Reproductive biology and plant systematics: the growth of a symbiotic association*

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Systematics and reproductive biology have been closely intertwined through botanical history because both rely on reproductive characters. We consider interconnections between systematics and reproductive biology from notable papers and reviews. In addition, a review of over 6,000 journals and millions of articles using the ISI Web of Science® demonstrates a steady growth in publication of papers on reproductive biology from 1975 to 2001. Furthermore, the rate of publications that link systematics with reproductive biology shows a steep increase from 1991 to the present. This increase is evident even when the overall increased rate of publica-tion is considered. We identify several current research themes, including the increasing use of phylogenetic data for interpreting the evolution of reproductive systems. Though studies of reproductive biology and of syste-matics have the potential for "reciprocal illumination", few have used reproductive biological data for under-standing the functional significance of morphology. Other fundamental areas where the combination of repro-ductive biology and systematics has proven valuable include studies of the nature of species, adaptation, spe-ciation and hybridization. These elements of reproductive biology, especially in the context of systematic stu-dies, will benefit from more comprehensive analyses within genera, and of taxa within communities through time and space.

KEYWORDS: breeding system, cladistics, evolution, phylogeny, pollination, reproductive biology, systema-tics.

INTRODUCTION

Systematics is devoted to the study of the diversity of life. At its center is taxonomy, a venerable field devot-ed to the formal description and classification of living things. As a consequence of Darwin's explanation for the origins of diversity, systematics broadened immensely, and since then has been central in the development of evolutionary biology, including many new fields of study. Systematists were among the first to recognize and interpret significant evolutionary patterns in nature. The importance of reproductive characters in systematic stud-ies of plants has been recognized since at least the time of the adoption of Linnaeus' sexual system of classifica-tion. In a brief paper in the early 20th century, Sprague (1925) pointed out that the majority of characters (20 of

the 24 he cited) employed in understanding angiosperm classification were those of the flowers, fruits and seeds. He also discussed functional interpretations of some of these characters, including their roles in pollination, in his analysis of "evolutionary progressions" (= more or less, polarity interpretations of these characters). Subsequently, Grant (1949) made the observation that floral characters (exclusive of the calyx) constitute 37–40% of those used in taxonomic treatments of species with specialized pollination systems, while in wind and "promiscuous" pollinated plants, they constituted only 4–15% of the characters. Lloyd (1965) and Ornduff (1969) emphasized the impact of pollination and breed-ing system on inflorescence, floral, seed and fruit char-acters via a list of character states that may better reflect breeding systems (autogamy vs. xenogamy in their

examples) than taxonomic groupings. Of course, reference to almost any monographic study, past or present, makes the same point that all of these authors have emphasized: reproductive characters are central in systematic treatments.

Even with this long history of association between systematics and reproductive biology, systematic studies often neglect or undervalue the potential for reciprocal illumination in linking these two: understanding reproductive biology helps to clarify the potential use and value of characters in systematic treatments, and a good phylogeny can clarify the origin of reproductive characters or syndromes. Most studies employ systematics to understand the origin and evolution of reproductive features or syndromes; such studies are becoming more common. However, we also emphasize that the reciprocal is of considerable value as well.

We present a brief history of the interconnections between systematics and reproductive biology through a summary of reviews and key papers on that topic, document trends in the rate of publications dealing with the linkage between reproductive biology and systematics, and finally consider some of the current and emerging research themes in the field.

The war-delayed publication of the 1942 Presidential Address of the American Society of Plant Taxonomists by Francis W. Pennell (1948) is one of the early papers, after Sprague (1925), to explicitly promote the study of pollination and the broader topic of plant reproductive biology, and to help understand the characters that are central in systematic analyses. Pennell lamented that the study of pollination "...came to be associated, not with taxonomy, but with that vague though intriguing study of the interrelationships of plants and animals and environment that is termed ecology" (Pennell, 1948: 3). His emphasis was on the great variation present in floral morphology, and the connections to pollination, as well as a call for more attention to the latter topic.

Ornduff's (1969) paper, like Pennell's previously, exhorted systematists and evolutionists to be more cognizant of reproductive biology in systematic and evolutionary studies. He highlighted the importance of reproductive characters and syndromes in systematic studies, in particular, biosystematic approaches. He emphasized that knowledge of the breeding system, e.g., incompatibility systems, is fundamental to understanding mating patterns, character evolution, and possibly even the potential for hybridization. Reflecting his own research experience, he emphasized the ramifications of heteromorphic (e.g., heterostylous) systems on reproductive morphology. He also made a special point of the dramatic effects mating systems can have on morphology in presenting an exhaustive list of the alternate states of 28 floral characters associated with autogamy vs.

xenogamy. Of course, systematic treatments based on reproductive characters can sometimes be misleading, as pointed out by Ornduff (1969) for the largely anemophilous "Amentiferae", and Anderson (1995) for two erroneously linked autogamous *Solanum* (Solanaceae) species. However, understanding the inheritance of a correlated set of reproductive characters in other instances not only makes systematic treatments more sound, but also points to the evolutionary forces that have shaped some groups. Ornduff cited examples from the genus *Aquilegia* (Ranunculaceae; red-flowered, bird-pollinated species, and white-flowered hawkmoth-pollinated species) and the family Onagraceae. Hodges (1997) later showed that the radiation of *Aquilegia* is closely associated with the evolution of an important element of the reproductive system, i.e., nectar spurs. Other examples of such radiation within genera include: *Disa* with 19 pollination systems occurring in the 27 species included in the phylogenetic analysis by Johnson & al. (1998); see Fig. 1A, 1B, 1D, 2B; *Nicotiana* (Solanaceae) with three main floral syndromes (Cocucci, 1999)— sphingophily (flowers with funnel-shaped corollas, slender tubes and broad star-shaped or discoidal limbs), chiropterophily (zygomorphic flowers with a tubular basal portion articulated with a broader campanulate region) and ornithophily (flowers with tubular corollas and reduced limb); and *Caesalpinia* (Fabaceae) which has melittophilous, psychophilous, sphingophilous and ornithophilous species each with characteristic structural and color variation (Vogel, 1991).

Webb (1984) carefully studied nearly 50 entomophilous species in the New Zealand flora to assess the stability of reproductive parts (e.g., flower size, stamens, pollen and ovules) in various lineages. This often overlooked paper demonstrates variation in reproductive systems within four New Zealand plant families. For instance, Webb noted that dioecy has evolved at least four times in Apiaceae; he also cited Raven's study (1979) of breeding systems in Onagraceae where self-pollination had well over 100 independent origins. He pointed out the potential errors that ensue in systematic treatments if the biological significance of character states, such as these reproductive characters, is not well understood, citing a study by Garnock-Jones (1976) where both autogamy and entomophily are found in a single species of *Parahebe* (Scrophulariaceae). It was the study of the functional significance of the characters that facilitated the correct treatment of the striking differences in floral morphology as associated with pollination systems within a single species, rather than taxonomic differences among species (see also Fig. 2C, D). Webb made a strong case for understanding reproductive biology as a prerequisite to studying the morphologically based systematics of a group.

Fig. 1. Pollinators and floral evolution. A, flowers of the orchid *Disa uniflora* are pollinated exclusively by the large mountain pride butterfly *Aeropetes tulbaghia* (Johnson & al., 1998). **B**, pollination by the butterfly *A. tulbaghia* has evolved twice in *Disa*, with the deceptive species *Disa ferruginea* shown here occurring in a separate clade to the rewarding (nectar) congener *D. uniflora* (in A; Johnson & al., 1998). **C**, the guild of ca. 20 South African plants pollinated by *A. tulbaghia* is characterized by large unscented red flowers and includes the amaryllid *Cyrtanthus elatus*. **D**, carpenter bees are the exclusive pollinator of *Disa graminifolia* in South Africa. The genus *Disa* has undergone spectacular adaptive radiation associated with shifts between pollination systems in this region (Johnson & al., 1998). **E**, convergent floral syndromes allow hypotheses to be generated about pollinators, as shown recently in *Massonia depressa*, a lily species whose similarity in floral traits to rodent-pollinated proteas, led researchers to the discovery of a new rodent pollination system (Johnson & al., 2001). **F**, *Zaluzianskya microsiphon*, a self-incompatible species pollinated by long-tongued flies evolved within a large clade of night-flowering moth-pollinated species (Johnson & al., 2002). Photos: Steve Johnson.
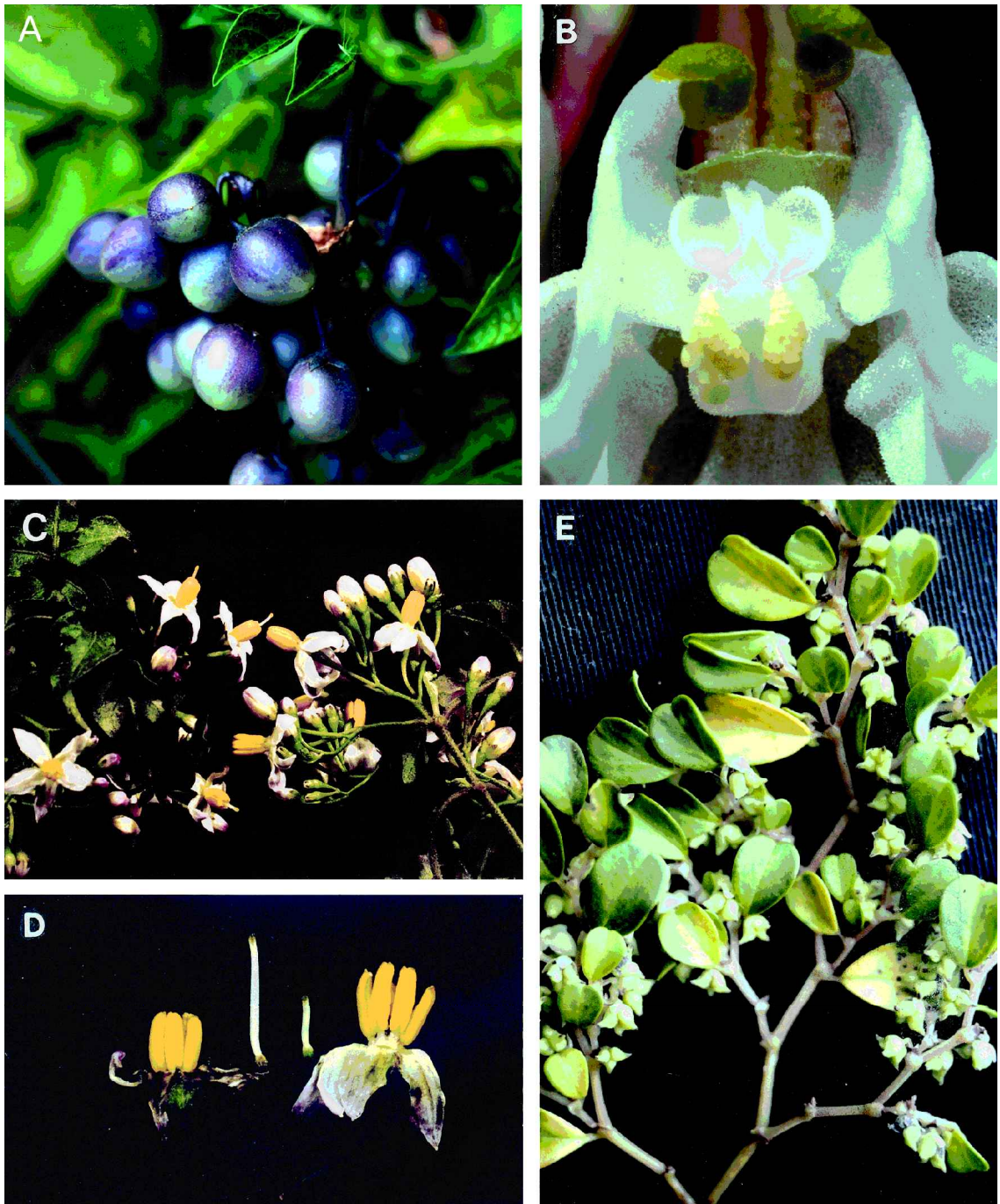
Fig. 2. Breeding systems and floral evolution. A, self-compatible, self-crossing species such as *Solanum fernandezia-num* (Solanaceae), whose fruits are shown here, and the *Disa* orchid in B often have relatively little (compared with out-crossers like the dioecious *Solanum* shown in C) within-population variation, and thus may require more populations to be sampled to assess variation (Anderson, 1995). B, the orchid *Disa rosea* grows in habitats that are marginal for insect activity, but obtains reproductive assurance when the pollinia flip onto the stigma resulting in autonomous self-pollination (Johnson & al., 1998). C, D, understanding breeding system characters is sometimes the key to the proper taxonomic treatment: the flowers of *Solanum appendiculatum* (Solanaceae; intact in C, styles dissected out in D) with short styles are functional males, those with long styles, from a different plant, are the functional females. Previously, these two morphs had been treated as separate, but closely related species (Anderson, 1979; Anderson & Levine, 1982). E, knowledge of the reproductive biology of island species like the Juan Fernandez endemic *Lactoris fernan-deziana* (Lactoridaceae) is essential not only to achieving the correct taxonomic treatment, but also to establishing effective conservation programs (Bernardello & al., 1999). Photos: Greg Anderson, Steve Johnson.

Speaking at the IOPB biosystematics conference (St. Louis) about a decade ago, Anderson outlined the conceptual interactions between systematics and reproductive biology and recognized the six categories summarized below (Anderson, 1995).

(1) Processes dictate patterns. — Processes such as speciation, which are directed by adaptation to new pollinators (vs. those induced by internal changes such as major chromosome rearrangements), can have major effects on character expression (as above). Pattern studies will be much better founded, therefore, and thus more informative, if based on a clear understanding of the forces driving character expression or change.

(2) The nature of species. — The questions associated with species definitions, if anything, are more hotly debated, and more complex in this "cladistic era" than they were previously. Central to some arguments in this debate is understanding the potential for gene flow (in all of its manifestations). Such an understanding is obviously most profound if based on an understanding of reproductive biology including breeding system, pollination and seed dispersal.

(3) Nature and range of variation. — In their classic plant systematics textbook, Davis & Heywood (1963) recognized links between taxonomy and reproductive systems when they stated, "The recombination of genetic variability is largely determined by the breeding system...." (p. 303). Anderson (1995) elaborated on this point by citing the classic examples of the distribution of variation among self-crossing plants (more electrophoretically detectable variation among populations) vs. plants that outcross (most variation within populations; Hamrick & Godt, 1990). Thus, in systematic and evolutionary studies, population sampling of species like the rare island endemic, *Solanum fernandezianum* (Ramanna & Hermsen, 1981; Bernardello & al., 2001) (e.g., Fig. 2A), that are autogamous, should be quite different than it is for a species like *Zaluzianskya microsiphon* (Scrophulariaceae; Fig. 1F) that is an obligate outcrosser.

(4) Anticipation of hybridization in lineages. — Knowledge of the compatibility system and the degree of specialization in pollination systems is useful as well for prediction of possible hybridization and the multiple impacts that this phenomenon can have on pattern studies.

(5) Evaluation of characters of systematic importance. — It is perhaps obvious that the vast majority of the morphological characters that systematists employ are often the same adaptations for attraction and morphological accommodation of biotic pollinators (based on many observations and experimental studies in pollination biology, e.g., Grant, 1949; Johnson, 1996). Thus, recognizing the functional role of characters in pollina-

tion, for instance, can help systematists evaluate their suitability for cladistic studies, in particular, to avoid or de-weight characters of the mating system that are particularly labile (e.g., Lloyd, 1965; Ornduff, 1969; Webb, 1984; Wyatt, 1988; Anderson & Jansen, 1998).

(6) Explanation of anagenetic changes. — Darwin (1862) and later Romero (1992) worked with orchid genera where dioecy greatly confounded the systematics. The staminate and pistillate forms of these *Catasetum* orchids were previously even treated as members of different genera; ultimately the understanding of the multiple and profound ramifications of the breeding system made clear the correct systematic interpretation. A similar, but less dramatic example of acquisition of a suite of characters associated with the breeding system, and of the systematic clarification ultimately resulting from the recognition of dioecy, is the discovery of dioecy in the genus *Solanum* where the functional male and female plants also were previously recognized as distinct species (Anderson, 1979; see Fig. 2C, D).

Ecology and systematics, which developed as quite separate fields (also see Pennell, 1948), have moved closer in the past two decades. Phylogenetic information for taxa is becoming commonplace, enabling ecologists to obtain historical insights into the adaptation of traits to the environment (Wanntorp, 1983). At the same time, systematists and evolutionary biologists are increasingly using ecological information to interpret patterns of character evolution (Givnish & Sytsma, 1997). The increasing interaction between ecology and systematics has led to the development of the new disciplines of comparative biology (Harvey & Pagel, 1991) and "ecophylogenetics" (Wanntorp, 1983; Sillén-Tullberg, 1988). This has led to renewed interest in, and a much deeper understanding of, the process of adaptive radiation (Givnish & Sytsma, 1997; Schluter, 2000). One field that has benefitted enormously from these new associations is plant reproductive biology. As we have described, there have always been strong links between plant reproductive biology and systematics, but these have been strengthened in recent years as cladistics and molecular biology together have provided the tools for constructing more reliable phylogenies.

In a summary of the interplay between comparative biology and reproductive systems, Barrett & al. (1996) analyzed the ways in which explicit phylogenies can help interpret reproductive characters or syndromes. Their paper focused on three examples. The authors combined results from recent molecular-based phylogenies with reproductive data from other studies. Within Polemoniaceae, they assessed selfing vs. outcrossing mating systems in six congeneric species pairs to evaluate allocation theory between pollen (P) and ovules (O) (manifest in P/O ratios), and pollen grain size. This phylogeneti-

cally independent analysis yielded the expected result that outcrossers have significantly higher P/O ratios, but surprisingly they also found that outcrossers tend to have larger pollen. The authors concluded that these results emphasize the need for increased attention to "...interactions between sex allocation, pollination, and post-pollination processes...." To that we would add that it also illustrates the value of systematists knowing what sort of impact mating systems might have on taxonomically significant characters. The second example concerns heterostyly in Pontederiaceae. Barrett & al. (1996) consider the issue of character weighting in phylogenetic studies and advocate its application especially when the biology indicates developmental or genetic complexity in floral syndromes such as tristyly. Finally, they used some of the then-nascent phylogenetic studies of all seed plants to evaluate growth form and breeding system. They found support for the hypothesis that perennial plants (woody or herbaceous) tend to outcross more than annuals. As described below, this kind of analysis where "biological" (functional, ecological, genetic, etc.) data are interpreted using phylogenies once again is becoming more common as phylogenetic analyses have become more routine.

The perspectives derived from comparison of taxa within a phylogenetic framework are where many of the most significant advances in reproductive biology have taken place. In particular, phylogenies have refined the formulation of evolutionary hypotheses about adaptation in floral traits. In an exhaustive review of cladistics and reproductive biology, Weller & Sakai (1999) considered conceptual issues and methodological approaches to using molecular data or morphological data, or a combination of the two, to evaluate reproductive systems and pollination. They carefully considered the contentious arguments regarding the inclusion in the data matrix of the characters/syndromes being studied. The analysis is focused primarily on how such phylogenetic studies inform the understanding of the evolution of reproductive characters or syndromes. However, Weller & Sakai also reviewed examples of the reciprocal—where the results from "microevolutionary studies" can inform character analyses/weighting in phylogenetic studies. In addition to the analysis of inclusion/exclusion of characters under study, they also evaluated the diverse literature on morphological/molecular data sets and elements of cladistic methodology (e.g., outgroup selection), character ordering and weighting, consideration of the sequence of events and character or syndrome homology. The heart of the paper is a table with 23 categories derived from their review of nearly 40 papers summarizing the distribution, loss, gains, order of acquisition of reproductive and pollination characters or syndromes.

TRENDS IN PUBLICATION IN REPRODUCTIVE BIOLOGY AND SYSTEMATICS

The preceding makes clear that there have been a number of significant reviews touting the interaction between systematics and reproductive biology that also offer insights and interpretations of the value of study of these interactions. In this part of the paper we have taken a new, broader approach to the topic to assess the overall activity and interest in research in plant reproductive biology, and in particular, publications that link with systematics. This approach was facilitated by searching the database now available from the Institute for Scientific Information ISI Web of Science® covering the literature from 1975–2002. The ISI database covers thousands of journals, and millions of articles. Each topic (as identified below) was searched from titles for 1975–2001 (the data for 2002 were incomplete at the time of the survey). The ISI data base was expanded to include abstracts and keywords beginning in 1991, so we also repeated the survey, searching titles, abstracts and key word lists for 1991–2001. The search procedure is summarized in Table 1. The resultant data are presented in tabular form in Appendices 1 and 2. Where appropriate, the data were transformed as needed for regression analysis using SAS® statistical procedures (Figs. 3–8).

PUBLICATION IN REPRODUCTIVE BIOLOGY IN GENERAL

Introductory comments. — In all the following analyses, it is important to note that the data are based on author-selected information—their titles, abstracts and keywords. Our interpretations in this part of the paper are of the data that result; we did not interject interpretation of the orientation or focus of the papers.

All journals. — The data in Appendices 1 and 2, illustrated in Figs. 3–5, show clearly that there is an increase in the number of publications in plant reproductive biology in the last 27 years. The review of titles for "all journals" for publications on "pollination" shows an increase averaging about 5% per year (i.e., an average increase of about 89 papers a year), and roughly a threefold increase in the number of papers published with "pollination" in their titles over the 27-year period (Appendix 1; Fig. 3). Clearly, the study of pollination biology is flourishing. We were unable to analyze the extent to which this increase simply reflects a general increase in scientific publication rate. The ISI data give the number of articles reviewed per year for each search, and that number certainly has gone up dramatically over the 27-year period. However, the number of articles reviewed is in the hundreds of thousands because all the scientific literature that the ISI Web of Science® covers

Table 1. Structure of the literature search to determine publication trends in plant reproductive biology and linkages to systematics.

Terms searched	Journals covered	Titles only (1975–2001)	Titles, keywords and abstracts (1991–2001)
Pollination[1]	"All Journals"[4]	Appendix 1 Fig. 1	Appendix 2 Fig. 2
Pollination[2] Reproductive Biology Breeding System	"10 Select"[5, 6] *American Journal of Botany*[7] *Systematic Botany* *Systematic Biology* *Plant Systematics and Evolution* *Taxon*	Appendix 1 Fig. 1	Appendix 2 Fig. 2
Pollination AND Systematics[3] Pollination AND Phylogeny Reproductive Biology AND Systematics Reproductive Biology AND Phylogeny Breeding System AND Systematics Breeding System AND Phylogeny	All Journals[4, 8] "10 Select"[5] *American Journal of Botany*[7] *Systematic Botany* *Systematic Biology* *Plant Systematics and Evolution* *Taxon*	Appendix 1	Appendix 2 Fig. 3

[1] *The articles identified were not vetted for "plant" vs. "animal", assuming that each article on "pollination" must have had at least some plant component. The terms "reproductive biology" and "breeding system" could not be used because they would also have encompassed a large number of animal, and particularly human medical, reproductive biology articles.*

[2] *Only one of these three terms was needed to recover an article from the database.*

[3] *Only one of these six combinations of terms was needed to recover an article from the database.*

[4] *All 5,700+ journals covered by the ISI® site at the time of the survey (April, May 2002).*

[5] *The 10 journals following were chosen because they represent international journals in which a large percentage of plant reproductive biology papers appear regularly, or they are leading systematic journals that include articles linking reproductive biology and systematics. Our journal selection was based on experience in the field, but is corroborated by an analysis of the literature cited in the Weller and Sakai annual review paper discussed above. They cite papers from at least 26 journals, including seven of the 10 we selected. However, 58% of the journal papers cited in that review come from the seven journals on our list. JOURNALS: American Journal of Botany, Annals of Botany, American Naturalist, Ecology, Evolution, Oecologia, Plant Systematics and Evolution, Systematic Botany, Systematic Biology, Taxon.*

[6] *For the "titles only" search over 1000 citations were found. A review of the first 100 articles yielded only a single paper on the reproductive biology of animals, so we did not vet the rest of the citations.*

[7] *Specialty plant or systematics journals each independently reviewed for the terms indicated:* American Journal of Botany, Systematic Botany *(from 1976 on; previously as* Brittonia, *which was not searched),* Systematic Biology *(from 1992 on; previously as* Systematic Zoology, *which was not searched),* Plant Systematics and Evolution, Taxon.

[8] *With this data set, we hand-eliminated all articles that treated the general topics of "reproductive biology" or "breeding systems" that referred exclusively to animals.*

is reviewed for each search. There is presently no way to select only the subset of potential pollination-relevant literature to review from the universe of scientific literature. However, as you will read below, we devised a (time intensive) method for measuring the publication rate for the selected journals we surveyed. The results show that generally the rate of increase of the publication of articles in reproductive biology exceeds the overall publication rate in relevant journals.

The more comprehensive review (including keywords and abstracts as well as titles) for the last 11 years (1991–2001) yielded twice as many articles as the titles-only search (Appendix 2), demonstrating the point that searches of titles for literature are much less effective.

The average increase per year is about 4% for a total of some 5100 articles. Thus, the more recent trends in the study of pollination biology are also significantly positive (Fig. 4).

Selected journals. — The survey of the titles of the "10 selected journals" shows an approximate doubling of articles with reproductive terms during the 27-year period, with an increase averaging about 13% per year (Appendix 1). However, the data are more variable; as a consequence the regression is not significant (Fig. 3). Three points in the middle of the distribution stand out—the especially high rates of publication for 1985–87. When these data points are deleted, and the analysis run again, the regression is highly significant
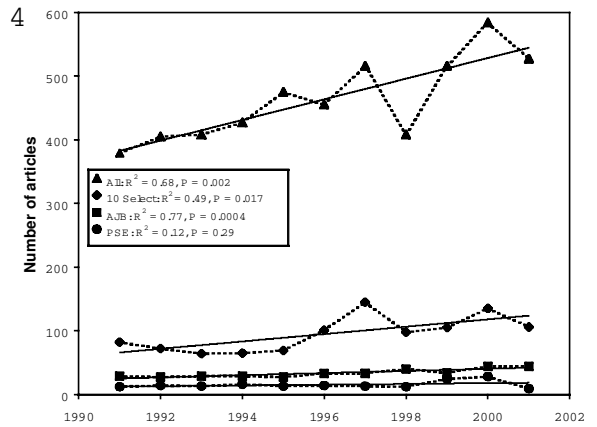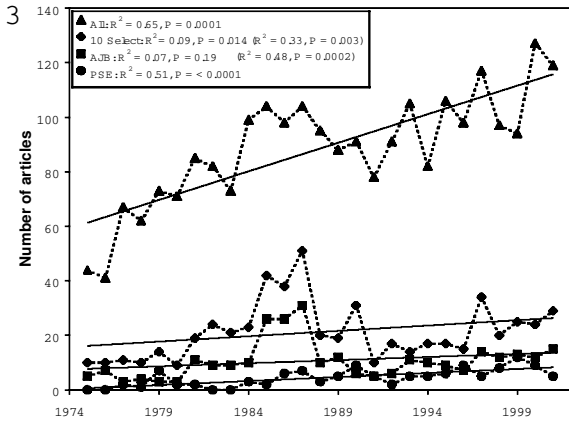
Figs. 3, 4. Titles-only (Fig. 3) and titles, keywords and abstracts (Fig. 4) searched for pollination (for all Journals), or pollination or reproductive biology, or breeding system. The 10 select journals are given in the text. AJB = *American Journal of Botany*, and PSE = *Plant Systematics and Evolution*. Dotted lines connect points among years for ease of comparison, and are of no statistical significance; solid lines are regression lines back-transformed into original units.
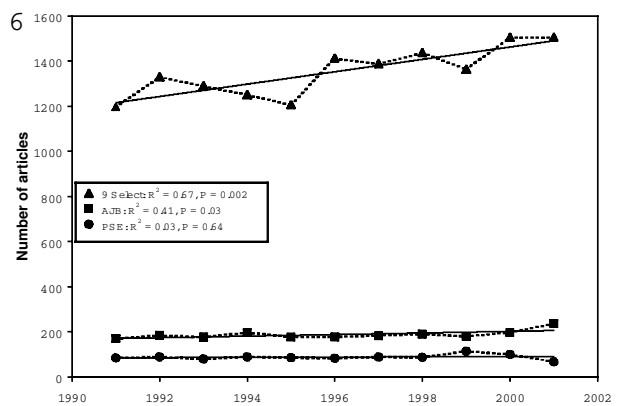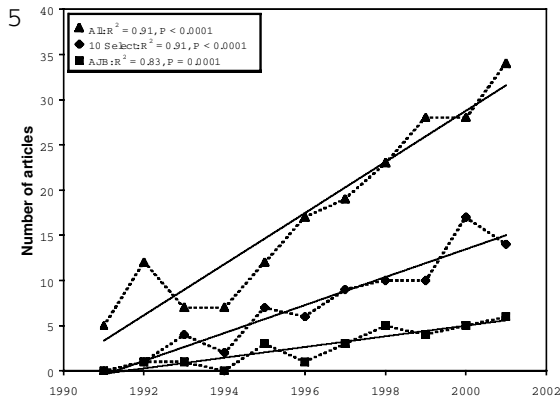
Figs. 5, 6. Titles, keywords and abstracts searched for the linkage of pollination (for all journals), or pollination or reproductive biology or breeding system (for all other categories) with either systematics or phylogeny. The 10 select journals given in the text (Fig. 5), and the total number of full articles published per year (Fig. 6; the nine select journals are given in the text). Abbreviations as in Fig. 3.
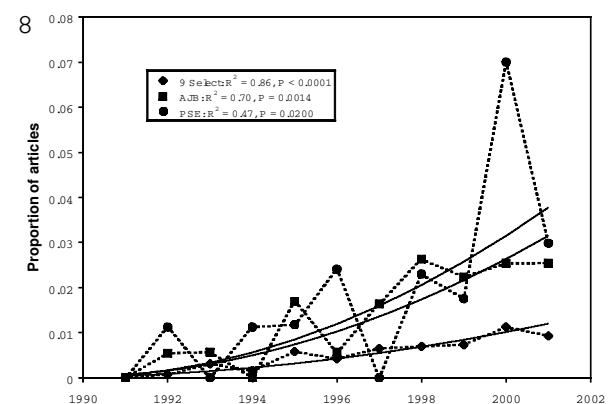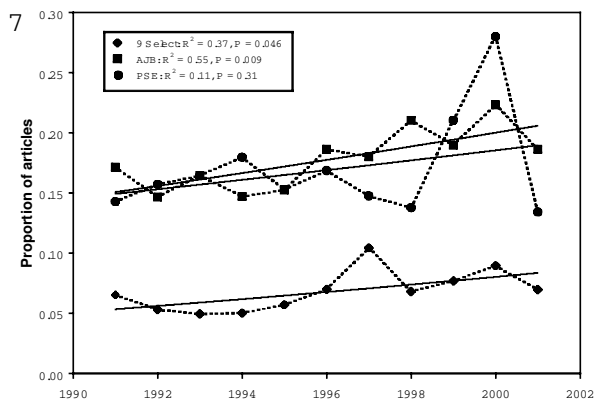
Fig. 7, 8. The proportion of articles published, which include pollination or reproductive biology or breeding system in their titles, keywords or abstracts (Fig. 7), and the proportion of articles published that link in their titles, keywords or abstracts systematics or phylogeny (Fig. 8). The nine select journals are given in the text. Abbreviations as in Fig. 3. Dotted lines connect points among the years for ease of comparison, and are of no statistical significance; solid lines are regression lines back transformed into original units.

($R^2 = 0.33$; $P = 0.003$). The explanation for the spike in reproductive biology publication in 1985–87 is not immediately apparent.

The analysis of titles, keywords and abstracts for 1991–2001 shows a highly significant regression value (Appendix 2; Fig. 4) similar to that generated with "all journals". These 10 journals are clearly significant venues for considerable numbers of plant reproductive biology papers.

To compare the relative rates of publication of articles on reproductive biology, we counted the full articles (excluding notes, book reviews, etc.) in nine of the journals for the 11-year period. *Taxon* was not included in this survey because its focus, particularly prior to 2000, was on nomenclatural issues, etc., and it would have required a much more subjective analysis to select only the articles with a broader focus. Accordingly, the seven entries in Appendix 2 for articles in *Taxon* that covered reproductive biology were deleted from the "10 Select Journals" totals before statistical comparisons were made. This group thus became "nine select Journals" for this analysis only.

Appendix 3 lists the number of articles counted. For the group as a whole, Fig. 6 shows a strong trend to more publication overall during the 1990s, with a highly significant regression. To determine whether the rate of publication of plant reproductive biology papers was the same, higher, or lower than this increase in overall publication rate, we calculated the proportion of the total articles that were in reproductive biology for each year [e.g., for the *American Journal of Botany* for 1991, 29 articles on reproductive biology (Appendix 2) divided by 169 total articles (Appendix 3) = 17%]. Figure 7 graphically portrays these results, showing an increasing proportion of publication of plant reproductive biology papers from 1991–2001 for the "nine select journals".

Specialty journals. — The two international journals with the broadest scope among those we selected for individual analysis, the *American Journal of Botany* (*AJB*), and *Plant Systematics and Evolution* (*PSE*), include a large number of reproductive biology articles (see more below; Figs. 3, 4, and Appendices 1, 2). There is a significant increase in the number of titles in *PSE* with reproductive terms during the last 27 years (Fig. 1); this is not the case with *AJB*. However, as in the data for the "10 select journals" (and likely attributable in large part to these *AJB* data), there are three years in the middle of the study period, 1985–87, that witnessed very large numbers of reproductive biology papers in *AJB*. When these three highly productive years are removed from the data, the R^2 goes up to 0.48 ($P = 0.0002$).

The comprehensive survey (titles, keywords and abstracts) of the last 11 years shows a highly significant increase for *AJB* (Fig. 4), but not for *PSE*, where there

has been a more constant (but substantial) rate of publication of about 15 papers per year. Impressively, *Systematic Botany* also includes a large number of articles, but the publication rate is fairly constant per year, so no significant trends were detected (Appendices 1, 2).

The orientation of *Taxon* and *Systematic Biology* is different and apparently plant scientists have rarely published reproductive biology papers in either of these journals. Appendix 1 shows that *Taxon*, more nomenclaturally focused in the past, included only nine articles with "pollination", "reproductive biology" or "breeding system" in their titles since 1975 (Appendix 1). The comprehensive analysis including searches of keywords and abstracts as well, turned up four additional articles in *Taxon*. There are only two papers in *Systematic Biology* (since it was re-titled in 1992) that deal with plant reproductive biology (Appendix 2).

An analysis of the data in Appendix 2 shows that *AJB* and *PSE* account for more than 50% of the plant reproductive biology papers cited in the comprehensive search since 1991 (*AJB* + *PSE* / "nine select journals" = 52%). Thus, as indicated above, these might be considered the two major journals for plant reproductive biology studies. Accordingly, our further analyses of publication rate (Appendix 3; Figs. 4, 5) were focused on these two journals. Figure 4 shows a fairly constant overall publication rate for *PSE*, but a significant increase in the number of papers in *AJB* over the 11-year sample period. Similarly, when the proportion of articles on reproductive biology is considered, there are highly significant regression values for *AJB*, but not for *PSE* (Fig. 7).

Thus, there is a continued and growing interest in plant reproductive biology studies—even as assayed here by these necessarily restricted means (i.e., such things as dispersal and associated fields were not surveyed).

PUBLICATION IN REPRODUCTIVE BIOLOGY LINKED TO SYSTEMATICS

Introductory comments. — We used the search terms "systematics" or "phylogeny" to identify systematics papers linked with reproductive biology. Review of data in the second part of Appendix 1 (the seven columns on the right) makes it very clear that title searches are even less useful for more complicated searches requiring linkage between terms. Although nearly 2,400 papers had "pollination" in their titles for "all journals", only eight also included the terms "systematics" or "phylogeny". Similarly, though nearly 600 papers in the "10 select journals" included "pollination", "reproductive biology" or "breeding system" in the title, only five titles in the 27-year study period also included "systematics" or "phylogeny". Even in the key journals (*AJB, PSE*), there are virtually no articles (n = 2 each) with "systematics"

or "phylogeny" linked to "pollination", "reproductive biology" or "breeding system" in titles. Fortunately, the ISI Web of Science® search engines began to include keywords and abstracts in 1991; accordingly, the following analysis is based only on the data from those 11 years (Appendix 2, Fig. 5).

Only about 4% of the articles from "all journals" included a linkage to systematics or phylogeny, and about twice that proportion among the "10 select journals" (7.7%; Appendix 2). However, these data show clearly that the number of papers linking systematics and reproductive biology over the last decade has grown dramatically (Fig. 5). The rate of publication of articles linking reproductive biology and systematics has increased even more rapidly than the publication rate of reproductive biology in general (Fig. 4). However, the articles linking reproductive biology and systematics are found in relatively few journals. Not surprisingly, most of the papers in journals with an ecological orientation tend not to have papers linking reproductive biology to systematics. More than 60 of the 80 papers in the "10 select journals" are from three sources: *American Journal of Botany*, *Plant Systematics and Evolution*, and *Systematic Botany*.

Selected journals and speciality journals. — We could not make comparisons of publication rate for "all journals" (see above), but could for the "nine select journals", and for *AJB* and *PSE*. For the "nine select journals", *AJB* and *PSE*, the proportional change in papers linking systematics and reproductive biology shows a strong upward slope, and significant regression values (Fig. 8). This implies that this broader view of systematics incorporating elements of reproductive biology is growing substantially. This is very likely a tribute to the "maturity" of the field of phylogenetic analysis, reflected in increased application of phylogenies to the study of other systematically relevant issues like character and syndrome analysis. This trend, utilizing robust phylogenies, often generated with molecular data sets, is increasingly evident in both articles published and in papers presented at international meetings. As phylogenetic techniques (and the molecular methods generating the data) have become more routine, there has been an extension beyond just the study of patterns of relationships to include, once again, the study of processes, character evolution, and of "biological" elements of species and other taxa.

■ EMERGING RESEARCH THEMES

Evolution of floral traits. — Apart from their obvious usefulness for classification, phylogenies based on cladistic methodology provide a powerful means of studying the pathways of trait evolution (Wanntorp, 1983; Donoghue, 1989). Concepts such as specialization, preadaptation, key innovations, and evolutionary constraint take on a clearer meaning when the actual sequence of trait evolution can be studied (Armbruster, 1992, 1998; McDade, 1992). Features that vary among organisms are termed "traits" by ecologists and "characters" by systematists. In ecology, these features require an explanation, while in systematics, historically, they have provided explanations. Thus, for example, the long tube of a flower may suggest an adaptation to a hawkmoth to an ecologist, while to a systematist the same feature may imply a relationship to another taxon that shares long flower tubes. Without phylogenetic information, both may be wrong. The long flower tube may be an ancestral trait that evolved before hawkmoth pollination (and is thus a preadaptation), or the two taxa may share long flower tubes because of convergent evolution (manifest as homoplasy on a properly constructed cladogram). Thus, a deeper understanding of the evolution of floral traits clearly requires the collaborative effort of reproductive biologists and systematists.

One of the insights that evolutionary biology has obtained from phylogenetics is that multiple origins of a trait provide better evidence for adaptation than the overall number of species possessing such a trait. Felsenstein (1985) was among the first to show that because of patterns of common descent, species cannot be treated as independent samples either when correlating traits among organisms or when correlating traits to environmental variables. Character mapping onto phylogenies has become the standard tool for tracing the evolution of traits. There are several examples where consideration of phylogeny has led to a new perspective on long-standing problems in reproductive biology (e.g.,Weller & Sakai, 1999). In one of the more notable cases, Donoghue (1989) was able to show that dioecy evolved concurrently with fleshy fruits, in contradiction to previous theoretical predictions that it should evolve after the innovation of fleshy fruits.

Gene flow and plant mating patterns. — While the scale of pollen dispersal distances away from plants received much attention in the 1970s and 1980s as a result of Ehrlich & Raven's (1969) influential paper arguing against gene flow as the mechanism uniting species, there was renewed interest in self-pollination in the 1990s. Biologists drew attention to the important and previously neglected phenomenon of pollinator-mediated self-pollination, particularly geitonogamy (pollen transfer between flowers on the same plant). Geitonogamy can reduce the pollen that is available for export to other plants ("pollen discounting", as in Holsinger & al., 1984) and also result in inbreeding depression in self-compatible plants. Thus, plant mating systems are a man-

ifestation not only of the capacity for autonomous self-pollination and compatibility systems, but also of the behavior of pollinators. The continuum between selfing and outcrossing in plants results in "mixed mating systems" (Holsinger, 1996).

In a controversial paper, Bell (1985) reached the radical conclusion that the advertising and reward traits of flowers serve mainly a male function. His premise, supported by some empirical studies, was that seed set is saturated in most plants by ample delivery of pollen to stigmas and thus that fitness will mainly be determined by the efficiency of pollen removal and export to other flowers. Bell's thesis has had to be modified in the light of further evidence that many species, perhaps the majority, do not in fact experience saturated female fitness as fruit and seed set is limited by pollen availability (Burd, 1994).

Adaptation, reproductive isolation and plant speciation. — It is widely accepted that evolutionary diversification in flowers and fruits has been a major feature of the radiation of the angiosperms. Indeed, it has been argued that adaptations for pollination and seed dispersal have been important driving forces in the evolution of the flowering plants (Grant & Grant, 1965; Stebbins, 1970; Basinger & Dilcher, 1984; Crepet & Friis, 1987; Dodd & al., 1999).

The patterns generated by processes of speciation are the primary focus of research in systematics. These patterns reveal much about the evolutionary processes that generated them. For example, taxa that are characterized by radiation in floral form are likely to have undergone pollinator-mediated selection, whereas radiation in vegetative characters is likely to reflect adaptation to the growth environment (Johnson, 1996). That pollinator-mediated selection drives the evolution of many floral traits has been clearly demonstrated in several studies (Galen, 1989; Alexandersson & Johnson, 2002). Much less clear is the manner in which such adaptive floral evolution leads to speciation (Johnson, 1996; Ollerton, 1996).

For Darwin, adaptations were responsible in a straight-forward manner for speciation, and it was thus a matter of personal taste where the lines that separate species should be drawn. Later, with the development of the biological species concept, speciation became envisaged as more than a process of adaptation; it was the process by which populations develop reproductive barriers that irrevocably split them from other populations. Reproductive biology was as much under the influence of the biological species concept as was systematics. There are many examples from the literature of the 1960s and 1970s with discussion of how pollinators and floral traits may serve to reproductively isolate species and thus play a role in the speciation process. In more recent

years reproductive biologists have begun to find fault with some premises of the reproductive isolation paradigm (Johnson, 1996; Waser, 1998). Criticism has focused on the implausibility of speciation via selection for isolating mechanisms. Thus, an emerging theme is that isolating mechanisms are incidental by-products of speciation, rather than subjects of selection per se (Grant, 1994). Waser (1998) argued that pollinators are seldom specialized enough for "ethological isolation", while Johnson (1996) drew attention to the need for processes, other than isolating mechanisms, that explain divergence in floral characters in allopatric populations. The primary form of selection imposed on reproductive traits is for increased reproductive output, e.g., to alleviate pollen-limitation, and not for reproductive isolation (Johnson, 1996). As traits diverge under these selection pressures in allopatric populations, isolating mechanisms inevitably develop as an incidental consequence, so that hybridization is minimized should the ranges of sister species subsequently overlap. The current consensus does not take anything away from studies of the importance of isolating mechanisms in species coexistence (cf. Fulton & Hodges, 1999). In fact, molecular markers and genome mapping have allowed much more detailed insights to be made into species integrity, hybridization and introgression (Bradshaw & al., 1995).

Convergent evolution of pollination syndromes. — One of the more lively debates in systematics has been between those who argue that evolutionary interpretations of traits should always be based on an "independent" phylogeny (i.e., one that does not include those same traits as characters, cf., Bremer & Eriksson, 1992), and others who argue that any interpretation of traits should be based on a phylogeny constructed from the "total evidence" available, even if this includes the same traits as part of a character matrix (Armbruster, 1993; Bruneau, 1997; Johnson & al., 1998; Kluge & Wolf, 1993; Luckow & Bruneau, 1997). The debate about circularity is directly relevant to the interpretation of reproductive traits, as floral and fruit characters are routinely included in morphology-based cladograms. Armbruster (1992) offered a way out of this impasse by showing that floral traits are nearly always less labile than pollination systems, and thus that they have utility for phylogenetic construction.

Patterns of convergence in floral traits (= pollination syndromes) were first described by Delpino in the late 1860s and early 1870s and further formalized in the classic book by Faegri & van der Pijl (1966). The notion that it is possible to discriminate between a flower adapted for one type of vector or another (e.g., butterflies vs. birds) is part of the concept of floral syndromes (see Fig. 1A–C). There has been much debate in the past few years about whether or not pollination syndromes are an

appropriate framework for describing pollination systems (Johnson & Steiner, 2000). Some have argued that syndromes oversimplify the mostly generalized nature of pollination systems (Ollerton, 1996; Waser & al., 1996), while others point to the continued utility of syndromes for generating testable hypotheses (Johnson & al., 2001; see Fig. 1E).

While convergent and divergent evolution both arise simultaneously from the process of adaptive evolution, the focus of systematics has been almost exclusively on divergence. There has even been a tendency for systematists to view convergent evolution as an annoying source of homoplasy in characters. Indeed, the likelihood of convergent evolution is one of the major reasons that morphological characters are often distrusted for phylogeny reconstruction (McDade, 1992; Givnish & Sytsma, 1997).

Coddington (1988) pointed out that patterns of convergence should be of special interest, as they provide powerful evidence for adaptation. Traits that arise in different lineages under similar selective pressures are often manifest as homoplasy in phylogenetic trees. Paradoxically, such homoplasy provides some of the most exciting opportunities to study the relationship between pattern and process in systematics. Johnson & al. (1998), for example, showed how flowers conforming to the same pollination syndrome and pollinated by the same vectors had arisen independently in many different lineages of the large orchid genus *Disa* (Fig. 1A, B, D). They argued that such findings are robust when morphological characters are used for phylogeny reconstruction, as homoplasy arising from convergence makes the detection of separate origins of traits less likely.

Some would argue that the debate about whether reproductive characters are suitable for phylogeny reconstruction is bound to recede as molecular data gradually replace morphology. However, systematists are unlikely to abandon morphological characters in the near future. Molecular and morphological data are often congruent and provide independent verification for phylogenetic hypotheses. Molecular data are also prone to homoplasy, especially in older lineages, and the resolution provided by molecular data remains poor for some rapidly evolving taxa (cf. Hodges, 1997). Morphological traits, of course, are also used to identify and recognize the species.

Comprehensive approaches to reproductive biology research. — The resolution of some issues requires a more comprehensive multidisciplinary approach, drawing on expertise not just from systematics, but also from ecology, geography and conservation biology. All stages of sexual reproduction—from pollination to seed dispersal—will benefit from studies with a comprehensive perspective, rather than one restricted to sin-

gle plant species and their visitors. Acquisition of these data will require a major effort, but such data will allow effective comparisons among groups and geographical areas to be made, and trends to be determined, that will facilitate firmer conclusions, for instance, regarding whether reproductive traits imply adaptation to pollinators, or represent conservative characters that reflect phylogenetic constraints. As our understanding of reproductive characters and syndromes is enhanced, so too is our effective application of these in systematic studies. Accordingly, future research should include the following.

(1) Studies at the community level will facilitate a better understanding of the complex interactions among pollinators and plants in a given area, scaling up to generate general trends that will allow comparisons among biomes, thereby providing a firm foundation for understanding reproductive characters (e.g., Momose & al., 1998).

(2) Comparative research on representative members of the same clade (e.g., several species of a genus, different genera of a tribe, different tribes of a family, etc., Galetto & al., 1998) will more effectively cover the whole range of variability in the group. This perspective is essential for understanding the evolutionary forces that have shaped floral traits. If pollinators provide the selective pressure, similar tendencies would be found in species pollinated by the same guilds (Baker & Baker, 1983; Vogel, 1991). Alternatively, members of a single clade would possess the same traits because they share a recent common ancestor (Armbruster, 1992, 1996; Silvertown & Dodd, 1996).

(3) Research on individual species, but throughout the geographic distribution, will allow assessment of variation of reproductive features in different parts of the species range; the distribution of pollinators and plants do not always coincide (Webb, 1984; Bawa, 1992). This kind of work would give an insight, for instance, into taxonomic variation, polymorphisms, etc., that will help systematists assess character stability.

(4) Research applied to resolve questions of viability, extinction, conservation, and management of endangered and vulnerable species must include analyses of reproductive biology. A central element of effective conservation of plants is knowledge of the reproductive system in all its manifestations—gene flow, compatibility, breeding systems, pollination, dispersal, etc. (Anderson & al., 2001). Conservation or restoration programs will not be effective without an understanding of breeding systems, pollination (Hamrick & al., 1991; Karron, 1991; Weller, 1994; Fig. 2A, 2E) and dispersal (Estrada & Fleming, 1986; Murray, 1986). Without such knowledge, conservation programs of communities or of individual species may well fail. In addition, reproductive data are fundamental for achieving the most effective interpreta-

tion of the molecular data on genetic diversity of rare species or communities (Crawford & al., 2001). Systematists and reproductive biologists have to work together in conservation biology, with systematists calling attention to endemisms (e.g., Fig. 2D), or rare or endangered species with few populations in the field, and reproductive biologists analyzing the basic aspects of those taxa that will be essential to manage and preserve populations and species.

CONCLUDING REMARKS

The trends identified in the literature analysis are positive indicators for reproductive biology studies per se, but also for the health and diversity of systematics as a whole. In a recent editorial in *Systematic Biology*, Donoghue (2001) took a very positive tack in his "wish list for systematic biology" (both the journal and the field) and expressed excitement over our task as systematic biologists, which he put as "...charting the diversity of life, in its entirety from the tiniest tips of the tree to every one of its branches". He also pointed out that the vitality of the enterprise depends on making connections to other disciplines. The trees we produce as systematists are incredibly important contributions to understanding the diversity of life, and the phylogenetic methods our field has developed have had revolutionary effects not only in systematics, but on much of science and even on fields outside pure science. But, this, the most recent innovation in systematics, resulted in a narrower perspective in the 1980s and early 1990s where the focus was almost exclusively on pattern studies, on the production of branching diagrams, often from molecular data. While responsible for some of its greatest successes, could molecular methods, by virtue of amenability to automation, also lead to the demise of traditional systematic expertise? Will there still be a place for systematics when the generation of phylogenies becomes a routine procedure carried out by machines and we know much of what there is to know about the relationships among taxa? If the *raison d'être* for systematics is restricted to creating a tree of life, this will come sooner rather than later. Reproductive biology as an integral component of systematics became less common during the era of the nearly exclusive phylogenetic focus. In one sense, the ambit of systematics has shrunk, while links between systematics and other disciplines, including reproductive biology, have become strengthened. Systematics, as conceived by one of the doyens of the previous generation, George Gaylord Simpson, was considered "most inclusive" because "...in its various guises and branches [systematics] eventually gathers together, utilizes, summarizes, and implements everything that is

known about [organisms]...." (Simpson, 1961: 8). The more restricted view prevalent in recent times missed the great value of synthesis from all data. Fields are defined not by limiting data sets, but by refining questions and using all data to seek answers; this is how innovations emerge. The long-term aim of systematics must be to understand the origins of diversity, a goal stretching the timetable for research well beyond the next century. The irony is that, now with the maturity of molecular-based cladistics in particular, it is the production of these elegant and well-supported branching diagrams that is very likely the stimulus for the increasingly frequent (as in Figs. 3, 6) "comparative biology" studies, such as those reviewed by Weller & Sakai (1999), in which analysis of reproductive biological features and other data sets is important. Indeed, we are sanguine that the automation of phylogenetic studies will allow systematists to return to the broader interpretation of evolutionary patterns as well. This enterprise will focus on character evolution, mating patterns, hybrid zones, species complexes and clinal variation, to name but a few. Most of these investigations will not be possible without the partnership of plant reproductive biology and systematics. The trends identified herein thus offer considerable hope that systematics is again realizing its full potential as a synthetic and far-reaching discipline.

ACKNOWLEDGMENTS

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Appendix 1. Numbers of journal articles recovered with searches of titles.

	Pollination or reproductive biology or breeding system							Pollination or reproductive biology or breeding system LINKED with phylogeny or systematics						
Year	All journals*	10 select	AJB	PSE	Syst Biol**	Syst Bot	Taxon	All journals	10 select	AJB	PSE	Syst Biol**	Syst Bot	Taxon
1975	44	10	5	0	-	0	0	0	0	0	0	-	0	0
1976	41	10	7	0	-	0	0	0	0	0	0	-	0	0
1977	67	11	3	2	-	1	0	0	0	0	0	-	0	0
1978	62	10	4	1	-	1	1	0	0	0	0	-	0	0
1979	73	14	3	7	-	0	0	0	0	0	0	-	0	0
1980	71	9	3	2	-	0	1	0	0	0	0	-	0	0
1981	85	19	11	2	-	0	0	0	0	0	0	-	0	0
1982	82	24	9	0	-	3	1	0	0	0	0	-	0	0
1983	73	21	9	0	-	4	1	0	0	0	0	-	0	0
1984	99	23	10	3	-	3	0	1	0	0	0	-	0	0
1985	104	42	26	2	-	1	1	0	0	0	0	-	0	0
1986	98	38	26	6	-	1	0	1	1	1	0	-	0	0
1987	104	51	31	7	-	1	0	1	1	0	1	-	0	0
1988	95	20	10	3	-	0	1	0	0	0	0	-	0	0
1989	88	19	12	5	-	1	0	0	0	0	0	-	0	0
1990	91	31	6	9	-	3	0	1	0	0	0	-	0	0
1991	78	10	5	5	-	1	1	0	0	0	0	-	0	0
1992	91	17	6	2	0	3	1	1	0	0	0	0	0	0
1993	105	14	11	5	0	0	0	0	0	0	0	0	0	0
1994	82	17	10	5	0	0	0	0	0	0	0	0	0	0
1995	106	17	9	6	0	0	0	0	0	0	0	0	0	0
1996	98	15	7	9	0	0	1	1	1	0	1	0	0	0
1997	117	34	14	5	1	0	0	0	0	0	0	0	0	0
1998	97	20	12	8	1	0	0	1	1	1	0	1	0	0
1999	94	25	13	12	0	2	0	0	0	0	0	0	0	0
2000	127	24	12	9	0	1	0	1	0	0	0	0	0	0
2001	119	29	15	5	0	1	0	0	0	0	0	0	0	1
Total	2391	574	289	120	2	27	9	8	4	2	2	1	0	1

Appendix 2. Numbers of journal articles recovered with searches of titles, keywords, and abstracts.

	Pollination or reproductive biology or breeding system							Pollination or reproductive biology or breeding system LINKED with phylogeny or systematics						
Year	All journals*	10 select	AJB	PSE	Syst Biol**	Syst Bot	Taxon	All journals	10 select	AJB	PSE	Syst Biol**	Syst Bot	Taxon
1991	379	82	29	12	-	3	1	5	0	0	0	-	1	0
1992	405	72	27	14	0	4	1	12	1	1	1	0	1	0
1993	408	64	29	13	0	4	0	7	4	1	0	0	2	0
1994	427	65	29	16	0	0	2	7	2	0	1	0	0	0
1995	475	69	27	13	0	3	0	12	7	3	1	0	2	0
1996	455	101	33	14	0	4	2	17	6	1	2	0	1	0
1997	516	145	33	13	1	2	0	19	9	3	0	0	2	0
1998	408	98	40	12	1	4	0	23	10	5	2	1	1	0
1999	516	105	34	24	0	4	0	28	10	4	2	0	1	0
2000	584	135	44	28	0	3	0	28	17	5	7	0	1	0
2001	527	106	44	9	0	4	1	34	14	6	2	0	3	1
Total	5100	1042	369	168	2	35	7	192	80	29	18	1	15	1

S*ee text for journals used in "all journals" and "10 select" categories.* AJB = American Journal of Botany, PSE = Plant Systematics and Evolution, Syst Biol = Systematic Biology, Syst Bot = Systematic Botany.

* *Searched for "pollination" only; see text.*

** Systematic Biology *began publication in 1992.*

Appendix 3. The total number of articles published in nine select journals.

Year	AJB	Am Nat	Ann Bot	Ecology	Evolution	Oecologia	PSE	Syst Biol *	Syst Bot	Total
1991	169	163	143	196	93	293	84	43	55	1196
1992	184	151	145	201	137	331	89	38	54	1292
1993	176	104	141	210	161	327	79	43	48	1246
1994	197	131	158	201	157	233	89	45	40	1206
1995	177	112	150	213	124	260	85	45	40	1161
1996	177	147	160	221	237	303	83	43	42	1370
1997	183	116	173	224	215	296	88	44	49	1344
1998	190	123	178	236	189	347	87	52	35	1385
1999	179	134	151	231	195	271	114	44	45	1320
2000	197	116	252	260	218	271	100	42	49	1463
2001	236	108	185	269	236	280	67	65	58	1439
Total	2065	1405	1836	2462	1962	3212	965	504	515	14422

AJB = American Journal of Botany, Am Nat = American Naturalist, Ann Bot = Annals of Botany, PSE = Plant Systematics and Evolution, Syst Biol = Systematic Biology, Syst Bot = Systematic Botany.

* Systematic Biology *began publication in 1992. Value given for 1991 and used in calculations is the mean of the first five years of publication.*