levin 1983, Barrett 1988, Ramamoorthy et al. 1992, Kirk 1993). Baker and Baker (1982) interpreted this correlation as a functional relationship between the energy storage capacity of pollen grains and the distance to ovules. Cruden and Lyon (1985) disputed this reasoning based on other data and demonstrations that pollen tubes obtain energy from stylar tissue. They concluded that pollen size was functionally related to stigma depth (the distance pollen tubes had to grow to reach stylar tissue) and that correlations between pollen size and style length represented analyses of closely related taxa in which style length was also correlated with stigma depth. They predicted that surveys including distantly related species would not show a correlation between pollen size and style length because different plant families showed different relationships between stigma depth and style length. They supported their hypothesis with a data set based on 15 distantly related species that showed a significant correlation ($r = 0.74$) between stigma depth and style length but not between pollen size and style length.

We did not measure stigma depth and thus we cannot compare the relative strength of these two correlations in our data set. In contrast to Cruden and Lyon (1985), we found a significant association between style length and pollen volume for distantly related taxa. Our survey included pollen volume and style length estimates for species in 83 genera and 50 plant families, and we found a strong association between pollen volume and style length after statistically removing taxonomic covariance ($r = 0.6$, reported earlier as a regression co-

efficient). It seems unlikely that a significant correlation of such strength across such a wide range of taxa after accounting for taxonomy is entirely spurious. This controversy, however, will not be resolved by finding the strongest correlation coefficient across the widest taxonomic surveys. Pollen volume itself does not explain how far pollen tubes can grow, but it may correlate with the storage capacity of particular nutrients that influence pollen tube growth. Baker and Baker (1979) suggested that pollen volume restricted energy storage and that differences in oil vs. starch as the primary storage compound influenced the amount of energy that could be stored in a pollen grain of a given size. Alternatively, the starch and oil content of pollen may reflect ecophysiological conditions rather than the amount of energy that pollen grains need to store for pollen tube growth. Pacini (1996) and Franchi et al. (1996) suggested that plant species in open habitats have starchless pollen because pollen grains are less susceptible to dehydration following starch hydrolysis.

We found that protein mass per pollen grain predicts style length slightly better than does pollen grain volume. Many pollen enzymes function during pollen tube germination and growth and we speculate that there may be a functional relationship between the amount of enzymes present and the distance or rate of pollen tube growth, especially since protein can account for more than 60% of the mass of a pollen grain. Confirmation of this awaits comparisons of enzyme types, abundances, and functions among plant taxa.

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APPENDIX

The table below reports the entire data set of pollen protein comparisons.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
PTERIDOPHYTA							
Equisetaceae							
Equisetum arvense L.	35.6	M[6]					
Lycopodiaceae							
Lycopodium clavatum L.	8.3	M[6]					
GYMNOSPERMAE							
Pinopsida							
Cupressaceae							
Cupressus arizonica Greene	2.3	M	wind				
C. macrocarpa Harw. ex Gord.	6.6	M	wind				
Juniperus californica Carr.	9	M	wind				
J. communis L.	8.8	M[6]	wind				
J. deppeana Steud.	5.1	B	wind			8.4	
J. monosperma (Engelm.) Sarg.	8.9	M	wind			4.2	
J. osteosperma (Torr.) Little	8.5	M	wind			3.7	
J. scopulorum Sarg.	8.7	M	wind			5.4	
Thuja occidentalis L.	9.8	M	wind				
Pinaceae							
Abies grandis (Dougl. ex D. Don) Lind.	24.1	M	wind				Page (1990*a*)
Cedrus deodara (Roxb. ex D. Don) G. Don	13.3	M	wind				Page (1990*a*)
Picea abies (L.) Karst.	20.9	M[6]	wind				Page (1990*a*)
Pinus contorta Dougl. ex Loud.	13	M[6,12]	wind				Page (1990*a*)
P. coulteri D. Don	9.25	M	wind				
P. halepensis Bieb.	14.7	M	wind				
P. edulis Engelm.	16.3	M	wind				Page (1990*a*)
P. mugo Turra	13.7	M[6]	wind				Page (1990*a*)
P. ponderosa P. & C. Lawson	11.7	M	wind			21.2	
P. radiata D. Don	13.5	M[12]	wind				Page (1990*a*)
P. sabiniana Dougl. ex Dougl.	11.4	M[12]	wind				Page (1990*a*)
P. sylvestris L.	15.7	M[6,7]	wind				Page (1990*a*)
P. taeda L.	15.9	B	wind			87.3	Page (1990*a*)
Taxodiaceae							
Sequoia sempervirens (Lamb. ex D. Don) Endl.	7.9	M	wind				Page (1990*b*)
Cycadopsida							
Zamiaceae							
Ceratozamia mexicana Brongn.	44.3	B				11.0	
Dioon califanoi P. de Luca & S. Sabato	31	B				7.4	
Encephalartos gratus Prain	44.9	B	ins?			4.6	
Gnetopsida							
Ephedraceae							
Ephedra trifurca Torr. ex S. Wats.	34.5	B	wind	+		9.1	Buchmann et al. (1989)
Welwitchiaceae							
Welwitschia mirabilis Hook.	53.6	C	ins				Kubitzki (1990)
ANGIOSPERMAE (order in parentheses)							
Dicotyledonae							
Acanthaceae (Scrophulariales)							
Aphelandra sinclairiana Nees in Benth.	57.3	B	hum		56.9	32.5	McDade (1992)
Justicia graciliflora (Standl.) D. Gibs.	36.1	B	hum		50.3	56.0	
J. secunda Sieber ex Steud.	36.2	B	hum		41.1	24.0	Linhart and Feinsinger (1980)
Aceraceae (Sapindales)							
Acer macrophyllum Pursh	46.2	M				21.0	
A. rubrum L.	39.4	B	bee/wind	+	3.6	14.7	Batra (1985)

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
Actinidiaceae (Ericales)							
Actinidia deliciosa (male flowers)	42.2		bee	+			Clark and Lintas (1992)
Aizoaceae (Caryophyllales)							
Faucaria longifolia L. Bolus	43.7	B				5.4	
Mesembryanthemum dolabriforme Linn.	30.5	B				2.6	
Delosperma nelii L. Bolus	32.1	B				2.8	
Vanheerdia divergens	36.4	B				4.9	
Amaranthaceae (Caryophyllales)							
Amaranthus hybridus L.	23.4	M				7.5	
A. palmeri S. Wats.	23.2	M	wind				Cane et al. (1992)
A. tuberculatus (Moq.) Sauer	27.4	M				5.0	
Anacardiaceae (Sapindales)							
Malosma laurina (Nutt.) Nutt. ex Abrams	12.7	B				5.4	
Pistacia vera Mill.	33.4	M	wind	+‖		10.9	Crane and Walker (1984), Niklas and Buchmann (1988)
Schinus molle L.	39.4	M		+‖		4.7	Eisikowitch and Masad (1982)
Spondias mombin L.	30.2	B	bee	+	0.8	21.5	Roubik (1995)
Apiaceae (Apiales)							
Anthriscus sylvestris (L.) Berhh.	29	M[6]	bee/fly	+			Müller (1883)
Apocynaceae (Gentianales)							
Allamanda cathartica L.	24.2	B			40.3	581.7	
Stemmadenia grandiflora (Jacq.) Miers	41.1	B	bee		19.6	26.2	Frankie et al. (1983)
Thevetia ahouai (L.) A. DC.	28.6	B	bee		33.2	500.1	Frankie et al. (1983)
Asclepiadaceae (Gentianales)							
Asclepias curassivica L.	16.4	B	but		3.2	94.4	Croat (1978)
Asteraceae (Asterales)							
Ambrosia ambrosoides (Cav.) Payne	22.9	B				8.4	
A. artemesiifolia L.	25.8	B	wind		0.8	3.1	Lundholm and Aarssen (1994)
A. chamissonis (Less.) E. Greene	26.7	M					
A. deltoidea (Torr.) Payne	23.0	M				6.0	
A. dumosa (Gray) Payne	22.5	M	wind			5.6	Colin and Jones (1980)
A. psilostachya DC.	23.2	M	wind				Bassett and Crompton (1975)
A. tenuifolia Spreng.	23.8	M					
A. trifida L.	30	M	wind	+‖			Robertson (1929), Colin and Jones (1980)
Anthemis arvensis L.	17.5	M[6]		+			Müller (1883)
A. cotula L.	27.7	M	wind	+			Robertson (1929), Colin and Jones (1980)
Artemisia californica Less.	23.4	M	wind				Moldenke (1976)
A. campestris L.	17.3	M[6]					
A. heterophylla Muhl. ex Willd.	23.2	M					
A. vulgaris L.	19.5	M[6]					
Centaurea cyanus L.	26.2	M[6]	bee	+			Müller (1883), Svensson and Wigren (1985)
C. solstitialis L.	25.3	M[12]	bee	+‖			Gary (1975), Harrod and Taylor (1995)
Chrysanthemum segetum L.	18.2	M[6]					
Chrysothamnus nauseosus (Pallas ex Pursh) Britt.	30.8	M	bee	+			Moldenke (1976)
Cirsium neomexicanum Gray	28.3	B	bee	+		27.2	Harder (1983)§
Dicoria canescens Gray	22.8	M					
Gutierrizia microcephala (DC.) Gray	22.8	M				5.0	
Helianthus annuus L.	30.6	B, M	bee	+	9.4	14.1	Hurd et al. (1980)

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
Hymenoclea monogrya Torr. & Gray ex Gray	24.2	M				6.0	
H. salsola Torr. & Gray ex Gray	26.3	M	wind				Colin and Jones (1980)
Iva annua L. var. *annua*	25.3	M				5.2	
I. axillaris Persh	28.9	M	wind				Colin and Jones (1980)
Leucanthemum vulgare Lam.	28	M	bee	+			Ginsberg (1984)
Matricaria perforata Mérat	15	M[6]					
Silybum marianum (L.) Gaertn.	34.3	M[12]					
Tanacetum vulgare L.	11.7	M[6]	bee?	+			Müller (1883)
Taraxacum officinale vulgare (Lam.) Schinz & R. Keller	19.2	M[6,12]			7.3		
Wulffia baccata (L.f.) O. Kuntze	25.8	B			4.3	8.7	
Xanthium spinosum L.	34.3	M		+‖		6.0	du Toit (1988)
Betulaceae (Fagales)							
Alnus glutinosa (L.) Gaertn.	24.2	M[6]	wind				Proctor et al. (1996)
A. incana (L.) Moench	23.5	M[6]					
A. rubra Bong.	22.1	M	wind				Tsukada (1982)
A. sp.	30.2	C	wind			3.9	
A. viridis (Vill.) Lam. & DC.	29.4	M[7]	wind		0.8		
Betula lenta L.	28.3	M[7]	wind			3.2	
B. pendula Roth	28.8	M[6]	wind				
Corylus avellana L.	30.2	M[7]	wind	+‖		6.7[14]	Müller (1883), Proctor et al. (1996)
C. cornuta californica (A. DC.) Sharp	27.7	M					
Ostrya virginiana (P. Mill.) K. Koch	26.8	B	wind		3.7	9.7	
Bignoniaceae (Scrophulariales)							
Anemopaegna sp.	40.5	B					
Campsis radicans (L.) Seem. ex Bureau	36.9	B	hum	+	53.4	10.6	Bertin (1982)
Catalpa speciosa (Warder) Warder ex Engelm.	37.8	B	bee/moth		22.9	0.9	Stephenson and Thomas (1977)
Chilopsis linearis (Cav.) Sweet	36.6	B	bee		21.7	22.4	Brown et al. (1981)
Clystostoma binatum (Thumb.) Sandw.	43.9	B			35.1	65.4	
Tabebuia guayacan (Seem.) Hemsl.	43.9	B	bee		31.8	4.3	
T. rosea (Bertol.) DC.	40.1	B	bee			24.6	Frankie et al. (1983)
Bixaceae (Malvales)							
Amorexia palmatifida Moc. & Sessé ex DC.	51.7	C	bee	+			Buchmann (1983)
Cochlospermum vitifolium (Willd.) Willd. ex Spreng.	53.8	C	bee	+	25.6	2.1	Snow and Roubik (1987)
Bombacaceae (Malvales)							
Bombacopsis quinata (Jacq.) Dug.	50.3	B	bat/bird/bee		95.2	4.4	Roubik (1995)
Ceiba sp.	30.2	B	bat?			26.4	
Chorisia speciosa St. Hil.	33.2	C				29.3	
Ochroma pyramidale (Cav. ex Lam.) Urban	41.7	C	bat			168.2	Jaeger (1974)
Pachira aquatica Aubl.	54.2	B	bat/moth		246.8	58.0	Roubik (1995)
Pseudobombax septanatum (Jacq.) Dug.	48.2	C	bat		82.6	24.8	Eguiarte and del Rio (1987)§
Brassicaceae (Capparales)							
Brassica napus L.	31.9	M[12]	bee	+‖			Rayner and Langridge (1985)
Brassica nigra (L.) W.D.J. Koch	33.6	M[12]	bee/fly	+	3.3	2.1	Conner and Neumeier (1995)
Brassica rapa L. var. *rapa*	44.1	M, M[12]	bee		5.8	5.9[8]	Singh and Singh (1992)
Sinapis arvensis L.	33.8	M[12]	bee/fly/but	+	7		Müller (1883), Kunin (1993)

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
Buxaceae (Buxales)							
Buxus sempervirens L.	29.5	M[7]			2.6		Free (1993)
Cactaceae (Caryophyllales)							
Carnegiea gigantea (Engelm.) Britt. & Rose	37.8	B	bee/bat	+	85	95.8	Schmidt and Buchmann (1986)
Cereus sp.	31.3	B					
Echinocereus engelmanii (Parry ex Engelm.) Lem.	33.7	B	bee	+	44.3	130.9	
Opuntia acanthocarpa Engelm. & Bigelow	24.9	B	bee	+	32.5	427.8	
O. arbuscula Engelm.	28.8	B	bee	+	22.2	414.2	
O. echios Howell	17.3	M[5]	bee	+			
O. ficus-indica (L.) P. Mill.	25.5	B	bee	+		614.5	
O. phaecantha Engelm.	22.2	B	bee	+	31.3	706.1	Osborn et al. (1988)
O. santa-rita (Griffiths & Hare) Rose	28.7	B	bee	+	39.3	434.7	
O. versicolor Engelm. ex Coult.	28	B	bee	+	27.1		
Pachycereus pringlei (Engelm.) Britt. & Rose	36.8	B	bat			134.0	Fleming et al. (1994)
Campanulaceae (Asterales)							
Centropogon coccineus Regel	51	B	hum		41.3	12.9	Stein (1992)§
C. panamensis Wilbur	53.4	B	hum			15.2	Stein (1992)§
Hippobroma longiflora (L.) G. Don	51	B	sph		102.9		Feinsinger and Swarm (1978)
Lobelia siphilitica L.	47.9	C	bee	+			Robertson (1929), Johnston (1991)
L. cardinalis propinqua (Paxton) Bowden	55	M[7]	hum			25.3	Müller (1883), Johnston (1991)
Cannabaceae (Urticales)							
Cannabis sativa L.	31.8	M, M[7]	wind		8.9	7.1	Colin and Jones (1980)
Caprifoliaceae (Dipsacales)							
Sambucus caerulea Raf. var. *caerulea*	46.3	M				1.9	
S. nigra L.	37.5	M[6]	ins	+‖			Ortiz-de-Boada and Cogua (1989), Proctor et al. (1996)
Chenopodiaceae (Caryophyllales)							
Allenrolfea occidentalis (S. Wats.) Kuntze	24.9	M				5.4	
Atriplex canescens (Pursh) Nutt.	20.1	M	wind			6.8	Blackwell and Powell (1981)
A. confertifolia (Torr. & Frém) S. Wats.	29.8	M	wind				Colin and Jones (1980)
A. lentiformis (Torr.) S. Wats.	25.3	M					
A. patula L.	17.1	M[6]	self?				Proctor et al. (1996)
Beta vulgaris L.	24.2	M[6]	bee/thrips/wind				Roubik (1995), Proctor et al. (1996)
Chenopodium album L.	28	M	wind			10.9	Müller (1883)
C. fremontii S. Wats.	22.5	M					
Kochia scoparia (L.) Shrad.	19.3	M	bee				Blackwell and Powell (1981)
Salsola kali L.	31.3	M	bee/wasp				Blackwell and Powell (1981)
Sarcocornia perennis (P. Mill.) A.J. Scott	28.3	M					
Sarcobatus vermiculatus (Hook.) Torr.	30.8	M	wind				Blackwell and Powell (1981)
Suaeda sp.	23	M	ins				Blackwell and Powell (1981)
Clusiaceae (Guttiferales)							
Hypericum perforatum L.	30.3	M[12]	bee	+	4.5	3.4[9]	Macior (1993)
Convolvulaceae (Solanales)							
Bonamia sp.	34.1	B				28.5	
Ipomoea squamosa Choisy in DC.	26.8	B	bee	+	26.1	130.9	

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
I. tiliacea (Willd.) Choisy	30.1	B	bee	+	41.3	253.2	
Merremia umbellata (L.) Hallier f.	38.1	B			20.3	166.0	
Crossosomataceae (Rosales)							
Crossosoma sp.	36.8	B				1.9	
Cucurbitaceae (Violales)							
Cucurbita foetidissima Kunth	39.1	B	bee	+	49.3	614.5	Ordway et al. (1987)
Cucurbita pepo L.	38.2	C	bee	+		775.3	Hurd et al. (1971)
Ericaceae (Ericales)							
Chimaphila umbellata (L.) W. Bart.	29.4	C	bee	+			Knudsen and Olesen (1993)
Vaccinium ashei Reade	43	B	bee	+		9.0	Cane and Payne (1988)
Euphorbiaceae (Euphorbiales)							
Ricinus communis L.	42.5	M[7]	wind	+‖	7.3	15.2	
Fabaceae (Fabales)							
Caesalpinia sp.	34.2	B	but			302.5	Cruden and Hermann-Parker (1979)§
Cercis canadensis L.	40	B	bee	+	7.2	4.4	Robertson (1929)
Crotalaria retusa L.	52.7	B	bee	+	18.3	8.2	Free (1993)§
C. sagittalis L.	51	B	bee		8	8.2	Robertson (1929)
Erythrina fusca Lour.	47.1	B	bird		35.6	22.4	Feinsinger and Swarm (1978)
E. gibbosa Cufod.	41.7	B	hum		48.7	20.6	
Lonchocarpus oliganthus F.S. Herm.	48.1	B	bee	+	8.4		
Olneya tesota Gray	44.4	B	bee	+	10.8	8.2	
Parkinsonia aculeata L.	33.4	B	bee	+	9.1	9.0	
P. microphylla Torr.	46.2	B	bee	+	7.2	5.3	Jones (1977)
Prosopis velutina Woot.	39	B	bee	+	3.9	14.0	Keys et al. (1995)
Pueraria montana lobata (Willd.) Maesen & Almeida	48.8	B	bee	+	14.56	8.0	Mangum and Brooks (1997)
Senna covesii (Gray) Irwin & Barnaby	42.8	C	bee	+			
S. fruticosa (Miller) Irwin & Barnaby	49.4	B	bee	+	13.3	23.4	Gottsberger and Silberbauer-Gottsberger (1988)§
S. obtusifolia (L.) Irwin & Barnaby	45.8	B	bee	+	14.96	17.2	
S. occidentalis (L.) Link	33.5	B	bee	+	11.9	21.9	
S. reticulata (Willd.) Irwin & Barnaby	51.6	B	bee	+	22.3	10.2	Snow and Roubik (1987)
Swainsona formosa (G. Don) J. Thompson	57.4	B				2.4	
Trifolium hybridum L.	13.7	M[6]	bee	+			Horne (1995)
Trifolium pratense L.	32.2	M[6]	bee	+			Schmid-Hempel and Stauffer (1998)
Trifolium repens L.	35.4	M[12]	bee	+	6.1	4.3	Robertson (1929)
Trifolium sp.	31.1	M[12]	bee	+			
Vicia grandiflora Scop.	42.8	B	bee	+	18	9.1	
Fagaceae (Fagales)							
Fagus sylvatica L.	17.4	M[6]	wind	+			Chambers (1945)
Quercus alba L.	38.6	B	wind	+		16.8	Colin and Jones (1980)
Q. arizonica Sarg.	32.5	M	wind				
Q. kelloggii Newberry	37.1	M, M[12]	wind	+			McCarthy and Quinn (1990)§
Q. michauxii Nutt.	38.5	C	wind	+		11.6	
Q. nigra L.	41.5	C	wind	+	2.1	5.9	
Q. robur L.	30.6	M[6,7]	wind	+		5.6[3]	
Q. rubra L.	40.6	C	wind	+	2.63	10.8	
Q. virginiana P. Mill.	35.4	M	wind	+			
Q. wislezeni A. DC.	37.7	M	wind				Colin and Jones (1980)
Flacourtiaceae (Violales)							
Zuelania guidonia (Sw.) Britt. & Millsp.	36	B			3.9	6.9	

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
Fouquieriaceae (Violales)							
Fouquieria splendens Engelm.	46.9	B	bee/hum	+	24.1	21.7	Waser (1979)
Garryaceae (Cornales)							
Garrya elliptica Dougl. ex Lindl.	28.6	M	wind			18.8	Moldenke (1976)
Gelsemiaceae (Rubiales)							
Gelsemium sempervirens St.-Hil.	42.3	B	bee		20.2	20.4	Ornduff (1979)
Hamamelidaceae (Hamamelidales)							
Liquidambar styraciflua L.	28.4	B	wind		7.1	24.6	Schmitt and Perry (1964)
Hippocastanaceae (Sapindales)							
Aesculus hippocastanum L.	26.7	M[6]	bee	+			Müller (1883)
A. pavia L.	49.2	B	hum	+	27	6.3	Wyatt and Lodwick (1981)
Hydrophyllaceae (Solanales)							
Phacelia campanularia Gray	59	B	bee	+	35	5.3	Tepedino and Torchio (1982)§
Juglandaceae (Juglandales)							
Carya illinoensis (Wangenh.) K. Koch	20	C	wind		3.1	57.9	McCarthy and Quinn (1990)
Juglans californica S. Wats.	27.1	M	wind			25.4	Colin and Jones (1980)
J. major (Torr.) Heller	27.6	M	wind				
J. nigra L.	23.6	B, M[12]	wind		9.8	18.8[3]	Rink et al. (1989)
J. regia L.	25.1	B				36.4	
Lamiaceae (Lamiales)							
Salvia sp.	22.8	M				6.2	
Loasaceae (Violales)							
Mentzelia pumila Nutt. ex Torr. & Gray	39.7	B	bee	+	26.5	4.5	Griswold and Parker (1988)
Magnoliaceae (Magnoliales)							
Liriodendron tulipifera L.	37.1	B		+		55.6	
Magnolia grandiflora L.	36.5	B	beetle			76.8	
Magnolia sp.	38.2	B	beetle			85.0	Thien (1974)
Malpighiaceae (Polygalales)							
Stigmaphyllon ellipticum (H.P.K.) Adr. Juss.	42.1	B	bee	+	4.6	29.9	Frankie et al. (1983)
Malvaceae (Malvales)							
Gossypium thurberi Todaro	21.1	B	bee	+		195.3	Buchmann and Shipman (1990)
Hibiscus laevis All.	23.7	B	bee	+	47.3	915.7	Robertson (1929)
Hibiscus rosa-sinensis L.	17.5	B	hum		110.6	849.0	
Malvaviscus drummondii Torr. & Gray	25.2	B	hum	+	59.5	715.7	Webb (1984)
Pavonia paniculata Cav.	20.3	B			9	706.1	
Sidalcea oregana ssp. *spicata* (Regel) C. Hitch.	14.4	M[1]	bee	+			Ashman and Stanton (1991)
Sphaeralcea ambigua Gray	29.4	B	bee	+	7.9	41.6	
Melastomataceae (Myrtales)							
Bellucia imperialis Sald. & Cogn ex Cogn	56.6	C	bee	+			Renner (1986)§
Miconia argentea (Sw.) DC.	52	B	bee	+	4.6	0.9	Mori and Pipoli (1984)§
Mouriri nervosa Pilg.	46.4	C					Buchmann (1986)
Rhexia mariana L.	60	B	bee	+		4.4	
Tococa sp.	37.6	C	bee	+			Laroca (1970)
Moraaee (Urticales)							
Broussonetia papyrifera (L.) L'Hér ex Vent.	19.6	M	wind			1.2	Bucholtz et al. (1991)
Morus rubra L.	32.8	B	wind		3.5	2.4	O'Neal and Waller (1984)§
Myricaceae (Juglandales)							
Myrica cerifera L.	17.8	B	wind		2.1	9.2	
M. gale L.	21.2	M[6]					
Myrtaceae (Myrtales)							
Eucalyptus globulus Labill.	37.8	M[12]	bird/bee	+‖	21.1		Roubik (1995)

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
Nymphaceae (Nymphaeles)							
Nuphar lutea (L.) Sm.	41.1	B	bee/syrph		10.2	44.1	Ervik et al. (1995)
Nymphaea sp.	55.8	B				12.1	Robertson (1929)§
Oleaceae (Scrophulariales)							
Fraxinus excelsior L.	33.3	M[6]	wind				Robertson (1929), Proctor et al. (1996)§
Olea europea L.	27.4	M[12]	wind	+‖	2.3	5.6[14]	Free (1993), Molina et al. (1996)
Syringa vulgaris L.	17.2	M[6]	ins				Müller (1883)
Onagraceae (Myrtales)							
Camissonia cardiophylla (Torr.) Raven	26.8	B				130.8	
Oenothera deltoides Torr. & Frém.	21	B	sph	+	53.3	1945.0	Linsley et al. (1973)
O. speciosa Nutt.	26	B	bee	+	41.7	138.7	Wolin et al. (1984)
Papaveraceae (Ranunculales)							
Argemone corymbosa Greene	45.3	B	bee	+	8.4	14.9	Schneider et al. (1987)§
Eschscholzia californica Cham.	43.1	M	bee	+		14.5	Bohart and Griswold (1987)
Passifloraceae (Violales)							
Passiflora sp.	30.1	B	bee			89.5	
P. vitifolia Kunth	34.6	B	hum	+	18.9	61.6	Snow (1982)
Plantaginaceae (Plantaginales)							
Plantago lanceolata L.	23.9	B, M, M[7]	bee/wind	+	4	6.8	Sharma et al. (1993)
Platanaceae (Hamamelidales)							
Platanus racemosa Nutt.	37.8	M	wind			2.6	Proctor et al. (1996)
Polygonaceae (Polygonales)							
Rumex acetosa L.	16.8	M[6]	wind?				Proctor et al. (1996)
R. acetosella L.	17.9	M	wind?				Proctor et al. (1996)
R. conglomeratus Murr.	25	M	wind?				Proctor et al. (1996)
R. crispus L.	20	B	wind			9.7	
R. hymenosepalus Torr.	25.5	M	wind				Colin and Jones (1980)
Portulaceae (Caryophyllales)							
Calandrinia ciliata (Ruiz & Pavón) DC.	27.1	M[12]					
Primulaceae (Primulales)							
Dodecatheon clevelandii Greene	61.7	M	bee	+			Buchmann (1983)
D. pulchella (Raf.) Merr.	47.5	B	bee			0.7	
Proteaceae (Proteales)							
Banksia integrifolia Schlecht.	39	M[13]	mar/bats				Turner (1984)
B. marginata Cav.	37	M[13]	mar				Turner (1984)
B. serrata Cav.	36	M[13]	mar/bird				Turner (1984)
B. spinulosa Sm.	42	M[13]	mar/bird/ins				Turner (1984)
Rhamnaceae (Rhamnales)							
Ceanothus crassifolius Torr.	43.7	M[12]	ins		1.7		Dobson (1993)[cong]
C. integerrimus Hook. & Arn.	37.1	M[12]	ins	+	1.1		Dobson (1993)[cong]
Rosaceae (Rosales)							
Adenostoma fasciculatum Hook. & Arn.	33.3	M	bee/beetle	+		3.0	Moldenke (1976)
Chamaebatia foliolosa Benth.	41.3	M[12]		+	5		Moldenke (1976)§
Prunus communis Huds.	43.6	M[12]	bee/fly	+			Müller (1883)
P. padus L.	28.5	M[6]	bee/fly				Müller (1883)
P. persica (L.) Batsch.	38	M[12]	bee	+‖	15.86	49.3	Free (1993)
Rosa woodsii Lindl.	44.5	M	bee			13.7	Robertson (1929), Kevan et al. (1990)§
Sorbus aucuparia L.	34.8	M[6]	fly?				Proctor et al. (1996)
Rubiaceae (Rubiales)							
Genipa americana L.	40.8	B	bee		27.1	9.2	Frankie et al. (1983)
Pentagonia macrophylla Benth.	45.8	B	hum			19.7	McDade (1986)
Salicaceae (Violales)							
Populus deltoides Bartr. ex Marsh.	39.5	B	wind	+‖	3.1	14.8	Robertson (1929), Proctor et al. (1996)
P. fremontii S. Wats.	43.1	M	wind				Colin and Jones (1980)

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
P. nigra L.	36.5	M[11]					
P. tremula L.	31.9	M[6]	wind				Hesse (1979)
Salix alba L.	43	M[7]		+	2.6		
S. caprea L.	36.8	M[6]	bee/wind	+			Müller (1883), Tollsten and Knudsen (1992)
S. lasiolepis Benth.	46.4	M				2.3	
S. nigra Marsh.	39.3	B, M[12]		+	2.6	2.7	Robertson (1929)
S. repens L.	38.7	M[6]	wind/bee	+			Müller (1883), Tollsten and Knudsen (1992)
Simaroubaceae (Sapindales)							
Quassia amara L.	36.8	B	hum		51.6	27.6	Roubik et al. (1985)
Simmondsiaceae (Buxales)							
Simmondisa chinensis (Link) Schneid.	35	B	wind	+	12.1	12.5	Niklas and Buchmann (1985)
Solanaceae (Solanales)							
Brugmansia candida Pers.	38.9	C			182.3	41.6	
Datura discolor Bernh.	45.9	M[4]			117.6	45.9	
Datura innoxia quiqucuspida	51.6	M[4]	sph		156.6	36.4	Kugler (1971)
Datura stramonium L.	45.2	B				54.3	
Datura wrightii Regel	52.7	B	sph	+	160.9	40.2	Linsley and Cazier (1970), Grant and Grant (1983)
Nicotiana glauca Graham	51.9	M[4]	hum		32	6.8	Galetto and Bernadello (1993)
Petunia axillaris (Lam.) B.S.P.	41.1	M[4]			41.5	12.6	
Solandra maxima (Seese & Moc.) P.S. Green	52.9	B	bat?			6.4	
Solanum appendiculatum Humb. & Bonpl. ex Dun.	46.2	M[4]	bee	+	5.5	7.5[2]	
S. atropurpureum Schrank	40.8	M[4]	bee	+			
S. aviculare G. Forst.	40.1	M[4]	bee	+			
S. basendopogon Bitter	40.4	M[4]	bee	+		3.6[2]	
S. carpiense Humb. & Bonpl. ex Dunal	50.8	M[4]	bee	+	6.8	2.8[2]	
S. citrullifolium A. Braun	52	M[4]	bee	+	16.4		
S. douglassii Dunal	53.4	M[4]	bee	+	7		Buchmann et al. (1977)
S. dulcamara L.	51.4	M[4]	bee	+	7.6	0.9[9]	Proctor et al. (1996)
S. eleagnifolium Cav.	39.2	M[4]	bee	+	12.7	10.3	Buchmann and Cane (1989)
S. gracilis Herter	49	M[4]	bee	+			
S. hayesii Fern.	50.9	B	bee	+	8.1		
S. lanceifolium Jacq.	46.7	B	bee	+	11.5	3.9	
S. lycopersicum L.	54.9	M[4]	bee	+	9.3	5.2	Buchmann (1986)
S. melongena L.	45.7	M[4]	bee	+			Torregrossa (1983)
S. muricatum Ait.	39.9	M[4]	bee	+			
S. pyracanthum Jacq.	50.8	M[4]	bee	+			
S. sisymbriifolium Lam.	46.6	M[4]	bee	+	11.1		
S. tabanoense Correll	34.1	M[4]	bee	+		2.6[2]	
S. xanti Gray	53	M[4]	bee	+	8.2		Buchmann et al. (1977)
Styracaceae (Theales)							
Halesia carolina L.	38.8	B			16.2	22.6	
Tiliaceae (Malvales)							
Luehea seemanii Tr. & Planch.	42.5	B	bee		8.7	7.5	Haber and Frankie (1982)
Ulmaceae (Urticales)							
Ulmus americana L.	28.9	M	wind				Colin and Jones (1980)
U. glabra Huds.	26.4	M[6]	wind	+‖			Daumann (1975)
Urticaceae (Urticales)							
Urtica dioica L.	17.5	M[6]	wind				Proctor et al. (1996)
Viscaceae (Santalales)							
Phoradendron californicum Nutt.	32.3	B	bee/ins			6.8	
Zygophyllaceae (Sapindales)							
Larrea tridentata (Sessé & Moc. ex DC.) Coville	45.4	B	bee	+	6.5	4.4	Simpson et al. (1977)

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
Monocotyledonae							
Agavaceae (Asparagales)							
Agave americana L.	31.8	C	bat			119.1	
A. chrysantha Peebles	40.9	C	bat			55.9	Freeman et al. (1983)
A. deserti Engelm.	45.8	C	bat			52.4	Freeman et al. (1983)
A. lechuguilla Torr.	45.1	C				72.9	Freeman and Reid (1985)
A. mckelveyana Gentry	43.9	C	bee			51.3	Sutherland (1987)
A. palmeri Engelm.	39.8	C	bat			74.6	Freeman et al. (1983)
A. parryi Engelm.	44.1	C	bat				
A. parryi huachucensis (Baker) Little ex L. Benson	44.8	C	bat			131.1	Freeman et al. (1983)
A. schottii Engelm.	42.9	C	bee		47.8	41.0	Schaffer and Schaffer (1977)
A. stricta Salm. Dyck	43.9	C				45.1	
Hesperocallis undulata Gray	41.5	B	sph			125.4	
Amaryllidaceae (Asparagales)							
Crinum erubescens Ait.	29.1	B	sph		309.2	108.1	Manasse and Stanton (1991)
Narcissus poeticus L.	44.4	M[7]	bee	+			Mahindre (1978)
Araceae (Arales)							
Arum sp.	12.5	B				13.4	
Arecaceae (Arecales)							
Cocos plumosa Lodd ex Loud	34.9	B				8.7	
Oenocarpus panamanus Bailey	23.8	C				20.6	
Phoenix dactylifera L.	35.5	M[12]	wind/ins	+‖		2.1	Free (1993), Proctor et al. (1996)
Asparagaceae (Asparagales)							
Asparagus officinalis L.	37	M[12]	bee	+	2.6	4.6	Robertson (1929), Free (1993)
Asphodelaceae (Asparagales)							
Aloe ferox Mill.	46.7	C	bird/bee	+‖		7.9	Hoffman (1988)
Bromeliaceae (Bromeliales)							
Pitcairnia sp.	48	B				21.1	
Cyperaceae (Cyperales)							
Carex acuta Linn.	21.9	M[7]	wind				Handel (1976)§
Eriophorum vaginatum L.	19.9	M[6]	wind				Moldenke (1976)
Scirpus microcarpus J. & K. Presl	21.6	M	wind				Colin and Jones (1980)
Dracaenaceae (Asparagales)							
Nolina sp.	38.7	B					
Haemodoraceae (Liliales)							
Anigozanthus manglesii D. Don.	42.1	C				19.2	
Juncaginaceae (Alismatales)							
Triglochin maritimum L.	22.2	B				8.0	
Liliaceae (Liliales)							
Lilium sp.	17.1	B				194.4	
Musaceae (Zingiberales)							
Heliconia sp.	13.7	B	hum			225.2	Feinsinger (1983)§
Strelitzia reginae Aitm.	23.1	C	bird			368.9	Skead (1975)
Poaceae (Cyperales)							
Agrostis capillaris L.	22.8	M, M[6]					
Avena barbata Pott ex Link	28.6	M	wind				Colin and Jones (1980)
Bromus carinatus Hook & Arn.	33.1	M					
B. inermis Leyss.	25.9	M	wind				Kevan and Tikhmenev (1996)
Calamagrostis arenaria L.	22	M[6]					
Cynodon dactylon (L.) Pers.	23.8	M, M[12]	wind	+‖	1.1	14.1	Erickson and Atmowidjojo (1997)
Dactylis glomerata L.	25.6	M, M[6]	wind				Colin and Jones (1980)
Festuca pratensis Huds.	24.6	M[6]	wind				Kevan and Tikhmenev (1996)

APPENDIX. Continued.

Species	Protein (%)	Analysis technique	Pollinator	Bees coll?†	Style length (mm)	Pollen volume‡	Reference
F. rubra L.	21.9	M[6]	wind				Kevan and Tikhmenev (1996)
Helictotrichon pubescens (Huds.) Pilger	25.9	M[6]					
Holcus lanatus L.	22.2	M, M[6]					
Leymus arenarius (L.) Hochst.	26.7	M[6]					
Lolium perenne L.	25.7	M, M[6]	wind				Proctor et al. (1996)
Pascopyrum smithii (Rydb.) A. Löve	32.4	M					
Paspalum notatum Fluegge	28.2	B	bee/wind	+	1.7	15.4	Adams et al. (1981)§
Phalaris arundinacea L.	19.8	M[6]					
P. minor Retz.	27.5	M	wind				Colin and Jones (1980)
Phleum pratense L.	27.5	M[6]	agametic				Proctor et al. (1996)
Poa annua L.	26.8	M	wind			11.8	Colin and Jones (1980)
P. nemoralis L.	20.7	M[6]					
P. pratensis L.	20.9	M[6]					
P. trivialis L.	20.7	M[6]					
Secale cereale L.	24.6	M[6]	wind	+			Müller (1883)
Sorghum halepense (L.) Pers.	29.9	M					
Trisetum flavescens (L.) Beauv.	19.7	M[6]					
Triticum aestivum L.	23.1	M[6]					
Zea mays L.	23.9	B, M, M[6,7,12]	wind/bee	+	95.8	293.9	Vaissiere and Vinson (1994)
Typhaceae (Typhales)							
Typha angustifolia L.	22	M[6]					
T. latifolia L.	19.2	C, M, M[6,10,12]	wind		3.2	6.9	Proctor et al. (1996)
Zingiberaceae (Zingiberales)							
Costus formosus	19.3	C				448.7	
C. laevis R. & P.	27.2	B	bee		66.6	455.8	Schemske (1981)
C. nutans K. Schum.	24	C				243.6	
C. pulverolentus Presl	26.8	B	hum			427.8	Sytsma and Pippen (1985)
Dimerocostus strobilaceus O. Kuntz	21.3	B	bee		87.8	463.0	D. Schemske, *personal communication*
Hedychium coronarium Koenig	47.5	B	moth		106.3		Knudsen et al. (1993)

Notes: Analysis technique is either Bradford Assay (B), Micro-Kjeldahl (M), or Combustion (C). Superscript numbers refer to the following sources from which protein values were taken from the literature: [1] Ashman and Baker (1992), [2] Anderson and Gensel (1976), [3] Bassett, J. I. et al. (1978), [4] Buchmann (1986), [5] Grant (1996), [6] Knight et al. (1972), [7] Lidforss (1899), [8] Lewis et al. (1983), [9] Punt and Clarke (1980), [10] Schmidt et al. (1989), [11] Standifer (1967), [12] Todd and Bretherick (1942), [13] Turner (1984), and [14] Wodehouse (1959). Abbreviations for pollinators are: hum = hummingbird, ins = insect, but = butterfly, sph = Sphingidae, syrph = Syrphidae, mar = marsupials. Synonyms under which protein values for several species were previously published: *Agropyron smithii = Pascopyrum smithii*; *Brassica kaber = Sinapis arvensis*; *Brassica campestris = B. rapa rapa*; *Datura meteloides = D. wrightii*; *Elymus arenarius = Leymus arenarius*; *Lobelia fulgens = L. cardinalis*; *Lycopersicon esculentum = Solanum lycopersicum*; *Petunia hybrida = P. axillaris*; *Solanum laciniatum = S. aviculare*; *S. sublobatum = S. gracilis*; *Sambucus glauca = S. caerulea caerulea*; *Triticum sativum = T. aestivum*; *Tripleurospermum maritimum inodorum = Matricaria perforata*; *Taraxacum vulgare = T. officinale vulgare.*

† This column reports whether bees were collected (indicated by ''+'' symbols).

‡ Pollen volume is reported in millionths of cubic centimeters (i.e., volume in cm^3 has been multiplied by 10^6).

§ Reference refers to a similar, congeneric species.

‖ Pollen collection noted for honey bees only.