



Pollination systems in the Asclepiadaceae: a survey and preliminary analysis

JEFF OLLERTON

School of Environmental Science, Nene College, Park Campus, Northampton, NN2 7AL

SIGRID LIEDE

Lehrstuhl f. Pflanzensystematik, University of Bayreuth, D-95440, Bayreuth, Germany

Received 13 February 1997; accepted for publication 28 August 1997

Using published and unpublished records of pollination in the dicot family Asclepiadaceae (the 'milkweeds') we offer a preliminary analysis of present-day pollination systems in the family. Variation in principal pollinators is apparent at and below the tribal level. The tribes Marsdenieae and Stapelieae and Asclepiadeae subtribe Gonolobineae are primarily Diptera-pollinated, a tentative conclusion also for the tribe Periploceae, and we emphasize the ubiquity and importance of fly pollination in the family. The rest of the tribe Asclepiadeae is pollinated in the main by Hymenoptera and Lepidoptera. Lack of data makes it impossible to draw even initial conclusions for the remaining tribes, Secamoneae and Fockeeae. Within the Asclepiadeae, there has been a trend towards more diverse pollination systems (incorporating butterflies and wasps) in the New World compared to the Old World. In terms of the taxonomic breadth of pollinators of individual species, Stapelieae is the most specialized tribe. We emphasize that this is only a preliminary account of pollination in the Asclepiadaceae, and detail areas where further work is urgently required.

© 1997 The Linnean Society of London

ADDITIONAL KEY WORDS:—Apocynaceae – diversification – Gentianales – reproductive ecology – specialization.

CONTENTS

Introduction	594
Methods	595
Results and Discussion	595
Quantity and quality of the available data	595
The pollinators of the Asclepiadaceae	598
The significance of fly pollination	602
Specialization and generalization in the family	604
Concluding remarks	606
Acknowledgements	607

Correspondence to: Dr J. Ollerton. email jeff.ollerton@nene.ac.uk.

References	607
Appendix	609

INTRODUCTION

Plant-animal pollination relationships have held the interest of scholars since the late 18th century (Sprengel, 1793) and played an important role in shaping early ideas about natural selection (Darwin, 1862, 1880; Muller, 1883). This long-standing preoccupation with the ways of plants and their pollinators has generated an enormous literature. Attempts to synthesize this work include reviews for discrete geographical areas (Armstrong, 1979; Prance, 1985; Feinsinger, 1987), in relation to specific biomes (Bawa, 1990) and life-forms (Gentry, 1991), or particular pollination and breeding systems (Dafni, 1984; Renner & Feil, 1993), or dealing with 'primitive' angiosperms (Bernhardt & Thien, 1987; Gottsberger, 1988). This is not an exhaustive list of review topics undertaken by pollination biologists, but one area which is open to much fuller exploitation is using the published and unpublished literature to assess the diversity of pollination systems at various systematic levels. There are few published family-level accounts of plant-pollinator interactions, for instance. One reason for this is that records of pollinators are scattered throughout the (often obscure) literature, or are secreted in researchers' note books, and compiling these data requires considerable effort. In this paper we present a quantitative analysis of pollination systems in the dicotyledonous family Asclepiadaceae (the 'milkweeds'), arguably one of the most highly evolved of all dicotyledon families, rivalling the monocotyledonous Orchidaceae in floral complexity. As in many orchids, asclepiad pollen is usually presented for a pollinator as a coherent mass (the pollinium). Exceptions to this are found in some members of the least derived tribe, the Periploceae, where pollen is shed in tetrads (a summary of current thinking on Asclepiadaceae systematics is presented in the Appendix). Specialized transportation devices (translators) have evolved to provide attachment of pollen to the pollinator, whilst pollination is usually brought about by insertion of the pollinium into modified anther organs (anther slits), though as noted there are exceptions to this, e.g. the tribe Periploceae. From this basic (though highly complex) ground plan, a range of floral forms has evolved. An overview of the morphological aspects of asclepiad pollination is given by Kunze (1991, 1995) and Endress (1994) has proposed a model of asclepiad floral evolution.

The last decade has seen a burgeoning interest in the systematics, evolution and ecology of the Asclepiadaceae. Despite advances in our understanding of asclepiad anatomy, morphology and phylogenetics, the pollination ecology of the family remains poorly understood, with the exception of the North American members of the genus *Asclepias* (for references see the review by Wyatt & Broyles, 1994). Much of the information about the pollinators of asclepiads is scattered amongst old and obscure publications. Here we draw together this information to present a coherent, state of the art overview of pollination in the family. Specifically, our aims were to: (1) assess the quantity and quality of information about pollination in the family; (2) to analyse the geographic and taxonomic coverage of these studies, thereby revealing areas where further field work is particularly required; (3) use existing information to build preliminary hypotheses concerning the diversity and evolution of pollination systems in the family, so that these hypotheses may be tested as further data become available.

We have almost certainly missed relevant information and would be grateful if

researchers would inform us of any published or unpublished omissions. Our work is intended to be ongoing: baptized the ASCLEPOL project, we will continue to catalogue pollinator records, and hope to re-review asclepiad pollination within the next decade.

METHODS

Information regarding pollination in members of the Asclepiadaceae was extracted from the published literature, or gleaned from the unpublished records of colleagues and of ourselves. Each record of pollination was coded on the basis of the quality of the information (cf. Adams & Lawson, 1993) as follows:

- (1) Identity of the pollinator proven. Insects with pollinia attached observed to bring about insertion of these pollinia into the guide rails of a flower of the same species, under natural conditions.
- (2) Identity of the pollinator inferred. Insects observed with pollinia attached, under natural conditions.
- (3) Identity of the pollinator inferred from circumstantial evidence. Insects observed to visit flowers, but not to pick up pollinia, under natural conditions.

In each case the taxonomic identity of the pollinator may have been more or less accurately determined. Ideally, a species name was available but if not, genus or family sufficed.

Where pollination had been observed under non-natural conditions, e.g. plants and/or pollinators outside of their natural range, this was noted and a coding 'B' appended to the record. Sometimes the published source was unclear; in such cases we made informed judgements as to the correct coding, based on the context of the study or with reference to other published work by the same authors. Where pollination records were restricted to order and family identity (e.g. Hymenoptera: Halictidae) we counted this as two species, except when the source indicated otherwise. Likewise some asclepiad records were for more than one un-named species (e.g. *Huernia* spp). and were recorded as two species. Where necessary plant generic and specific names have been modernized from the original records.

For the sake of brevity we have kept to a minimum citations of individual pollination studies; a catalogue of data on pollinator–plant relationships in the Asclepiadaceae has been compiled (the ASCLEPOL database) and is freely available from the first author.

RESULTS AND DISCUSSION

Quantity and quality of the available data

Our survey of published and unpublished pollination studies yielded 929 records of pollinators and visitors to a total of 150 species of asclepiads in 54 genera. This is a sample size of 5.8% of the total estimated number of species in the family (Table 1; data based on unpublished survey by S. Liede). Generic delimitations

TABLE 1. Summary of pollinator/visitor information available for the six tribes plus one subtribe of the Asclepiadaceae, based on records in the ASCLEPOL database. All data quality codes (1,2,3 and B) are included in these totals. * Excluding subtribe Gonolobinae

	Approximate number of species in the taxon	Number of species for which data are available	% sample of species
Periploceae	180	6	3.3
Secamoneae	100	2	2.0
Fockeeae	10	0	0.0
Marsdenieae	500	10	2.0
Stapeliaceae	650	57	8.8
Asclepiadeae*	900	65	7.2
Gonolobinae	250	10	4.0
Totals	2590	150	5.8

within the family are currently subject to some disagreement, but our data probably represent about 18% of accepted genera. We possess data for five of the six tribes; no data were available for Fockeeae, the smallest tribe.

The number of species in a tribe (including subtribe Gonolobinae—see below) for which pollination data were available was closely correlated with the total number of species in that tribe (Pearson's Correlation = 0.92; $df=6$; $P=0.04$), probably reflecting the rather haphazard way in which asclepiad pollination research has been conducted (i.e. larger tribes have a greater probability of having their species studied). For most species the only data available are from single populations over a restricted period. Since geographical and temporal variation in the identity of pollinators is a feature of many plant species (see references in Ollerton, 1996) the range of pollinators is probably wider than those so far recorded. This, together with the small sample sizes available for all tribes, means that our conclusions regarding the range of pollination systems within the family must necessarily be tentative.

The veracity of our initial conclusions regarding the diversity of pollination systems in the Asclepiadaceae is also dependent on data quality. Thus, a proportion of species for which we had data could not be used because the observations were made outside of the normal range of the plants or pollinators (see Methods). However, much useful information can be gleaned from these studies. As a general rule, the same orders of insects visit asclepiads inside and outside their native ranges. For example, *Asclepias curassavica* is pollinated mainly by butterflies (Lepidoptera) in Central America and the Caribbean, where it is native, and in India where it is introduced (Chaturvedi & Pant, 1986). Similarly, *Vincetoxicum hirundinaria* is pollinated in Europe mainly by Diptera, as is *V. nigrum*, a closely related introduction to North America (Lumer & Yost, 1995). The most striking examples of this, probably because of the narrowness of the pollinator spectrum (see later discussion), belong to the succulent stapeliads (*sensu* Meve & Liede, 1994): species of *Huerniopsis*, *Orbeopsis* and *Stapelia* are pollinated by the same families (occasionally the same genera) of Diptera in European glass-houses and in their native Africa (reviewed by Meve & Liede, 1994). Thus, data on pollinators of species outside of their natural range can sometimes reinforce natural observations.

Another variable of data quality concerns the type of observation—was it purely a visitation (code 3), or were the visitors seen to pick up or have attached (code 2)

TABLE 2. Summary of the quality of information on asclepiad pollinators for the six tribes plus one subtribe of the Asclepiadaceae. Figures are numbers of records of pollinators in the ASCLEPOL database. Refer to Methods for details of the coding system.

Code:	Peri	Seca	Fock	Mars	Stap	Ascl	Gono
1	3	0	0	2	0	11	0
2	2	0	0	64	37	545	13
3	3	2	0	0	21	120	1
B	5	0	0	2	35	51	12

Abbreviations are: Peri = Periploceae; Seca = Secamoneae; Fock = Fockeeae; Mars = Marsdeniae; Stap = Stapeliaceae; Ascl = Asclepiadeae (excluding Gonolobinae); Gono = Gonolobinae.

TABLE 3. Geographic ranges of the studies of asclepiad pollination included in the ASCLEPOL database, excluding those of plants outside their natural ranges. Figures refer to numbers of studies

Africa + Madagascar + Aldabra	43
Middle East + Israel + Pakistan	9
India + Indonesia	29
Australia	5
South and Central America + Caribbean	9
U.S.A. + Mexico	28
Europe + Russia	4

or deposited (code 1) pollinia? Most observations were of code 2, fewer were of code 1 (Table 2). This is not surprising as observing the act of pollination is more difficult than simply catching visitors and looking for attached pollinia. It is pleasing to see the rather small numbers of code 3 observations—the dangers of assuming that all floral visitors are legitimate pollinators are well known.

Visitors that can extract and carry pollinia may also be able to deposit them, and hence pollinate the plant. Thus, we have only used records of code 1 or 2 for all subsequent analyses, except where otherwise stated. It follows that in the rest of this account the term ‘pollinator’ refers to any record coded 1 or 2.

Classifying a plant’s pollination system simply on the basis of which taxa are the apparent pollinators may be misleading, as it takes no account of the relative effectiveness of those pollinators. For example, *Asclepias tuberosa* is visited by a wider range of butterfly than bee species (Fishbein & Venable, 1996). However, *Bombus sonorus* (Hymenoptera: Apidae) was the most effective pollinator because of its high frequency of visitation and efficiency of pollinia transfer. This kind of in-depth data is available for few asclepiad species and thus cannot be factored into the preliminary conclusions presented here.

An interesting conservation spin-off from the data-set concerns the activities of honeybees (*Apis mellifera*) outside of their natural range. Of the investigations of asclepiad pollination conducted beyond the natural range of honeybees which identified visitors to species level (excluding the apparently exclusively fly-pollinated stapeliads and ceropegiads—see later section), some 40% (29 of 73) recorded pollinia transfer by *A. mellifera*. This as an indicator of the ubiquity of this import, and of its important role in the pollination of plants beyond its usual range. The possible dangers of honeybees to native pollinators and their plants have been highlighted in the past (Roubik, 1978; Paton, 1993; Liede, 1994a).

The geographical range of the data is rather imbalanced (Table 3). It reflects the

working ranges of asclepiad students more than the numbers of species in various areas (compare with family distribution data in Good, 1952). U.S.A. + Mexico, India + Indonesia and Africa + Madagascar + Aldabra have the greatest concentration of studies, due respectively to work on *Asclepias*, *Calotropis* and the stapeliads. South and Central America represents a significant gap, with few studies from this asclepiad-rich area. Europe possesses only 15 species of Asclepiadaceae, but it is surprising that so little should be known about their pollinators; they have not caught the imagination of European ecologists in quite the same way as *Asclepias* has that of the ecologists of North America.

The pollinators of the Asclepiadaceae

From available information, asclepiads are pollinated exclusively by insects belonging to six orders (Fig. 1). There are, however, a number of records of birds visiting asclepiad flowers (e.g. Woodell, 1979; P.I. Forster, pers. comm.) though their role as pollinators must remain doubtful. Pollination by Hymenoptera is most common, with Lepidoptera and Diptera having a secondary, but still important, role. The remaining three orders are probably of minor importance: none of the records are observations of pollinium insertion (i.e. code 1). Coleoptera may be the principal pollinators of some species, but Hemiptera (sap feeders and predators) and Neuroptera (predators) are unlikely major pollinators of any species.

Hymenoptera, Lepidoptera and Diptera are the primary pollinators of the angiosperms as a whole, so it is not surprising that they should dominate asclepiad reproduction. This overview of the relative importance of these orders, however, masks a great deal of variation within and between tribes. In the remainder of this paper we will concentrate on pollination at and below the tribal level. A recent review of the subtribal classification of the tribe Asclepiadeae by the second author (Liede, 1997) has led to the tribe Gonolobeae being subsumed as subtribe Gonolobinae (see Appendix). However, the Gonolobinae is so distinctive within the Asclepiadeae that we have opted to discuss it separately from the rest of the Asclepiadeae.

Only Lepidoptera (hawkmoths) and Diptera are recorded as legitimate pollinators in the Periploceae (Fig. 1), but this is based on scant information and the actual range of pollinators may be much broader. For example *Polistes* wasps are known to visit *Periploca aphylla* in Oman, but they have never been observed carrying translators (Bert Jonkers, pers. comm.). Diptera pollination is probably the norm in some other *Periploca* species, judging by the botanic gardens observations of Schick (1982). These fly pollinated species would fit into the 'open-access fly pollination' system described in Concluding remarks, below.

There are frustratingly few records of flower visitors to Secamoneae. Beetle visitation, though not pollinia transfer, to *Secamone fryeri* has been recorded by Woodell (1979). What appeared to be dipteran flies have been observed, from a distance, landing on flowers of the Australian species *Secamone elliptica* and in Gabon, a small hymenopteran was seen visiting flowers of *Toxocarpus letouzeanus* (Ollerton, pers. obs.) but no specimens could be captured in either case. Further field work is urgently required for the Secamoneae.

We could find no records of pollination in the Fockeeae, either under natural circumstances or in cultivation. Judging from its dark purple-spotted flowers, *Cibirhiza*

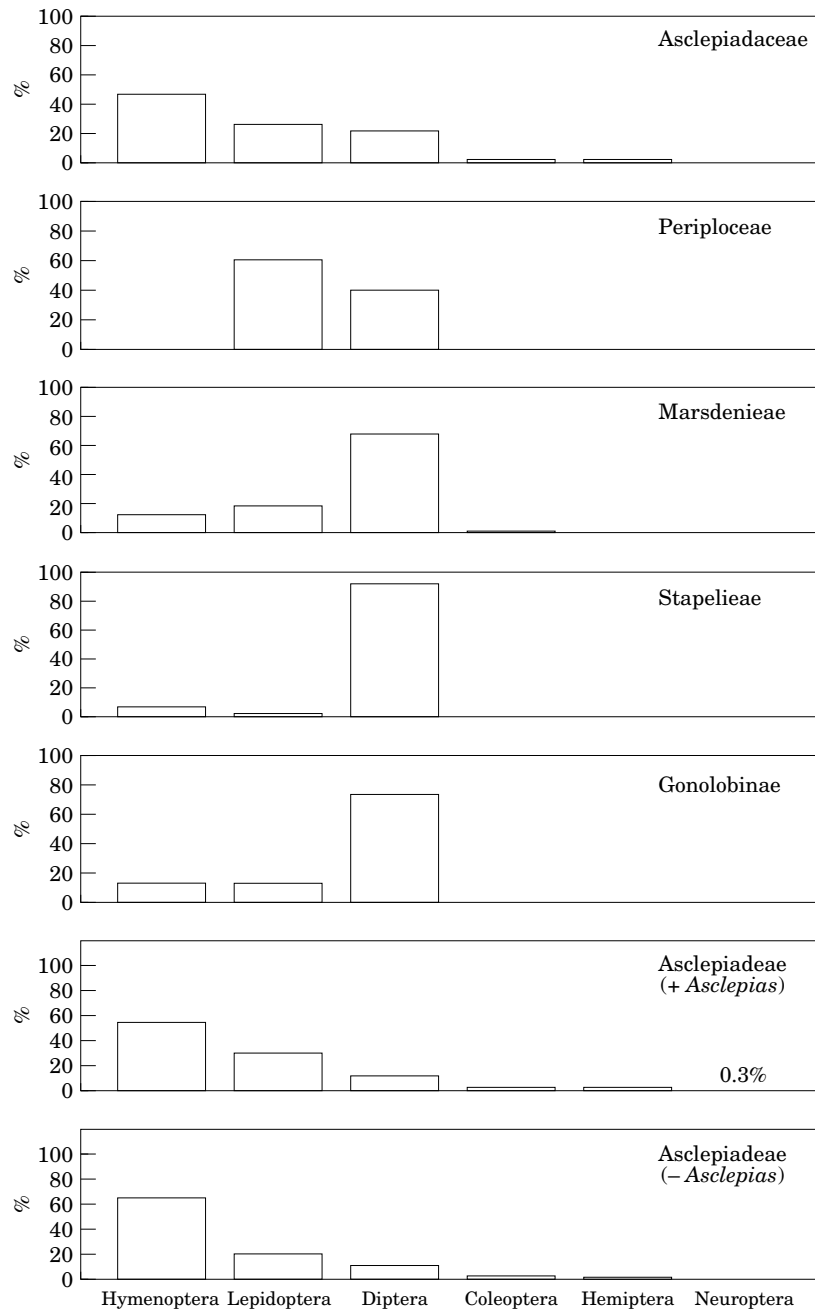


Figure 1. Frequency of pollination records for different insect orders; each record represents 1 species of insect from that order that has been recorded as inserting pollinia or with pollinia attached under natural circumstances (i.e. code 1 or 2). Duplicated records involving the same insect on the same species of asclepiad in a different study have been scored only once. Data are presented for the Asclepiadaceae as a whole and for individual tribes plus one subtribe. Neuroptera were rarely recorded, and therefore do not clearly register on the graph; the actual frequency is shown. Sample sizes (number of records) are: Asclepiadaceae=895; Periploceae=5; Marsdenieae=76; Stapelieae=43; Gonolobinae=16; Asclepiadeae (+ *Asclepias*)=755; Asclepiadeae (- *Asclepias*)=161. Data for Asclepiadeae do not include Gonolobinae.

may fit the 'open access fly pollination' system (see Concluding remarks, below) but we have no information for the only other genus, *Fockea*. Once again, field studies for this group are a priority.

Open access fly pollination predominates in the Marsdenieae, with a lesser contribution of Hymenoptera, Lepidoptera and Coleoptera (Fig. 1). Moth pollination may also be common in the tribe: *Telosma pallida* appears to be pollinated only by noctuid moths, whilst the evening emission of scent in *Hoya carmosa* and *Stephanotis floribunda* (Matile & Altenburger, 1989) strongly implicates nocturnal insects as pollinators. The white, tubular flowers of *S. floribunda* certainly correspond to the classic idea of a moth-pollinated plant (Faegri & van der Pijl, 1966).

The Stapelieae can be naturally divided into three groups. Stapeliads (*sensu* Meve & Liedt, 1994) are all succulent-stemmed taxa, many of which have foul-smelling 'carrion' flowers. Ceropegiads (*Ceropegia*, *Brachystelma* and allies) are (sometimes succulent) climbers and scramblers, and tuberous geophytes. The remaining genera constitute a rag-bag of shrubs, climbers and scramblers which, in contrast to the previous two groups, are not close phylogenetically. Indeed, some species in the latter group appear more closely related to the marsdeniads than to the stapeliads or ceropegiads (Ulrich Meve, pers. comm.).

These divisions are reflected to some extent by pollination systems in the groups. Stapeliads are almost exclusively Diptera-pollinated (recently reviewed by Meve & Liedt, 1994). Many fit the classic carrion fly pollination system, though a range of floral colours and odours exists in the group, not only those associated with carrion mimicry. This, plus records such as Coleoptera visiting *Caralluma flava* (Jonkers, 1990) and moths visiting *Huerniopsis atosanguinea* (Plowes, 1989) suggests a wider range of actual pollinators. Ceropegiads appear to be exclusively fly-pollinated, based on information for a few species of *Ceropegia* and cultivated *Brachystelma*. Fly pollination in *Ceropegia* represents a system distinct from that of the stapeliads and *Brachystelma*; very small Diptera (typically less than 3 mm in length; Ollerton, unpublished) are attracted into the ceropegiad trap flowers by floral scents emitted from more or less elaborate osmophores (Vogel, 1990a). The flies are retained until pollination and/or pollinium removal has occurred. Though this system is clearly different from that of the stapeliad flower mimicking decaying matter, there are obvious links between the two, particularly with respect to the range of floral colours (often garish reds, yellows and purples or sombre browns and blacks) and the fruity scents produced by some species. Also, although *Brachystelma* is apparently phylogenetically close to *Ceropegia*, many species possess traits of a decay-attraction fly pollination system. Little is known of pollinator relationships within the final group of the Stapelieae. The only data are for *Leptadenia reticulata*, which seems to be mainly bee pollinated (Pant *et al.*, 1982) and *Orphanthera albida*, which is apparently moth pollinated (Nel, 1995).

We have the most data for Asclepiadeae, principally because of the observations accumulated over the past 100 years for *Asclepias* in North America (see Wyatt & Broyles, 1994) though with significant contributions from other Old World genera, especially *Calotropis* (e.g. Ramakrishna & Arekal, 1979). The tribe is pollinated mainly by Hymenoptera, with strong Lepidoptera and lesser Diptera components (Fig. 1). Fly pollination is relatively unimportant in the Asclepiadeae as a whole, but is characteristic of at least some groups (see below). There is a danger that over-dependence on information about *Asclepias* may bias our conclusions about the Asclepiadeae as a whole. However, the pollinator spectra for Asclepiadeae with and

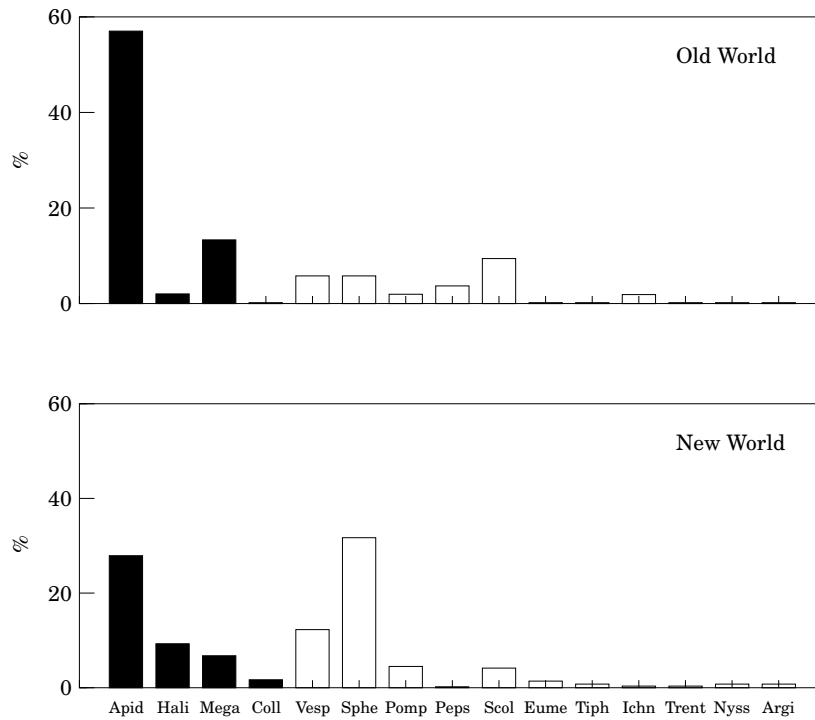


Figure 2. Hymenoptera pollination records for the tribe Asclepiadeae, subdivided between Old World and New World. Abbreviations refer to the following families, respectively: Apidae, Halictidae, Megachilidae, Colletidae, Vespidae, Sphecidae, Pompilidae, Pepsidae, Scolidae, Eumenidae, Tiphidae, Ichneumonidae, Tenthredinidae, Nyssonidae, Argidae. The filled bars indicate families of bees. Sample sizes (number of records) are 337 for the New World and 53 for the Old World.

without the inclusion of the *Asclepias* data (Fig. 1) do not significantly differ ($G = 6.40$; $df = 4$; $P > 0.05$ —calculated excluding Neuroptera which is only recorded from *Asclepias*).

Pollination by bees (Apidae + Halictidae + Megachilidae + Colletidae) dominates Old World Asclepiadeae (Fig. 2). Bees are also the primary New World pollinators, but ‘wasp’ (Vespidae + Sphecidae + Pompilidae + Pepsidae + Scolidae + Eumenidae) pollination is also important. These differences are statistically significant ($G_{adj} = 13.02$; $df = 1$; $P < 0.001$). Thus, there is an apparent New World/Old World division here. A difference between Old and New Worlds in the proportion of Lepidoptera pollinators is also noticeable. Pollination by butterflies (Danaidae + Nymphalidae + Heliconidae + Pieridae + Papilionidae + Satyridae + Lycaenidae + Libytheidae + Hesperidae) is almost exclusively a New World phenomenon, whereas moth (Noctuidae + Spingidae + Ctenuchidae + Arctidae + Crambidae + Lymantridae + Pyraustidae + Geometridae) pollination is shared between Old and New Worlds (Fig. 3). These differences are again highly statistically significant ($G_{adj} = 57.76$; $df = 1$; $P < 0.001$). A lack of bee pollinators in the New World does not seem to explain this pattern—bee diversity is quite similar in New and Old Worlds (Michener, 1979). Differences in the relative diversities of these wasp and butterfly families may possibly account for the New World/Old World disparity

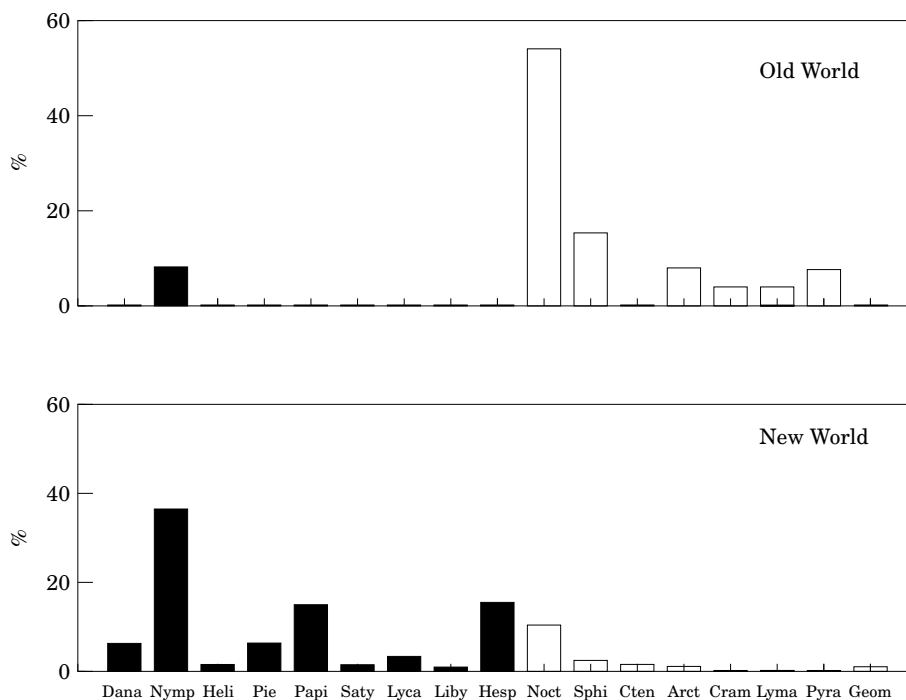


Figure 3. Lepidoptera pollination records for the tribe Asclepiadeae, subdivided between Old World and New World. Abbreviations refer to the following families, respectively: Heliconidae, Pieridae, Papilionidae, Satyridae, Lycaenidae, Hesperidae, Noctuidae, Spingidae, Ctenuchidae, Arctidae, Crambidae, Lymantridae, Pyraustidae, Geometridae. The filled bars indicate families of butterflies. Sample sizes (number of records) are 171 for the New World and 26 for the Old World.

and this deserves closer study. If these trends are real, and not an artefact of biased and small sample sizes, New World Asclepiadeae appear to have a much more diverse range of pollinators than Old World species.

The subtribe Gonolobinae of the Asclepiadeae is distinct in that it is predominantly Diptera pollinated (Fig. 1), fitting the 'open access fly pollination' system described in Concluding remarks. This is based on records for species of *Gonolobus* and *Matelea* (Drapalik, 1969). The only other information available for this subtribe is for *Fischeria funebris* which is pollinated by bees and butterflies in Costa Rica (Skutch, 1988). Open access fly pollination also occurs in *Vincetoxicum* (subtribe Astephaninae) and there may be scattered occurrences in other subtribes, e.g. *Tweedia* (Oxypetalinae) and *Pentarrhinum* (Metastelminae), though the data are far from definitive.

The significance of fly pollination

Pollination by Diptera features in all tribes for which pollinator data are available, although the relative importance varies between tribes (Fig. 1). The tribes Marsdenieae and Stapelieae and the subtribe Gonolobinae (Asclepiadeae) are the most prominently Diptera-served groups. Fourteen dipteran families are recorded as pollinators of asclepiads, with the seven commonest families being recorded from

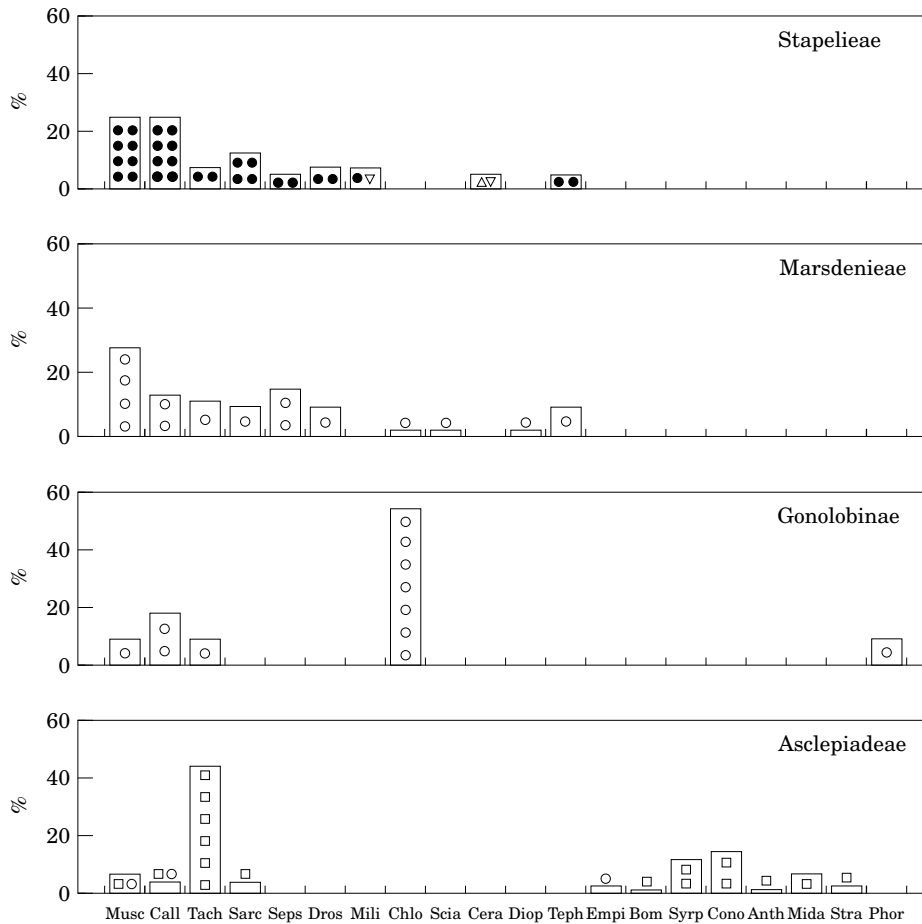


Figure 4. Diptera families recorded as pollinators for the tribes Stapelieae, Marsdenieae and Asclepiadeae and the subtribe Gonolobinae. Abbreviations refer to the following families, respectively: Muscidae, Calliphoridae, Tachinidae, Sarcophagidae, Sepsidae, Drosophilidae, Milichidae, Chloropidae, Sciaridae, Ceratopogonidae, Diopsidae, Tephritidae, Empidae, Bombyliidae, Syrphidae, Conopidae, Anthomyiidae, Midasidae, Stratiomyidae, Phoridae. Distinct pollination systems (see Concluding remarks) and the families associated with them are indicated as follows: (●) decay-attraction; (▽) trap-flower; (○) open-access; (□) generalized insect. Sample sizes (number of records) are: Stapelieae = 40; Marsdenieae = 54; Asclepiadeae = 75; Gonolobinae = 11.

at least two asclepiad tribes (Fig. 4). There appears to be little specialization on particular dipteran families and a similar range of families is exploited by Marsdenieae and Stapelieae in particular. It is interesting to note that there are few records of pollination by specialized flower-visiting flies (e.g. Syrphidae and Bombyliidae). They are occasional pollinators of *Asclepias* in North America whilst Syrphidae visit *Gomphocarpus* sp. in Britain (Ollerton, pers. obs.) and *Cynanchum acutum* (Volovnik, 1982) but are not strong enough to remove pollinia.

It is unusual to encounter such a large family in which pollination by flies is so important (though see the survey of fly pollination in the Orchidaceae presented by Christensen, 1994). Most Diptera are usually considered to be inefficient pollinators

relative to the bees, for instance, on account of the small amounts of pollen they transfer and their apparent lack of floral constancy (Proctor, Yeo & Lack, 1996). From a phylogenetic perspective, it is interesting to note that fly pollination does occur within the putative sister group of the Asclepiadaceae, tribe Apocynae of the Apocynaceae; pollination of *Apocynum* by flies has been reported and some species are apparently foul smelling (references in Scotti, 1911; Schick, 1982). It is presently impossible to say how common fly pollination is within this tribe, or indeed the Apocynaceae as a whole; data on the pollinators of this family are not as abundant as for the Asclepiadaceae. The basal-most asclepiad tribe (Periploceae) contains at least one genus (*Periploca*) which has some fly pollinated species, though other genera are, for example, moth pollinated (e.g. *Cryptostegia*; Walther, 1994). This pattern of a mixture of strictly fly pollinated and non-fly pollinated species occurring within the same clade recurs throughout the family. In some tribes the fly-pollinated taxa are in a minority, e.g. in Asclepiadeae; in other tribes they are in the majority, i.e. Stapelieae. The ceropegiads and stapeliads in the latter tribe are closely related and almost certainly comprise a monophyletic group; it is likely that fly pollination has arisen only once and persisted throughout the clade. The exact relationships between the fly-pollinated genera in the other tribes are not known for certain: *Gonolobus* and *Matelea* (Gonolobeae) are certainly very close and may be sister taxa, whilst Forster (1995) considers *Marsdenia* and *Gymnema* (Marsdenieae) to be synonymous. If fly pollinated genera within tribes are closely related, it suggests that this pollination system has a single origin in these tribes. This in turn begs questions about the evolution of fly pollination in the family as a whole—is it a primitive feature (derived from an apocynaceous ancestor?) which has persisted throughout the family, in which case the bee, butterfly and moth pollination of other genera are derived systems? Or does it have multiple origins, with parallel evolution between tribes? Our current feeling is that both of these ideas may be correct—fly pollination is primitive within the Asclepiadaceae, but has been subsequently lost and regained a number of times throughout the family. If true, this implies that asclepiads possess a suite of floral traits (colour, odour, ornamentation, nectar characteristics, etc.) which pre-adapts them to pollination by Dipteran flies. In order to address some of these issues, our future work on pollination in the Asclepiadaceae will address the evolution of pollination systems in more explicitly phylogenetic terms.

Specialization and generalization in the family

The degree of pollinator specificity exhibited by a plant species is determined by its morphological and ecological specialization and the taxonomic breadth of the potential pollinators within its community. In the angiosperms this ranges from plants that use both vertebrate and invertebrate vectors through to obligate mutualisms such as *Ficus* (Moraceae) and agaonid wasps, or *Yucca* (Agavaceae) and *Tegeticula* moths. Highly specialized systems are rare and more generalized relationships are common (Waser *et al.*, 1996). One measure of the specialization of a plant family is the frequency distribution of the numbers of recorded pollinators per species in that family. In common with the few other families for which this analysis has been attempted (Ranunculaceae, Polemoniaceae, Orchidaceae; Waser *et al.*, 1996) the distribution is strongly right-skewed, with most Asclepiadaceae having between 1

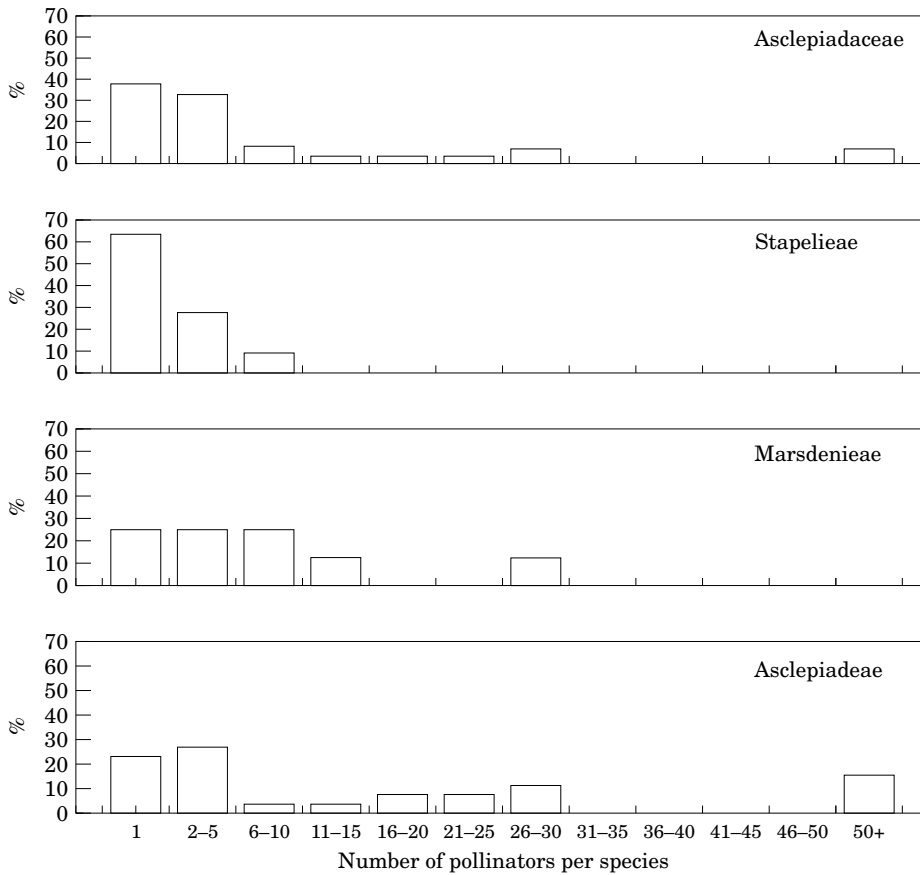


Figure 5. Frequency distributions of numbers of recorded pollinators of species of Asclepiadaceae. Data are presented individually for three tribes and combined for the Asclepiadaceae as a whole. Records of single pollinators are presented separately as this class of plant–pollinator relationship is the most specialized and of particular interest. Sample sizes are: Asclepiadaceae = 32 species; Marsdenieae = 8 species; Stapelieae = 21 species; Asclepiadeae = 66 species.

and 5 pollinators (Fig. 5). The record for number of pollinators goes to *Asclepias verticillata* with an amazing 126 recorded pollen vectors. The median (mean) number of pollinators is 3.0 (11.8) which is rather lower than the 7.9 (8.0) calculated for the Orchidaceae (Waser *et al.*, 1996). However the orchid data comprised total visiting species whereas our asclepiad data are restricted to proven or likely pollinators (codes 1 and 2). A more extensive compilation of orchid pollinator data by Tremblay (1992), using quality criteria similar to ours, revealed a mean number of pollinators of 3.4 (no median was given). Thus the Orchidaceae seems to show a greater degree of pollinator specialization than the Asclepiadaceae.

Dividing the frequency distribution data between the component tribes reveals differences in specialization among tribes (Fig. 5). There are sufficient suitable pollination records for only three tribes. Stapelieae is significantly more specialized than Marsdenieae (Mann–Whitney $U=37.0$; $n=21,8$; $P<0.05$) and Asclepiadeae (Mann–Whitney $U=91.5$; $n=21,32$; $P<0.05$) and the tribes Asclepiadeae and

Marsdenieae show similar levels of specialization (Mann–Whitney $U=109$; $n=32$, 8; $P>0.05$).

Stapelieae may be the most specialized tribe in terms of numbers of pollinating insect species, but the among-species taxonomic diversity of pollinators is low for stapeliads. Of the 12 species of stapeliad pollinated by identified genera, 10 are visited by *Musca domestica* or species of *Sarcophaga* and *Calliphora*. The ubiquity of *M. domestica* must be due to its now pan-global distribution as a result of human movement and activities. The low diversity and high specialization of pollinators may be a result of low insect diversity in the semi-arid habitats in which stapeliads grow (e.g. Cox, 1991).

Concluding remarks

In the Asclepiadaceae, at least eight pollination systems can be identified, utilizing distinct pollen vectors and with more or less specialized floral attributes. The systems are currently defined mainly by the major pollinators, rather than by reference to any pseudo-predictive ‘syndrome’ concept (*sensu* van der Pijl, 1961). These systems, together with examples of genera which contain representative species, are listed below:

- (1) Generalized insect: e.g. *Asclepias*.
- (2) Large Hymenoptera: e.g. *Asclepias*, *Calotropis*, *Gomphocarpus*.
- (3) Wasp pollination: e.g. *Cynanchum*, *Morrenia*.
- (4) Butterfly: e.g. *Asclepias*.
- (5) Night-flying moths: e.g. *Telosma*, *Cryptostegia*.
- (6) Open-access fly pollination: e.g. *Marsdenia*, *Matelea*, *Gonolobus*, *Vincetoxicum*.
- (7) Decay–attraction fly pollination: e.g. *Stapelia*, *Caralluma*.
- (8) Trap–flower fly pollination: e.g. *Ceropegia*.

Some of these categories will need to be sub-divided as more data accumulate; for example, ‘decay–attraction fly pollination’ includes the carrion-mimicking species as well as plants which produce odours reminiscent of rotting fruit or ‘sour beer’ (Agnew, 1976) and which are visited mainly by fruit flies (Meve & Liedtke, 1994). As research progresses we anticipate that other systems will come to light, particularly specialized beetle pollination.

The Asclepiadaceae possesses a diversity of pollination systems, in common with other angiosperm families that have been studied in any depth, for example: Arecaceae (Silberbauer-Gottsberger, 1980; Henderson, 1986), Epacridaceae (Keighery, 1996), Lamiaceae (Huck, 1992), Melastomataceae (Renner, 1989), Onagraceae (Raven, 1979), Orchidaceae (van der Pijl & Dodson, 1966; Dafni & Bernhardt, 1990; Adams & Lawson, 1993), Pandanaceae (Cox, 1990), Polemoniaceae (Grant & Grant, 1965) and Scrophulariaceae (Kampny, 1995). Most of these families utilize a diverse array of pollinators, with specialization on particular pollinators occurring principally at the level of genus and below. Exceptions to this pattern include the exclusively bee pollinated families Malpighiaceae (Vogel, 1990b) and Memecylaceae (Renner, 1989). However, the latter family is very small and coherent, containing few genera. Further detailed family-level studies of the kind presented here are required to determine the commonness of this pattern and we would urge any

workers planning to survey the pollination systems of specific families to take a more quantitative approach than has sometimes been used in previous studies.

ACKNOWLEDGEMENTS

Thanks to Paul Forster (Queensland Herbarium) for his input during the early stages of this work. For permission to use unpublished data we are grateful to: Dr Ulrich Meve (Münster), Dr Doug Yanega (Illinois Natural History Survey), Prof. L. T. Wasserthal and Dr Regina Walther (Erlangen), Dr Bert Jonkers (British Antarctic Survey) and Dr Mark Fishbein (University of Arizona). Dr Colin C. Walker (Open University), Phil Clark (International Asclepiad Society), Paul Forster and Prof. G. Gottsberger (University of Ulm) helped with obscure published sources. Constructive comments on the work and the manuscript were made by Dr Ulrich Meve, Dr Bert Jonkers, Dr Tim Shreeve (Oxford Brookes University), Prof. Nick Waser (University of California, Riverside), Dr Andrew Lack (Oxford Brookes University), Prof. Scott Armbruster (Norwegian University of Science and Technology), Dr Susan Kephart (Willamette University), Dr Laure Civeyrel (University of Montpellier II) and an anonymous referee.

Note: Through its journal *Asklepios*, The International Asclepiad Society exists to promote scientific and popular interest in the family Asclepiadaceae. It can be contacted via: The Secretary, 2 Keymer Court, Burgess Hill, West Sussex, RH15 0AA.

REFERENCES

- Adams PB, Lawson SD. 1993.** Pollination in Australian orchids: a critical assessment of the literature 1882–1992. *Australian Journal of Botany* **41**: 553–575.
- Agnew JD. 1976.** A case of myophily involving Drosophilidae (Diptera). *Journal of South African Botany* **42**: 85–95.
- Armstrong JA. 1979.** Biotic pollination mechanisms in Australian flora – a review. *New Zealand Journal of Botany* **17**: 467–508.
- Bawa SK. 1990.** Plant–pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* **21**: 399–422.
- Bernhardt P, Thien LB. 1987.** Self–isolation and insect pollination in the primitive angiosperms: New evaluations of older hypotheses. *Plant Systematics and Evolution* **156**: 159–176.
- Bruyns PV, Forster PI. 1991.** Recircumscription of the Stapelieae (Asclepiadaceae). *Taxon* **40**: 381–391.
- Chaturvedi SK, Pant DD. 1986.** Further studies in the pollination of some Indian asclepiads. *Bulletin of the Botanical Survey of India* **28**: 23–30.
- Christensen DE. 1994.** Fly pollination in the Orchidaceae. In: Arditti J, ed. *Orchid biology: Reviews and perspectives VI*. London: John Wiley & Sons, 415–454.
- Cox PA. 1990.** Pollination and the evolution of breeding systems in Pandanaceae. *Annals of the Missouri Botanical Garden* **77**: 816–840.
- Cox PA. 1991.** Abiotic pollination: An evolutionary escape for animal–pollinated angiosperms. *Philosophical Transactions of the Royal Society of London, B* **333**: 217–224.
- Dafni A. 1984.** Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* **15**: 259–278.
- Dafni A, Bernhardt P. 1990.** Pollination of terrestrial orchids of Southern Australia and the Mediterranean region, systematic, ecological and evolutionary implications. *Evolutionary Biology* **24**: 193–252.

- Darwin C. 1862.** *The various contrivances by which orchids are fertilized by insects.* London: Murray.
- Darwin C. 1880.** *The different forms of flowers on plants of the same species.* London: Murray.
- Drapalik DJ. 1969.** A biosystematic study of the genus *Matelea* in the southeastern United States. Unpublished Ph.D. Thesis, University of North Carolina at Chapel Hill.
- Endress PK. 1994.** Diversity and evolutionary biology of tropical flowers. Cambridge: Cambridge University Press.
- Faegri K. & van der Pijl L. 1966.** *The principles of pollination ecology.* Pergamon: Oxford.
- Feinsinger P. 1987.** Approaches to nectarivore–plant interactions in the New World. *Revista Chilena Historia Natural* **60**: 285–319.
- Fishbein M, Venable DL. 1996.** Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* **77**: 1061–1073.
- Forster PI. 1995.** Circumscription of *Marsdenia* (Asclepiadaceae, Marsdenieae), with a revision of the genus in Australia and Papuaia. *Australian Systematic Botany* **8**: 703–933.
- Gentry AH. 1991.** Breeding and dispersal systems of lianas. In: Putz FE, Mooney MA, eds. *The biology of vines.* Cambridge: Cambridge University Press, 393–423.
- Good R. 1952.** An atlas of the Asclepiadaceae. *New Phytologist* **51**: 198–209.
- Gottsberger G. 1988.** The reproductive biology of primitive angiosperms. *Taxon* **37**: 630–643.
- Grant V, Grant KA. 1965.** *Flower pollination in the phlox family.* New York: Columbia University Press.
- Henderson A. 1986.** A review of pollination studies in the Palmae. *The Botanical Review* **52**: 221–259.
- Huck RB. 1992.** Overview of pollination biology in the Lamiaceae. In: Harley RM, Reynolds T, eds. *Advances in labiate science.* Kew: Royal Botanic Gardens, 167–181.
- Jonkers B. 1990.** *Cavallumas* – gems of the mountainside. *Petroleum Development Oman News* **2**: 7–11.
- Judd WS, Sanders RW, Donoghue MJ. 1994.** Angiosperm family pairs: Preliminary phylogenetic analysis. *Harvard Papers in Botany* **5**: 1–51.
- Kampny CM. 1995.** Pollination and flower diversity in Scrophulariaceae. *Botanical Review* **61**: 350–366.
- Keighery GJ. 1996.** Phytogeography, biology and conservation of Western Australian Epacridaceae. *Annals of Botany* **77**: 347–355.
- Kunze H. 1991.** Structure and function in asclepiad pollination. *Plant Systematics and Evolution* **176**: 227–253.
- Kunze H. 1995.** Bau und Funktion der Asclepiadaceenblüte. *Phyton (Austria)* **35**: 1–24.
- Kunze H, Meve U, Liede S. 1994.** *Cibirhiza albersiana*, a new species of Asclepiadaceae, and establishment of the tribe Fockeeae. *Taxon* **43**: 367–376.
- Liede S. 1994a.** Some observations on pollination in Mexican Asclepiadaceae. *Madroño* **41**: 266–276.
- Liede S. 1994b.** Myth and reality of the subtribe Astephaninae (Decne.) Schumann (Asclepiadaceae). *Botanical Journal of the Linnean Society* **114**: 81–98.
- Liede S. 1996.** Anther differentiation in the Asclepiadaceae–Asclepiadeae: form and function. In: D'Arcy WG, Keating RC. eds. *The anther: form, function and phylogeny.* Cambridge: Cambridge University Press, 221–235.
- Liede S. 1997.** Subtribes and genera of the Asclepiadeae (Apocynaceae, Asclepiadoideae) – A synopsis. *Taxon* **46**: 233–247.
- Liede S, Albers F. 1994.** Tribal disposition of genera in the Asclepiadaceae. *Taxon* **43**: 201–231.
- Lumer C, Yost SE. 1995.** The reproductive biology of *Vincetoxicum nigrum* (L.) Moench (Asclepiadaceae), a Mediterranean weed in New York State. *Bulletin of the Torrey Botanical Club* **122**: 12–23.
- Matile P, Altenburger R. 1989.** Floral fragrance and its rhythmic emission in *Hoya carcosa* and *Stephanotis floribunda*. *Asklepios* **47**: 8–12.
- Meve U, Liede S. 1994.** Floral biology and pollination in stapeliads – New results and a literature review. *Plant Systematics and Evolution* **192**: 99–116.
- Michener CD. 1979.** Biogeography of the bees. *Annals of the Missouri Botanic Garden* **66**: 277–347.
- Müller H. 1883.** *The fertilisation of flowers.* London.
- Nel M. 1995.** Rare and interesting plants of the Namib desert, part 2: three desert plants. *Veld & Flora* **81**: 14–15.
- Nilsson S, Endress ME, Grafström E. 1993.** On the relationships of the Apocynaceae and Periplocaceae. *Grana, Suppl.* **2**: 3–20.
- Ollerton J. 1996.** Reconciling ecological processes with phylogenetic patterns: The apparent paradox of plant–pollinator systems. *Journal of Ecology* **84**: 767–769.
- Pant DD, Nautiyal DD, Chaturvedi SK. 1982.** Pollination ecology of some Indian asclepiads. *Phytomorphology* **32**: 302–313.
- Paton DC. 1993.** Honeybees in the Australian environment. *BioScience* **43**: 95–103.

- van der Pijl L.** 1961. Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution* **15**: 44–59.
- van der Pijl L, Dodson CH.** 1966. *Orchid flowers – their pollination and evolution*. Florida: University of Miami Press.
- Plowes DHC.** 1989. Succulents in Botswana. *Excelsa* **14**: 85–89.
- Prance GT.** 1985. The pollination of Amazonian plants. In: Prance GT, Lovejoy TE, eds. *Key environments: Amazonia*. Oxford: Pergamon Press, 166–191.
- Proctor M, Yeo P, Lack A.** 1996. *The natural history of pollination*. London: HarperCollins.
- Ramakrishna TM, Arekal GD.** 1979. Pollination biology of *Calotropis gigantea* (L.) R.Br. *Current Science* **48**: 212–213.
- Raven PH.** 1979. A survey of reproductive biology in Onagraceae. *New Zealand Journal of Botany* **17**: 575–593.
- Renner SS.** 1989. A survey of reproductive biology in neotropical Melastomataceae and Mimosaceae. *Annals of the Missouri Botanic Garden* **76**: 496–518.
- Renner SS, Feil JP.** 1993. Pollinators of tropical dioecious angiosperms. *American Journal Botany* **80**: 1100–1107.
- Roubik DW.** 1978. Competitive interactions between neotropical pollinators and Africanised honey bees. *Science* **201**: 1030–1032.
- Schick B.** 1982. Zur Morphologie, Entwicklung, Feinstruktur und Funktion des Translocators von *Periploca* L. (Asclepiadaceae). *Tropische und Subtropische Pflanzenwelt* **40**: 513–553.
- Scotti L.** 1911. Contribuzioni all biologia florale delle ‘Contortae’. *Annali di Botanica (Roma)* **9**: 199–314.
- Sennblad B, Bremer B.** 1996. The familial and subfamilial relationships of Apocynaceae and Asclepiadaceae evaluated with *rbcL* data. *Plant Systematics and Evolution* **202**: 153–175.
- Silberbauer-Gottsberger I.** 1980. Pollination and evolution in palms. *Phyton (Austria)* **30**: 213–234.
- Skutch AF.** 1988. Flowering and seed-production of *Fischeria funebris* (Asclepiadaceae). *Brenesia* **30**: 13–17.
- Sprengel CK.** 1793. *Das entdeckte Geheimnis der Natur im Bau in der Befruchtung der Blumen. [The secret of nature in the form and fertilisation of flowers discovered]*. Berlin: F. Vieweg.
- Sundell E.** 1980. The subfamilial, tribal and subtribal nomenclature of the Asclepiadaceae. *Taxon* **29**: 257–265.
- Swarupanandan K, Mangaly JK, Sonny TK, Kishorekumar K, Basha SC.** 1996. The subfamilial and tribal classification of the family Asclepiadaceae. *Botanical Journal of the Linnean Society* **120**: 327–369.
- Thorne RF.** 1992. Classification and geography of the flowering plants. *Botanical Review* **58**: 225–348.
- Tremblay RL.** 1992. Trends in the pollination ecology of the Orchidaceae: Evolution and systematics. *Canadian Journal of Botany* **70**: 642–650.
- Vogel S.** 1990a. *The role of scent glands in pollination*. Rotterdam: AA Balkema.
- Vogel S.** 1990b. History of the Malpighiaceae in the light of pollination ecology. *Memoirs of the New York Botanical Garden* **55**: 130–142.
- Volovnik S.** 1982. On biocoenotic relations between *Cynanchum acutum* and some insects. *Zhurnal Obshchei Biologii* **43**: 729–731.
- Walther R.** 1994. Pollenfrucht als Indikator fuer Ressourcennutzung und Einnischung bei Madagassischen Schwaermern (Lepidoptera). PhD thesis, Friedrich-Alexander University, Erlangen–Nuernberg.
- Waser NW, Chittka L, Price MV, Williams N, Ollerton J.** 1996. Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043–1060.
- Woodell SRJ.** 1979. The role of unspecialized pollinators in the reproductive success of Aldabran plants. *Philosophical Transactions of the Royal Society, series B.* **286**: 99–108.
- Wyatt R, Broyles SB.** 1994. Ecology and evolution of reproduction in milkweeds. *Annual Review of Ecology and Systematics* **25**: 423–441.

APPENDIX

Summary of current systematic understanding of the Asclepiadaceae

Recent higher-level treatments of the Asclepiadaceae (e.g. Bruyns & Forster, 1991; Liede & Albers, 1994) recognize 3 subfamilies, subdivided into 7 tribes, though see Swarupanandan *et al.* (1996) for

some divergent views. Subtribal nomenclature is less well defined (Sundell, 1980; Liede, 1994b) but progress has recently been made on the tribe Asclepiadeae (Liede, 1997). In this latter system, the tribe Gonolobeae is reduced to a subtribe of Asclepiadeae, the Gonolobineae (Table 1a).

TABLE 1a. Higher-level systematics of the family Asclepiadaceae, based on Bruyns & Forster, 1991, Liede & Albers, 1994 and Liede, 1997.

Subfamily	Tribe	subtribe	representative genera	
Periplocoideae	Periploceae	—	<i>Periploca</i> , <i>Raphionacme</i>	
Secamonoideae	Secamoneae	—	<i>Secamone</i> , <i>Toxocarpus</i>	
Asclepiadoideae	Fockeae	—	<i>Fockea</i> , <i>Cibirhiza</i>	
	Marsdeniaceae	—	<i>Hoya</i> , <i>Dischidia</i>	
	Stapeliaceae	—	<i>Stapelia</i> , <i>Ceropegia</i>	
	Asclepiadeae	Asclepiadinae	—	<i>Asclepias</i> , <i>Calotropis</i>
		Astephaninae	—	<i>Tylophora</i> , <i>Vincetoxicum</i>
		Glossonematinae	—	<i>Glossonema</i> , <i>Odontanthera</i>
		Gonolobinae	—	<i>Gonolobus</i> , <i>Matelea</i>
Metastelminae	—	<i>Cynanchum</i> , <i>Sarcostemma</i>		
Oxypetalinae	—	<i>Araujia</i> , <i>Tweedia</i>		

The subfamilies appear to comprise a natural sequence linking the Apocynaceae (sister family to the Asclepiadaceae) to the more highly evolved tribes of the Asclepiadoideae, in the order Apocynaceae (Apocynoideae)→Periplocoideae→Secamonoideae→Asclepiadoideae (Endress, 1994). However, there is some controversy over the exact systematic placement of these taxa and their evolutionary relationships, which has recently been addressed by Swarupanandan *et al.* (1996), though morphological and molecular phylogenies (Liede, 1996; Sennblad & Bremer, 1996) do support this broad sequence. The Periplocoideae is often considered a family in its own right (the Periplocaceae), whilst Thorne (1992), in the most recent overhaul of the Angiosperms, considers the Asclepiadaceae to be a subfamily of the Apocynaceae. The family status of the Asclepiadaceae has also been challenged by Nilsson, Endress & Grafström (1993) and Judd, Sanders & Donoghue (1994); according to this scenario the Apocynaceae comprises five subfamilies, of which Periplocoideae and Asclepiadoideae constitute the Asclepiadaceae as it is considered in this paper. This latter system is probably correct from a strictly phylogenetic view point, as the Apocynaceae as it stands is paraphyletic. However, this does not alter the fact that the asclepiad clade is probably monophyletic (though see Swarupanandan *et al.*, 1996).

The phylogenetic integrity of some tribes is well established, though the precise relationships between others are poorly resolved in recent cladistic analyses (Liede, 1996; Sennblad & Bremer, 1996). The exact circumscription of some tribes is also in flux (e.g. Bruyns & Forster, 1991), new tribes have recently been erected (Kunze, Meve & Liede, 1994) and old ones demolished (Liede, 1997).