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Tobacco to tomatoes: a phylogenetic perspective on fruit diversity in the Solanaceae

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Abstract

The Solanaceae contains many species of agricultural importance. Several of these are cultivated for their fruits, such as the tomato, the pepper and the aubergine. The family is very diverse in fruit type with capsules, drupes, pyrenes, berries, and several sorts of dehiscent non-capsular fruits occurring in the 90+ genera. In this paper, recent work on fruit type evolution in angiosperms is reviewed in relation to dispersal agents and habitat ecology. Defining fruit types in the Solanaceae in a simple five state system, then mapping them onto a previously published molecular phylogeny based on chloroplast DNA allows discussion of the evolution of these fruit types in a phylogenetic framework. Capsules are plesiomorphic in the family, and although berries are a synapomorphy (shared derived character) for a large clade including the genus *Solanum* (tomatoes and aubergines), they have arisen several times in the family as a whole. Problems with homology of drupes and pyrenes are discussed, and areas for future investigation of fruit structure homology identified. The distribution of fruit types in the large and diverse genus *Solanum* is also discussed in the light of monophyletic groups identified using chloroplast gene sequences. This variety is related to recent advances in the understanding of the molecular biology of fruit development. Finally, several key areas of future comparative, phylogenetic investigation into fruit type evolution in the family are highlighted.

Key words: Dehiscence, diversity, fruit type, morphology, phylogeny, seed dispersal, Solanaceae, tobacco, tomato.

Introduction

Today's terrestrial habitats are dominated by the angiosperms – flowering plants, one of whose key features is the possession of fruits of a wide range of forms and types. Angiosperms today exhibit an enormous range of fruit types, from dry single-seeded achenes like sunflowers (Asteraceae), to huge fleshy fruits like those of *Annona* (the cherimoya; Annonaceae) or *Artocarpus* (the breadfruit; Moraceae). Complex classifications of this huge variety of fruit types have been suggested (Spujt, 1994), with almost every variation being given a special name. However, mere description of fruits, though important for the accurate recording of variation in nature, is perhaps of less interest than an understanding of the evolution of such a variety, particularly in the light of an increased understanding of the genetic and developmental control of various floral features of angiosperms (Schwarz-Sommer *et al.*, 1990; Weigel and Meyerowitz, 1994; Reichmann and Meyerowitz, 1997; Theissen *et al.*, 2000; Becker *et al.*, 2000; Ng and Yanofsky, 2001). The evolution of such a wide array of fruit types and the degree to which the pattern of fruit types seems highly homoplasious has long intrigued both systematists and evolutionary biologists.

The diversification of the angiosperms in the Cretaceous and Tertiary was accompanied by explosive diversification in a variety of features (Friis *et al.*, 1987). Rapid diversification in co-evolved pollination systems in the Cretaceous occurred concomitantly with a rapid diversification of the insects (Friis and Crepet, 1987; Wing and Boucher, 1998). Other reproductive features of angiosperms, such as fruit and seed diversity, however, remained relatively unchanged through the Cretaceous (Eriksson *et al.*, 2000). Early angiosperm fruits were apocarpous, with several free carpels. Syncarpous fruits, with fused carpels, only appear in the middle Cretaceous (Albian-Cenomanian), some 97 million years ago. Fossil fruits from the early to middle Cretaceous were all dry and show no obvious modifications for dispersal (Friis and Crepet, 1987). Drupes and berries, the classic fleshy fruits, first appeared in the late Cretaceous or early Tertiary (Friis

Fig. 1. Representative fruit types in the Solanaceae. (A) Drupe of *Duckeodendron cestroides* Kuhlm. (base of fruit in upper right corner). (B) Capsules of *Schizanthus pinnatus* Ruiz and Pav. (C) Capsules of *Sessea corymbiflora* Taylor and Phillips. Scale bars=1 cm.

Fig. 2. Representative fruit types in the Solanaceae: dehiscent non-capsular fruit (pyxidia). (A) *Physochlaina orientalis*, unripe fruit. (B) *Anisodus luridus*, unripe fruit with the calyx cut away. (C) *Przewalskia tangutica* Maxim., ripe fruit showing line of dehiscence. (D) Fruit after dehiscence showing seeds (photographs courtesy of M Gilbert).

and Crepet, 1987). Tiffney (1984) suggested that the relatively rapid evolution of a wide variety of fruit and seed types and sizes in the Paleocene (65–56 Ma) and Eocene (56–35 Ma) was correlated with the rise of mammals and birds, primary dispersers of today's angiosperms. Fruits are the mechanism by which seeds are dispersed, and so both fruit type (mainly fleshy versus dry) and seed size have been discussed in the context of the diversification of angiosperm fruits (Eriksson *et al.*, 2000). Seed sizes were relatively small through the Cretaceous, with a drastic increase at approximately the Cretaceous-Tertiary boundary (about 65 Ma), both in median seed size

and in the range of seed sizes (Eriksson *et al.*, 2000). This increase has been interpreted as a response to the increasing dominance of vertebrates, mostly mammals, and thus to coevolution with seed dispersers (Tiffney, 1984). The proportion of fleshy, and presumably animal dispersed fruits increased through the Cretaceous, and the proportion of wind dispersed (dry) fruits fluctuated, showing several peaks (see Fig. 2B in Eriksson *et al.*, 2000). The combination of these two results led Eriksson *et al.* (2000) to reject the hypothesis that fruit and seed size were driven by co-evolution with the dispersers, but instead to suggest that the trends in overall fruit type and seed size were driven by climate and vegetation change around the Cretaceous–Tertiary boundary. Plants with larger seeds tend to be correlated with wet forest habitats (Westoby *et al.*, 1996) and the warm and increasingly wet climates of the Eocene supported the development of extensive closed canopy forests. The changing recruitment environment for seedlings, with the dry climates of the Cretaceous favouring small seeded plants, and the wetter and more closed canopy forests of the Eocene favouring larger seeded plants, is seen by Eriksson *et al.* (2000) as the primary factor driving the evolution of seed size and fruit in angiosperms as a whole. Plants with large seeds that were favoured in closed canopy environments would have a reduced dispersal capacity unless secondary animal dispersal evolved (Eriksson *et al.*, 2000). The evolution of specialized frugivores such as bats, birds and rodents during the Tertiary was a secondary phenomenon, related to the abundance of a large-seeded resource, rather than the primary cause of the increase in fruit and seed size among angiosperms (Eriksson *et al.*, 2000). Variation in the characters related to dispersal effectiveness are perhaps too limited to strongly affect the intensity of selection (Schemske, 1983) and thus are not the primary driving force in the evolution of broad patterns of fruit and seed size in angiosperms. It has been suggested that the interaction between plants and their animal dispersers is manifested at a level higher than the species (Howe, 1984; Herrera, 1985), so patterns of coevolution might be expected to occur at the family level in flowering plants.

The use of fruit types as important taxonomic characters has, to a certain extent, confounded the rigorous study of patterns of fruit type evolution. Fruit types are sometimes considered to be evolutionarily conservative (Spujt, 1994) and are thus given a high taxonomic weight. Recent studies, however, using phylogenetic methods, have shown that, in many families of angiosperms, fruit type is highly homoplasious (i.e Apiaceae, Plunkett *et al.*, 1996; Spalik *et al.*, 2001; Cunoniaceae, Bradford and Barnes, 2001; Lamiales, Wagstaff and Olmstead, 1997; Myrtaceae, Johnson and Briggs, 1994; Ranunculaceae, Hoot, 1995; Rosaceae, Morgan *et al.* 1994), and fleshy fruits in particular have evolved repeatedly in a wide variety of clades (Amaryllidaceae, Snijman and Linder, 1996;

Rubiaceae, Bremer and Eriksson, 1992; Bremer *et al.*, 1995; Melastomataceae, Clausing *et al.*, 2000; Malpighiaceae, Davis *et al.*, 2001). Using trees derived from the sequences of various chloroplast and/or nuclear genes (see Soltis *et al.*, 1998, for a discussion of DNA sequencing and its application to angiosperm phylogeny), it has been demonstrated that, in Rubiaceae for example, fleshy fruits have arisen 12 times independently (Bremer *et al.*, 1995). Clausing *et al.* (2000) have shown that previous classifications of the family Melastomataceae that relied heavily on fruit type (dry capsules considered plesiomorphic or ancestral and fleshy true berries as apomorphic or derived) were misleading, since the fleshy fruits in the family were not all equivalent or homologous. Homology is of critical importance in the assessment of characters for phylogenetic analysis, for example, in the Melastomataceae, soft berries are anatomically quite variable and have arisen from the development of fleshiness of different parts of the developing ovary (Clausing *et al.*, 2000) and very slightly different developmental trajectories in some Rosaceae can lead to what appear to be radically diffferent fruit types (Evans and Dickinson, 1999). Thus, the character 'fruit a soft berry' is not the same thing in every clade where it occurs. The accurate interpretation of fruit types is also important, in some groups it has been found that fruits previously thought to be berries (i.e. indehiscent) were incorrectly designated as such (Barnes and Rozefelds, 2000), and correct assessment of fruit type has resulted in a better understanding of the relationships and patterns of character evolution.

Fruits are more than simply characteristics of angiosperms—they are the means by which seeds are dispersed and as such are clearly under strong selective pressure. Fruit type, however, is not the only important fruit trait that potentially affects seed dispersal. It has been suggested that tight co-evolution between plants and their seed dispersers would result in fruit quality being directly related to seed dispersal quality (McKey, 1975), with specialist seed dispersers feeding on nutritionally higher quality fruits. This paradigm had much in common with that thought to be controlling plant–pollinator interactions, which do indeed show such tight and specific relationships. It has sometimes been assumed that differences in quality of seed dispersal can fully explain variation in fruit traits (Schupp, 1992). Wheelwright and Orians (1992), however, felt that expectations of such tight co-evolution were highly misguided, as the target for seeds (a good germination site) was much less obvious than that for pollen (a con-specific stigma) and that frugivores are 'paid in advance' for future services. Studies on plants and their seed dispersers undertaken since these paradigms were suggested have shown that if co-evolution does exist it is a much more diffuse phenonomen, with convergence on broad suites of fruit traits and fruit-feeding behaviours

occurring in natural communities (Murray *et al.*, 2000). Recent studies have also failed to corroborate the assumption that differences in quality determine fruit trait variation (Cipollini and Levey, 1997*a*). Fruit quality, however, is important to frugivores, and will affect seed dispersal in some way. Quality can be assessed in a variety of ways using protein or fat content (McKey, 1975), caloric value or levels of secondary metabolites (Cipollini and Levey, 1997*a*). This latter measurement of fruit quality is often not considered, but toxins in fruit are of great importance not only to natural frugivores, but to humans who cultivate fruits for their own purposes.

Solanaceae contain many taxa of importance, both agronomically (potatoes, tomatoes, peppers) and medicinally (mandrake, tobacco, deadly nightshade, henbane). Members of the family occur worldwide, but the highest species diversity is found in the Neotropics. The family is very diverse, both in terms of life form, with species ranging from ephemeral herbs (*Leptoglossis* and *Schizanthus* of the Chilean deserts) to large forest trees (*Duckeodendron* of the Amazon), and in flower morphology (Knapp, 2002*a*). Estimates of species diversity in the family range from 9000–10 000 species, with about 2000 of those being species of the large cosmopolitan genus *Solanum* (see Knapp, 2002*a*, for a review of genera in the family). Taxonomic work in the family largely proceeded at the generic level and the last complete treatment was that of Dunal (1852). Recently, Hunziker (2001) has provided a complete treatment of the family at the generic level, including a new classification system.

In recent years, three advances have contributed significantly to the understanding of the relationships of flowering plants: (1) an explicit framework for interpreting phylogeny (cladistics; Hennig, 1966; Kitching *et al.*, 1998), (2) the incorporation of data from the DNA sequences of a variety of regions of the genome, both from the nucleus and the chloroplast, to construct phylogenetic hypotheses in the form of trees, and (3) computer technology that is able to handle such large data sets. Systematic studies in the Solanaceae have benefited greatly from these advances, with phylogenetic studies being published for a variety of genera and species groups (Knapp, 1989; Mione *et al.*, 1994; Bruneau *et al.*, 1995; Axelius, 1996; Knapp and Helgason, 1997; Estrada and Martínez, 1999; Bohs, 2001; Peralta and Spooner, 2001) and the resolution of the relationships of several enigmatic genera (i.e. *Duckeodendron*, Fay *et al.*, 1998; *Schizanthus*, Olmstead *et al.*, 1999; *Sclerophylax*, L Bohs, personal communication) whose inclusion in the family has been the subject of much debate (D'Arcy, 1991). Molecular studies have also shown that the tomatoes, previously recognized as the segregate genus *Lycopersicon* Mill., are deeply nested with the genus *Solanum* (Spooner *et al.*, 1993; Peralta and Spooner, 2001), as are the tree tomatoes

(ex *Cyphomandra* Sendtn.; Bohs, 1995, 2002; Bohs and Olmstead, 1997). Some disagreement still exists as to the utility of these new classifications (Hunziker, 2001; Chetelat, personal communication), but as more gene sequences from both the chloroplast and the nucleus are analysed, the results are being shown to be robust (L Bohs, personal communication; RG Olmstead, personal communication). Although differences in taxonomic arrangement are perceived as being disruptive in the short term, the robustness of phylogenetic hypotheses allows the accurate and rigorous examination of character evolution, thus leading to a better understanding of how members of the family have evolved and are related.

Solanum is by far the largest and most diverse genus in the family, with between 1000 and 2000 species growing in all habitats from rainforests to the world's driest deserts. Floral morphology in *Solanum* follows a basic radially symmetrical plan (but see Knapp, 2001, 2002*a*), and solanums in flower are remarkably easy to recognize. The genus was last treated taxonomically by Dunal (1852), and has traditionally been divided into two major groups, the spiny solanums (with attenuate anthers and usually spiny foliage and stems) and the non-spiny solanums (with oblong anthers and no spines) (D'Arcy, 1972; Bohs and Olmstead, 1999; Knapp, 2001). The non-spiny solanums are clearly a paraphyletic group (a group containing some, but not all of the descendants of a common ancestor), and recent work using a variety of chloroplast and nuclear genes by L Bohs (University of Utah) has gone a long way towards defining monophyletic groups within the genus (Bohs, 2002). Several segregate genera traditionally treated, apart from *Solanum*, have recently been found to be nested within the genus and those species have been formally transferred (Spooner *et al.*, 1993; Bohs, 1995). In the discussions here, these species are treated as part of the larger, monophyletic *Solanum*.

In this paper, the patterns of fruit evolution in the economically important family Solanaceae are examined using a recently published molecular phylogeny (Fay *et al.*, 1998; Olmstead *et al.*, 1999). This examination in a phylogenetic framework is used specifically to address the following questions: (1) what is the range of fruit types found in the family? (2) how many independent origins of distinct fruit characters can be inferred from the phylogeny of the family? (3) are there any instances where homology of a particular fruit type is questionable? and (4) are there trends in fruit type that can be associated with habitat or dispersers? In addition, there will be a close examination of fruit type diversity and fruit chemistry in the large genus *Solanum*, where greater understanding of the molecular mechanisms of fruit development gained from studies of agronomically important crops may help in the understanding of evolutionary patterns, particularly in relation to fruit dispersal modes.

Table 1. *Fruit type definitions used for the Solanaceae, with equivalents in the systems of Spujt (1984) in parentheses*

Fruit type category	Definition
Capsule	A multicarpellate fruit opening into more or less equal valves along longitudinal sutures; septicidal capsules open along ventral suture, each valve is a single carpel+placenta; loculicidal capsules open along dorsal suture, each valve is composed of half of two carpels (septicidal capsules, loculicidal capsules)
Berry	A fleshy fruit with a pulpy interior, no stony layer and many seeds (bacca; carcerulus; diclesium)
Berry with stone cells	As above, but with sclerified inclusions in the fleshy portion of the fruit
Drupe or pyrene	A fleshy fruit with one or more stones; seeds enclosed by a stony layer, the endocarp (drupe)
Non-capsular dehiscent fruit	A fruit that is dry at maturity, opening variously, but not along longitidunal sutures (foraminicidal capsule; pyxidium)
Mericarps (nutlets)	A usually dry fruit with single- or multi-seeded units that are separate at maturity (achenarium; drupetum?)

Materials and methods

Solanaceae: evolution and phylogeny

Olmstead *et al.* (1999) produced a phylogenetic classification of the Solanaceae using two types of cpDNA data, (1) restriction site analysis of the entire chloroplast genome, and (2) DNA sequencing of two chloroplast genes, *rbcL* and *ndhF* (for details see Fay *et al.*, 1998; Olmstead *et al.*, 1999). Fay *et al.* (1998) included in this large data set the genus *Duckeodendron*, previously segregated as the family Duckeodendraceae (Kuhlmann, 1947; Thorne, 1992: Fay *et al.*'s study was completed after that of Olmstead *et al.*, but published before it). *Duckeodendron* is included here in the Olmstead *et al.* (1999) classification, at the rank of tribe (as suggested by Fay *et al.*, 1998; but see Bremer *et al.*, 2001). The phylogenetic classification presented in Olmstead *et al.* (1999) unfortunately used Latinized tribal and subfamilial ranks, but without validation. In Table 2 the Olmstead *et al.* (1999) classification is presented, with the names used in parentheses to indicate their use here as *sensu* Olmstead *et al.* only. Each of the monophyletic groupings has also been given an informal name (i.e. the Petunia clade) to facilitate discussion. These informal clade names will be used throughout this paper. Genera are listed in each clade in alphabetic order in Table 2, following Olmstead *et al.* (1999). Several segregate genera have been described recently (Hunziker, 2000*a, b*) and are included in the clade with the genus from which they have been distinguished. The Olmstead *et al.* (1999) classification has been used here rather than the more recent Hunziker (2001) scheme, not because molecular data are necessarily a better indicator of relationship, but because Hunziker's classification recognizes many paraphyletic and some polyphyletic groups and in so doing becomes less useful for the examination of evolutionary patterns than the Olmstead *et al.* classification, which is based on monophyly. Monophyletic groups are natural taxa, containing all the descendants of a common ancestor, while paraphyletic groups contain only some of the descendants of a common ancestor (birds are a classic example; Wiley, 1981) and polyphyletic groups contain taxa who do not share a close common ancestor. Monophyletic groups are more informative for the examination of character evolution.

For each genus, the possession of one or many of five fruit types has been recorded, defined *a priori* as relatively broad categories and in line with usage in other phylogenetic frameworks (Bremer and Eriksson, 1992; Clausing *et al.*, 2000; Bradford and Barnes, 2001). Table 1 provides definitions for the fruit types identified here for the Solanaceae, with an indication of some of the terms used by Spujt (1994) that have been subsumed here under these categories (the list

is not by any means exhaustive). Berries (with and without stone cells, see below and Table 1; Figs 3E, F, 4B, C, D), capsules (Figs 1B, C, 3A–D), dehiscent non-capsular fruits (Fig. 2), mericarps (Fig. 4A), and drupes or pyrenes (Fig. 1A) have been used as the five basic fruit types in the family based on initial homology assessments in the literature and from examination of both live and preserved specimens. Fruiting specimens have been examined of all genera in the herbaria of the Natural History Museum, London (BM), the Missouri Botanical Garden (MO) and the Royal Botanic Gardens, Kew (K), leading to some differences with fruit types published in the literature (e.g. the fruit of the rare Nevada endemic *Oryctes* is considered to be a non-capsular dehiscent fruit, while Hunziker, 2001, states that it is a capsule). Table 2 lists all the genera in the family and the fruit types found within them; if a genus has several different fruit types, it is indicated here. Figures 1–4 illustrate some of the fruit type diversity within the family.

In order to assess the distribution of fruit types in the family, the framework molecular phylogeny of Olmstead *et al.* (1999) has been used here, using as the terminals the monophyletic groups of their classification (Figs 5–7). Olmstead *et al.* (1999) did not have molecular data for all the genera of the family, but subsequent sampling has by and large confirmed the monophyletic groupings they identified (RG Olmstead, personal communication). Where newly sampled genera have been found to be members of different groups, this has been indicated in the notes to Table 2. Fruit characters have been mapped onto the framework tree using MacClade version 3.06 (Madison and Madison, 1996) showing all most parsimonious states at each node. The topology of this tree should not be interpreted as the true phylogeny of the family, but instead as a heuristic device with which to examine the distribution of fruit types in the family. Those interested in the more complex trees resulting from the molecular analyses are referred to the original literature (Olmstead *et al.*, 1999; Fay *et al.* 1998).

The genus Solanum: evolution and phylogeny

To examine the distribution of fruit types with relation to phylogeny at another hierarchical level in the same set of data, fruit types in the genus *Solanum* have been recorded using the monophyletic groups identified by Bohs (2002) using sequences of the chloroplast gene *ndhF*. Although these groups are preliminary, they represent the first attempt to assess monophyly in the genus and are largely supported by both morphological (S Knapp, personal observation) and other molecular data, both chloroplast (Bohs and Olmstead, 1997, 1999; Olmstead and Palmer, 1997) and nuclear (L Bohs, personal communication). Since the relationships of these monophyletic groups are not yet robustly supported, the consensus tree has not

Table 2. *Fruit type diversity in the Solanaceae arranged by genus*

Generic arrangement follows that of Olmstead *et al.* (1999), except where footnoted.

Clades referred to in text and figures; names in parentheses are those fide Olmstead *et al.* (1999); Fay *et al.* (1998)	Genus	Capsule	Berry	Berry with stone cells	Non-capsular dehiscent	Drupe or pyrene	Mericarps (nutlets)
Schwenkia clade (Schwenkioideae)	*Schwenkia* L.	X					
	Protoschwenkia Solereder[a]	X					
	Melananthus Walp.	X					
	Heteranthia Nees and Mart.	X					
Schizanthus (Schizanthoideae)	*Schizanthus* Ruiz and Pav.	X					
Duckeodendron (Duckeodendreae)	*Duckeodendron* Kuhlm.					X	
Goetzea clade (Goetzeoideae)	*Goetzea* Wydl.					X	
	Espadaea A.Rich.					X	
	Coeloneurum Radlk.					X	
	Henoonia Griseb.					X	
Petunia clade (Petunioideae)	*Benthamiella* Speg.	X					
	Bouchetia Dunal	X					
	Brunfelsia L.	X					
	Calibrachoa La Llave and Lex.	X					
	Combera Sandw.	X					
	Fabiana Ruiz and Pav.	X					
	Hunzikeria D'Arcy	X					
	Latua Phil.[b]		X				
	Leptoglossis Benth.	X					
	Nierembergia Ruiz and Pav.	X					
	Pantacantha Speg.	X					
	Petunia Juss.	X					
	Plowmania Hunz. and Subils	X					
Salpiglossis clade (Cestroideae: Salpiglossideae)	*Salpiglossis* Ruiz and Pav.	X					
	Reyesia Gay	X					
Browallia clade (Cestroideae: Browallieae)	*Browallia* L.	X					
	Streptosolen Miers	X					
Cestrum clade (Cestroideae: Cestreae)	*Cestrum* L.		X				
	Sessea Ruiz and Pav.	X					
	Metternichia Mikan[c]	X					
	Vestia Willd.	X					
Anthocercis clade (Nicotianoideae: Anthocercideae)	*Anthocercis* Labill.	X					
	Anthotroche Endl.	X					
	Crenidium Haegi	X					
	Cyphanthera Miers	X					
	Duboisia R. Br.		X				
	Grammosolen Haegi	X					
	Symonanthus Haegi	X					
Nicotiana (Nicotianoideae: Nicotianeae)	*Nicotiana* L.	X					
Capsicum clade (Solanoideae: Capsiceae)	*Capsicum* L.		X	X			
	Lycianthes (Dunal) Hassl.		X	X		X	
Datura clade (Solanoideae: Datureae)	*Datura* L.	X					
	Brugmansia Pers.		X				
Hyoscyamus clade (Solanoideae: Hyoscyameae)	*Anisodus* Link				X		
	Atropa L.		X				
	Atropanthe Pascher				X		
	Hyoscyamus L.				X		
	Physochlaina G. Don				X		
	Przewalskia Maxim.				X		
	Scopolia Jacq.				X		
Jaborosa (Solanoideae: Jaboroseae)	*Jaborosa* Juss.		X				
Solandra clade (Solanoideae: Solandreae)	*Dyssochroma* Miers		X				
	Juanulloa Ruiz and Pav.		X				
	Markea A. Rich.		X				
	Merinthopodium Donn. Sm.		X				
	Schultesianthus Hunz.		X				
	Solandra Sw.		X				
	Trianaea Planch. and Linden		X				
Lycium clade (Solanoideae: Lycieae)	*Grabowskia* Schltdl.					X	
	Lycium L.		X			X	
	Phrodus Miers		X	X			
Mandragora (Solanoideae: Mandragoreae)	*Mandragora* L.		X				

Table 2. *Continued*

Clades referred to in text and figures; names in parentheses are those fide Olmstead *et al.* (1999); Fay *et al.* (1998)	Genus	Capsule	Berry	Berry with stone cells	Non-capsular dehiscent	Drupe or pyrene	Mericarps (nutlets)
Nicandra clade (Solanoideae: Nicandreae)	*Exodeconus* Raf.		X	X			
	Nicandra Adans.		X	X			
Nolana (Solanoideae: Nolaneae)	*Nolana* L. (incl. *Alona*)						X
Iochroma clade (Solanoideae: Physaleae: Iochrominae)	*Acnistus* Schott		X	X			
	Dunalia Kunth		X	X			
	Iochroma Benth.		X	X			
	Saracha Ruiz and Pav.		X	X			
	Vassobia Rusby		X	X			
Physalis clade (Solanoideae: Physaleae: Physalinae)	*Brachistus* Miers		X	X			
	Chamaesaracha (A. Gray) Benth.		X				
	Leucophysalis Rydb.		X	X			
	Oryctes S. Watson				X		
	Physalis L. (incl. *Quincula* Raf.)		X	X			
	Witheringia L'Her.		X				
Salpichroa clade (Solanoideae: Physaleae: Salpichroinae)	*Nectouxia* Kunth		X				
	Salpichroa Miers		X				
Withania clade (Solanoideae: Physaleae: Withaninae)	*Athenaea* Sendt.		X				
	Aureliana Sendt.		X	X			
	Cuatresia Hunz.		X				
	Darcyanthus Hunz.[d]		X	X			
	Deprea Raf.		X	X			
	Eriolarynx (Hunz.) Hunz.[e]		X	X			
	Larnax Miers		X	X			
	Physalistrum Makino		X				
	Tubocapsicum (Wetts.) Makino		X				
	Withania Pauq.(incl. *Mellissia* Hook. f.)		X	X			
Solanum clade (Solanoideae: Solaneae)	*Discopodium* Hochst.		X				
	Jaltomata Schltdl.		X				
	Nothocestrum A. Gray		X				
	Solanum L. (incl. *Cyphomandra* Mart. ex Sendtn., *Lycopersicon* Mill., *Normania* Lowe, *Triguera* Cav.)		X	X	X		

[a] *Protoschwenkia* may be more closely related to members of the *Cestrum* and *Browallia* clades (RG Olmstead, personal communication).

[b] *Latua* has been excluded from the character mapping analysis, as I am extremely doubtful as to its inclusion in the Petunia clade based on both flower morphology and chemistry. The relationships of *Latua* are of great interest, not only due to its use as a hallucinogen (Plowman *et al.*, 1971), but due to its enigmatic status (Cosa Gastiazoro, 1991).

[c] *Metternichia* may be related to *Duckeodendron* and members of the Goetzea clade (Fay *et al.*, 1998; RG Olmstead, personal communication).

[d] *Darcyanthus* was previously considered a species of *Physalis* (*P. spruceana* Hunz.; see Hunziker, 2000*a*).

[e] *Eriolaryx* was previously part of *Vassobia* (section *Eriolaryx* Hunz.; see Hunziker, 2000*b*).

been reproduced (Bohs, 2002; for a tree produced with a much smaller sample see Bohs and Olmstead, 1997, 1999). Several group relationships, however, are robustly supported by all these molecular studies; (1) the segregate genera *Cyphomandra* and *Lycopersicon* form part of a monophyletic *Solanum* and should be included, (2) the spiny solanums form a robustly supported monophyletic group and are derived within the genus, and (3) traditional subgeneric classifications of the genus were largely composed of paraphyletic and polyphyletic groups (see Bohs and Olmstead, 1997, for a discussion). Species of *Solanum* as delimited here all possess berries (Table 2; Fig. 5), but within that category diversity is immense. Mature *Solanum* berries are of several basic kinds; (1) soft, brightly coloured, juicy berries (e.g. *S. dulcamara*; Figs 8D, 9A, D), (2) brightly coloured relatively dry berries (e.g. *S. pseudocapsicum*; the Jerusalem cherry), (3) soft, greenish berries (e.g. *S. mite*; Knapp and Helgason, 1997; Figs 8A, E, 9B), (4) hard, greenish or yellowish berries (e.g. *S. carolinense*; Cipollini and Levey, 1997*a*; Fig. 8B), or (5) dry berries enclosed in an accrescent calyx (e.g. *S. rostratum*; Fig. 9E, F). This last category includes those berries identified as censer fruits (Symon, 1984; Lester and Symon, 1989); dry berries borne on long flexible stalks where seeds are shaken out by wind or impact.

Results

Solanaceae: evolution and phylogeny

The sister group (most closely related family) for the Solanaceae is the Convolvulaceae (Savolainen *et al.*, 2000), where capsular fruits are the norm (Cronquist, 1981). Outgroup comparison with the sister group thus would indicate that capsular fruits were the plesiomorphic state in the Solanaceae, and capsules occur in most of the basal clades of the tree (Fig. 5A). The only other occurrence of capsular fruits in the family is in the Datura clade, where the genus *Datura* has large, usually spiny capsules (Fig. 3E, F) with relatively large, ant-dispersed seeds (Persson *et al.*, 1999). From the phylogeny this can be seen to represent a secondary derivation of the capsule from a berry-fruited ancestor (see below).

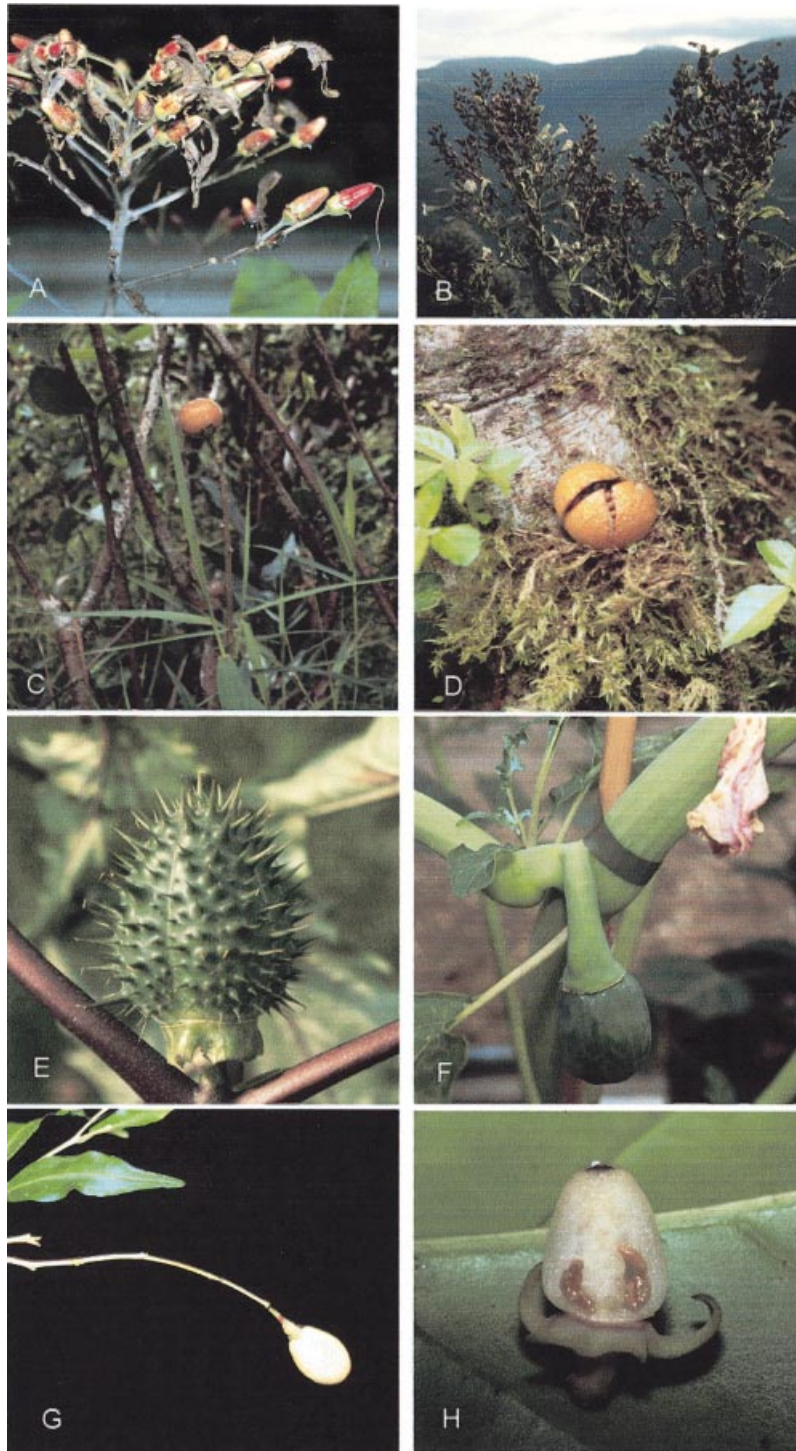Two basal clades however, *Duckeodendron* and the Goetzea clade both possess drupes (Fig. 5B). Similarities

Fig. 3. Representative fruit types in the Solanaceae. (A) *Nicotiana tomentosa* Ruiz and Pav., unripe capsules. (B) *Nicotiana tabacum* L., ripe and opened capsules. (C) *Brunfelsia lactea*, bright orange ripe fruit on plant. (D) *Brunfelsia lactea*, fruit showing dehiscence and dry seeds. (E) *Datura stramonium* L., unripe spiny capsule. (F) *Datura ceratocaula* Ortega, unripe green capsule. (G) *Cestrum fragile* Francey, white ripe berry. (H) *Markea panamense* Standl., ripe juicy berry.

of these drupaceous fruits have been noted by Carlquist (1988), but significant differences in the large size and fibrous mesocarp of *Duckeodendron* perhaps mean they are derived differently. Baehni (1943) used the fact that the drupe of *Goetzea* was derived from a single locule, rather than from two locules, to exclude it and its close relatives from the Solanaceae. Both *Lycium* and *Grabowskia* (the Lycium clade) have fruits that are defined as pyrenes—

Fig. 4. Representative fruit types in the Solanaceae. (A) Immature mericarps of *Nolana carnosa* (Lindl.) Miers ex Dunal (photograph courtesy of MO Dillon). (B) *Atropa belladonna* L., ripe fleshy berry. (C) *Capsicum* fruits. (D) *Solanum lycopersicum* L., ripe berries.

having one or two seeds enclosed in indurate endocarp and surrounded by fleshy exocarp. This clade is not closely related to either the Goetzea clade or to *Duckeodendron*, so it is perhaps important to assess the homology of this fruit type in the family. Further to the distribution of drupes/pyrene-type fruits is the case of *Lycianthes*, where one subgenus (*Eulycianthes* Bitter) has few (*c*. 8, as opposed to the many in the rest of the genus) seeds, each of which is enclosed in a bony endocarp superficially analogous to the situation in *Lycium* (Symon, 1987). The fruit of *Saracha* (in the Iochroma clade), although scored here as a berry, has most of the seeds surrounded by a bony substance, apparently derived from the copious stone cells (personal observation; Alvárez, 1996).

Berries are clearly derived in the family and seem to have three separate origins (Fig. 6A). Two equally parsimonious possibilities exist for this pattern. Either berries define a monophyletic clade and they have been lost three times, or berries have three separate origins, in

Cestrum of the Cestrum clade, in *Duboisia* of the Anthocercis clade and in the subfamily 'Solanoideae', where berries do occur in all terminal taxa (Table 2; Fig. 6). The first of these two scenarios involves four steps, while the second involves only three and is thus preferable using the criterion of parsimony. This is somewhat like the case in the Rubiaceae (Bremer and Eriksson, 1992) or Melastomataceae (Clausing *et al.*, 2000), where soft berries have clearly evolved many times independently. *Latua*, an unusual and rare Chilean endemic which would represent an independent origin of berries (Table 2), has not been analysed using molecular methods and Olmstead *et al.* (1999) provisionally included it in the Petunia clade. The relationships of *Latua* are unclear and it has been excluded from the analysis until more detailed molecular and morphological studies are undertaken. The berries of *Cestrum* (Cestrum clade) are unusual in the family in that in a few taxa they are occasionally somewhat capsular at the apex (Francey, 1935; Benítez de Rojas and D'Arcy,
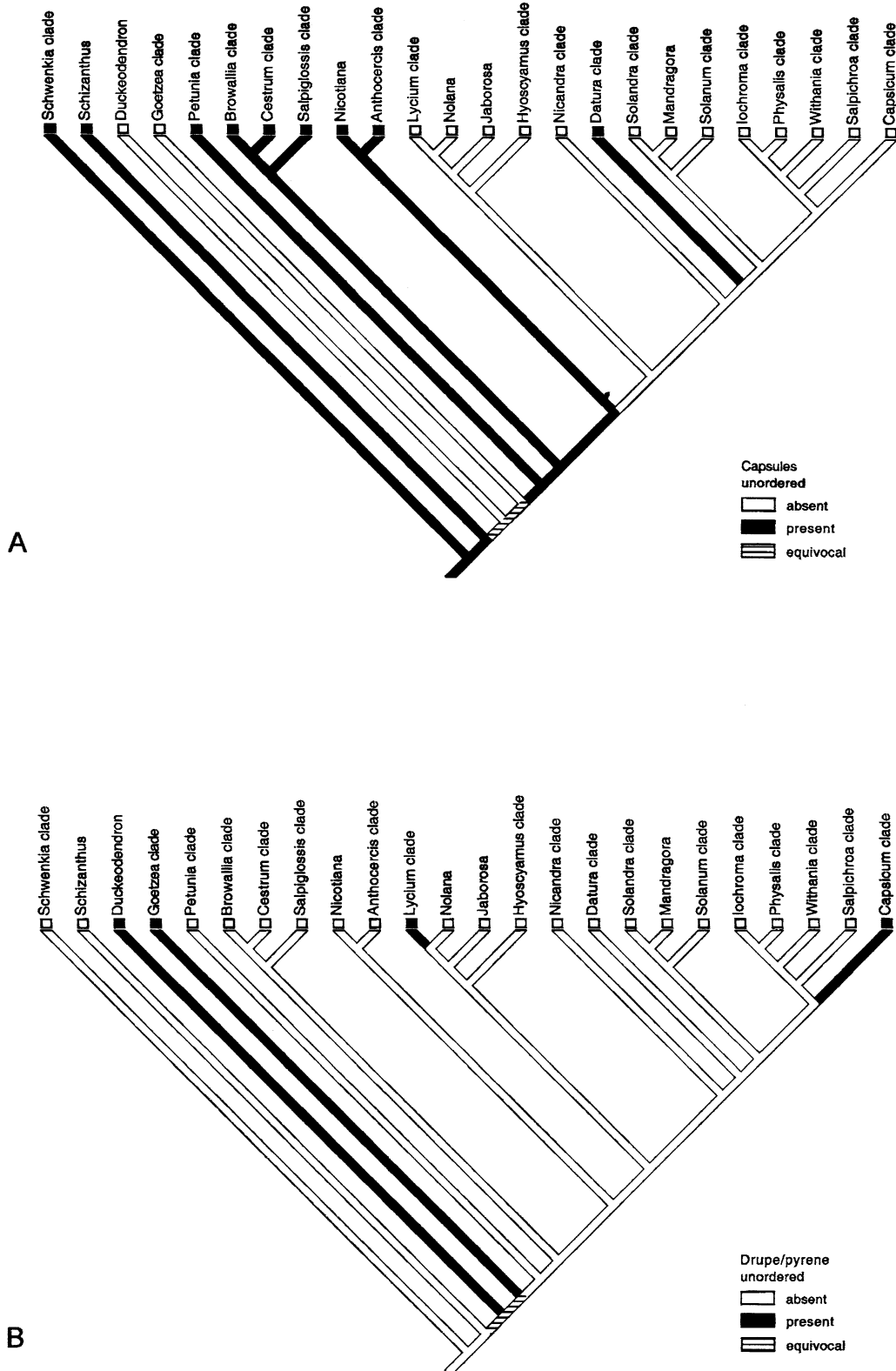
Fig. 5. (A) Distribution of capsular fruits on the framework molecular phylogeny. (B) Distribution of drupes and pyrenes on the framework molecular phylogeny.
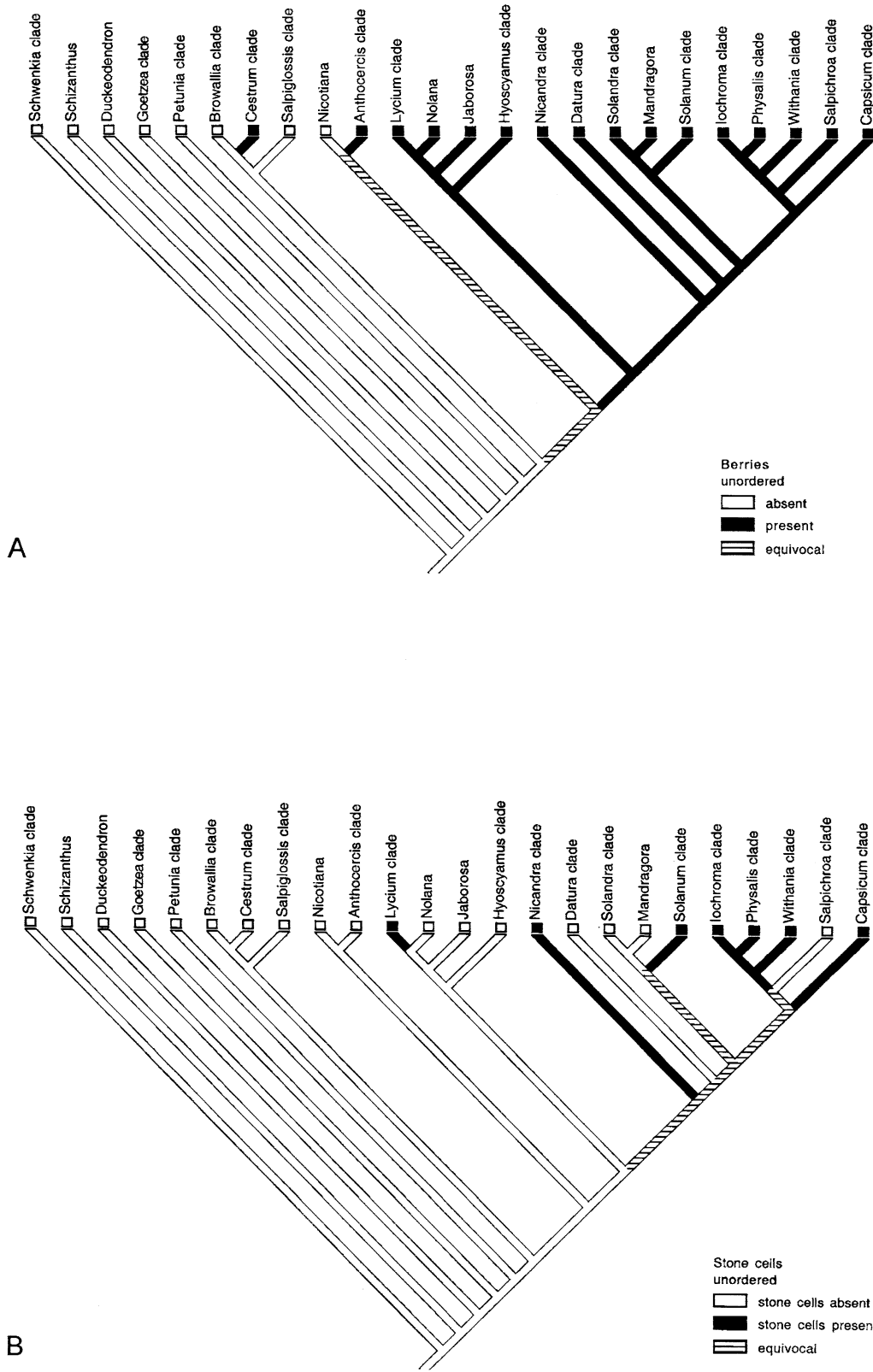
Fig. 6. (A) Distribution of berries on the framework molecular phylogeny. (B) Distribution of berries with stone cells on the framework molecular phylogeny.
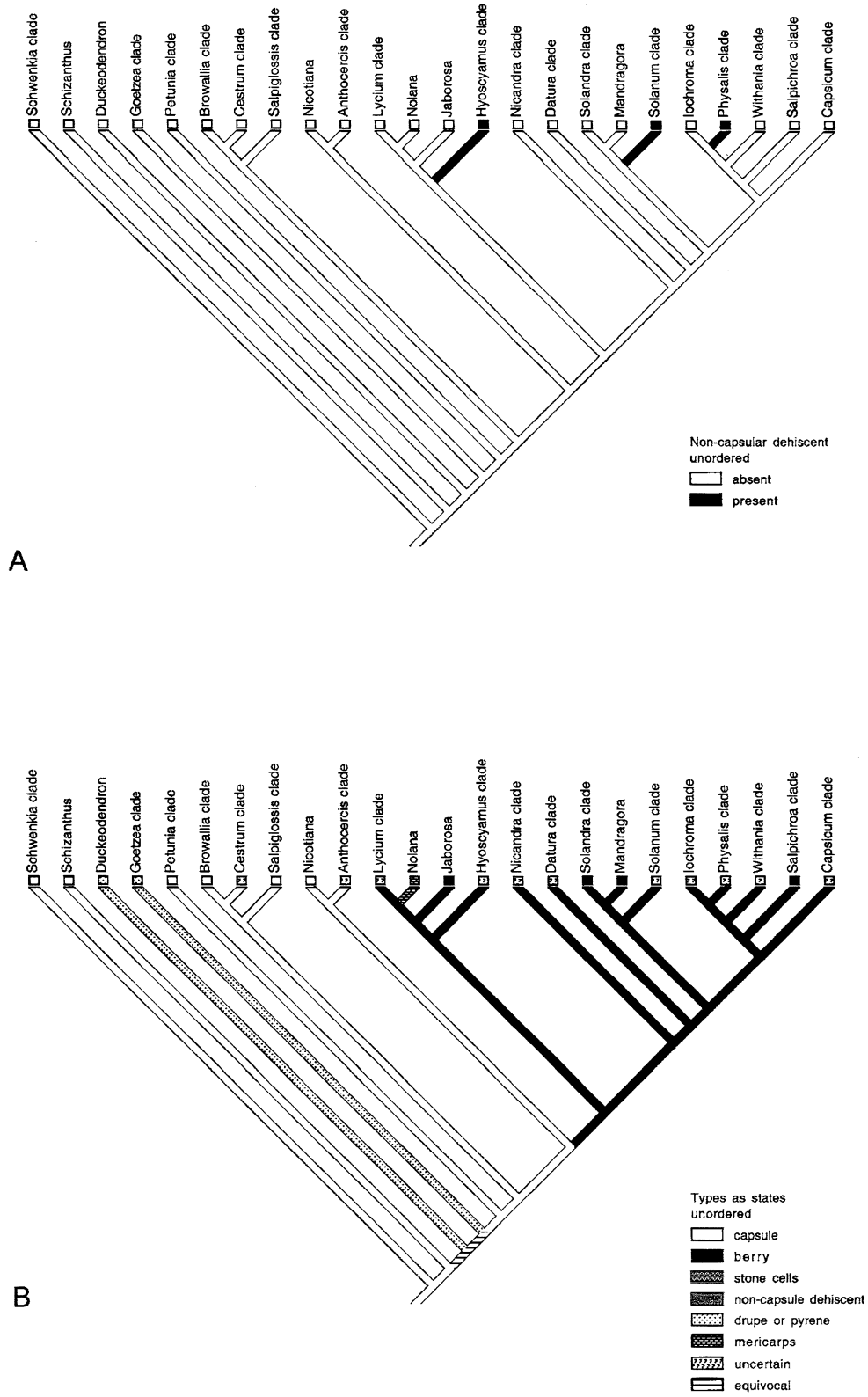
Fig. 7. (A) Distribution of non-capsular dehiscent fruit on the framework molecular phylogeny. (B) Fruit types coded as states (see legend in figure) and mapped onto the framework molecular phylogeny.
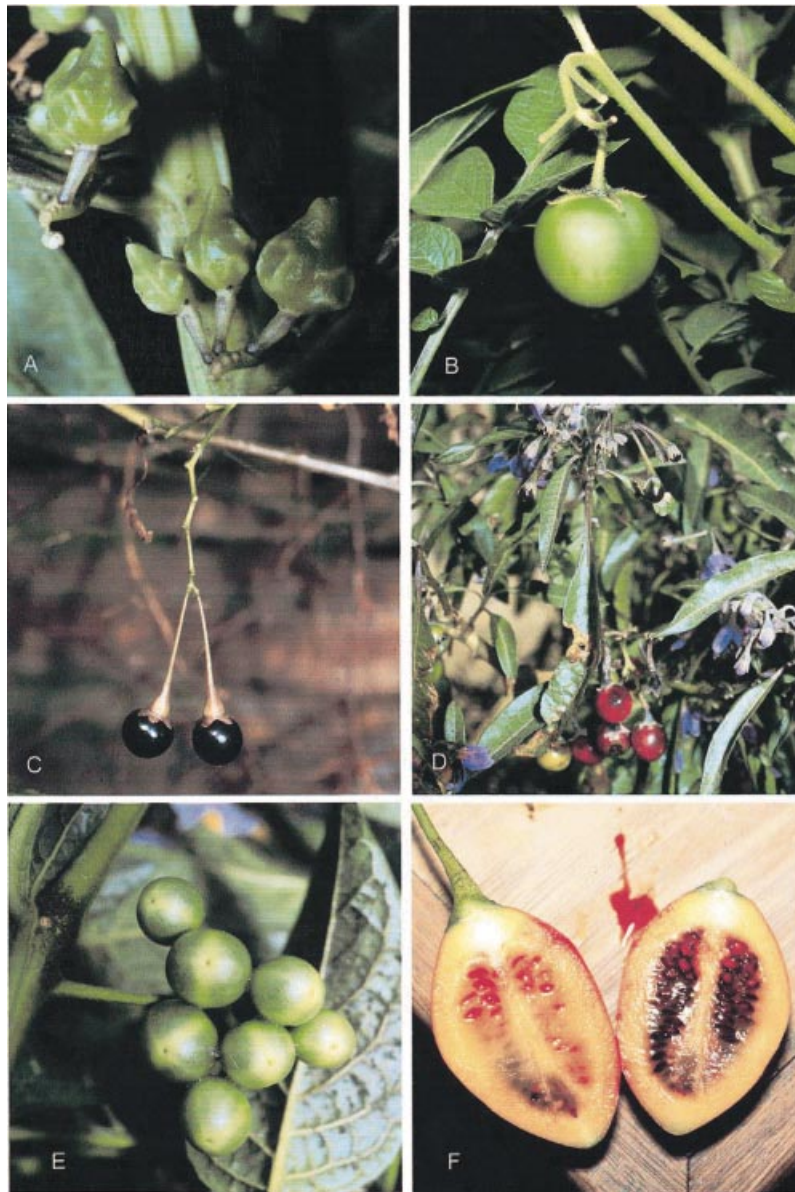
Fig. 8. Fruit types in *Solanum*. (A) *S. angustialatum* Bitter (potato clade) green berry with unusual verrucose pericarp. (B) *S. tuberosum* L. (potato clade), green relatively hard berry. (C) *S. jasminoides* Paxt. (Dulcamaroid clade), shiny black juicy berry. (D) *S. nitidum* Ruiz and Pav. (Dulcamaroid clade), berries turing from green to bright red at maturity. (E) *Solanum* sp. (Morelloid clade), green unripe fruits showing darker lines at locule margins. (F) *S. betaceum* Cav. (Cyphomandra clade) brightly colored berry with juicy pulp.

1998). *Sessea*, the sister group of *Cestrum*, has strictly capsular fruits with winged seeds. The berries in the most derived clade (Olmstead *et al.*'s subfamily 'Solanoideae') are all morphologically similar, with two carpels, axile placentation and mostly lenticular seeds (Symon, 1987). Many of the genera in this large clade contain stone cells (Fig. 6B), accretions of sclerenchyma that occur in the fleshy part of the berry (Bitter, 1911, 1914). In some cases these stone cells can be quite numerous, *Solanum multivenosum* Symon (an Australian species of the Archaeosolanum clade, see below) has an average of 180 (range: 162–1110) stone cells per fruit (Symon, 1987,

1994). Bitter (1911, 1914) suggested that these structures were the remnants of a once stony endocarp (i.e. that the ancestral fruit type in the family was a drupe). Bohs (1994) found that stone cells in the Cyphomandra clade (including *Solanum betaceum* Cav., see below) were lignified with high concentrations of sodium and calcium. From the distribution of stone cells in berries (Fig. 6B), it is clear that they are a derived character relative to the possession of berries, and have apparently been either gained or lost several times.

The unusual sclerified mericarps of *Nolana* are an autapomorphy (unique derived character) of that clade
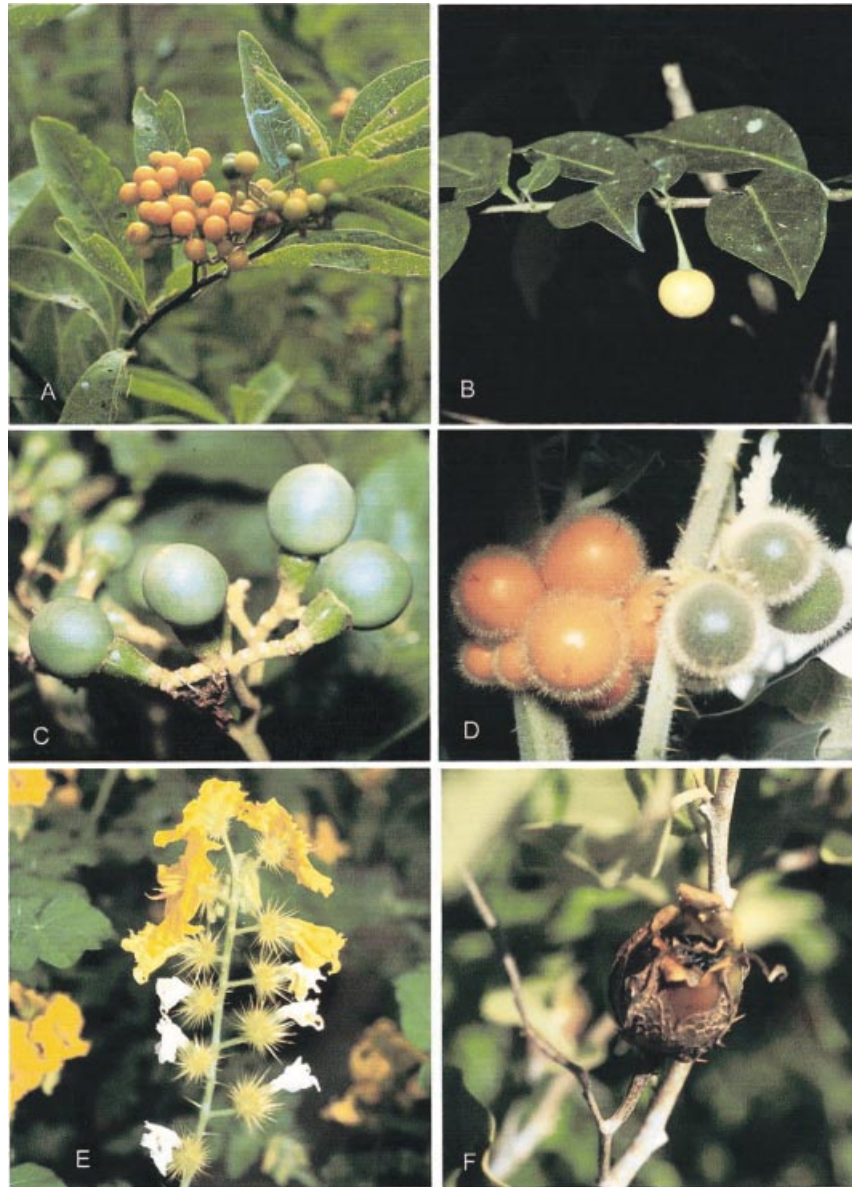
Fig. 9. Fruit types in *Solanum*. (A) *S. argentinum* Bitter and Lillo (Geminata clade), bright orange berry (B) *S. falconense* S. Knapp (Geminata clade) yellow soft berry. (C) *S. oblongifolium* Dunal (Geminata clade) woody, hard green berry. (D) *S. candidum* Dunal (spiny solanum clade) bright orange densely pubescent berries. (E) *S. rostratum* Dunal (spiny solanum clade), spiny accrescent calyces holding dry berries. (F) *S. tridynamum* Dunal (spiny solanum clade), splash cup or censer fruit (dry berry).

(Fig. 7B; Tago-Nakazawa and Dillon, 1999). These peculiar fruits, which are generally composed of 5–15 carpels (Di Fulvio, 1971; Bruno, 1994) are the principal reason some authors have maintained the genus at the family level (Nolanaceae; Mesa, 1981; Hunziker, 2001). *Nicandra*, however (the Nicandra clade; Fig. 7B; Table 2), also has a 5-carpellar ovary and the fruit is a fleshy berry. The mericarps of *Nolana* are variously connate (Fig. 4A) when immature, and vary from laterally united and multi-seeded to completely free and single-seeded (Tago-Nakazawa and Dillon, 1999).

Non-capsular dehiscent fruits occur in the Hyoscyamus clade, where most of the genera (with the exception of *Atropa*; Fig. 4B; Table 2) have pyxidia—fruit of this sort has been usually classified as a type of capsule (Roth, 1977; Spujt, 1994), but in the Solanaceae immature fruits of these genera are indistinguishable from immature berries (Fig. 2A, B). The dehiscence line around the circumference develops only as the pericarp dries out, and the entire structure is held tightly or loosely in an accrescent calyx (Fig. 2C, D). Although these sorts of dehiscent fruits have traditionally been considered to be

Table 3. *Monophyletic clades in* Solanum *as defined by Bohs (2002) with the distribution of fruit types in each*

See text for discussion of fruit types.

Clade	No. of species, distribution	Fruit types	Berry colour
Archaesolanum clade	c. 8 spp, Australia, New Guinea, New Zealand	Fleshy berries with copious stone cells	Red or purple
Normania clade	c. 3 spp, Macaronesia, Mediterranean	Fleshy berries with no stone cells	Bright red
African non-spiny clade	c. 7 spp, Africa	Fleshy berries with no stone cells	Red
Potato clade (incl. *Solanum tuberosum* L., *S. lycopersicum* L.)	c. 200–250 spp, New World	Hard or fleshy berries with no stone cells	Mainly green, brightly coloured only in the tomatoes
Morelloid/dulcamaroid clade (incl. *Solanum nigrum* L., *S. duclamara* L.)	c. 130 spp, worldwide	Morelloids: fleshy berries with stone cells	Morelloids: brightly coloured, black red or orange
		Dulcamaroids: fleshy berries without stone cells	Dulcamaroids: bright red, black
Wendlandii/Allophyllum clade	c. 10 spp, New World	Hard and fleshy berries	Green or yellowish
Cyphomandra clade (incl. *Solanum betaceum*)	c. 50 spp, New World	Fleshy berries with copious stone cells	Red, yellow or green
Geminata clade	c. 140–150 spp, New World (mostly)	Mostly hard berries, a few fleshy berries, all without stone cells	Green or yellowish, occasionally red or orange
Brevantherum clade	c. 60 spp, New World	Soft fleshy berries, with stone cells	Green or yellowish, occasionally orange
Lepstemonum clade (the spiny solanums, incl. *Solanum melongena* L.)	c. 450 spp, worldwide	Soft fleshy berries, hard berries, all without stone cells; variously modified non-capsular dehiscent fruits (censer fruits, tumbleweeds)	Green or yellowish, orange or red; dry fruits brownish

capsular (Roth, 1977; Spujt, 1994), it is clear at least in the case of the Solanaceae that pyxidia are highly modified berries. The distribution of this fruit type on the phylogeny shows that it has arisen three times independently, in the Hyoscyamus clade, in *Oryctes* of the Physalis clade and several times (see below) in the genus *Solanum*.

The genus Solanum: evolution and phylogeny

Despite the apparent uniformity of fruit type in this large genus, fruits in *Solanum* show a remarkable range of subtle variation. The colour of berries in *Solanum* varies from black, through red and orange to yellow and green (Table 3; Figs 8, 9). In general, brightly coloured berries tend to be juicy and extremely soft, while those berries that are green at maturity are harder, and are occasionally extremely woody (Symon, 1987). Many of the green berries suddenly become yellower and soft over a period of several hours, at which point they are taken by birds or bats (Knapp, 2002*b*). Bright colour is derived in the tomatoes (Peralta and Spooner, 2001), with the cultivated tomato *Solanum lycopersicum* L. and its close relatives the only taxa in the group with red or orange fruits (Marshall *et al.*, 2001). In other clades of *Solanum*, patterns of fruit colour evolution have not been specifically investigated and are not well understood. As in the Solanaceae as a whole, stone cells (Bitter, 1911, 1914) are widely distributed in the genus *Solanum*, and appear to be confined to particular monophyletic groups (Table 3).

Fruit size in *Solanum* also varies considerably; cultivated varieties of *Solanum lycopersicum* (the tomato) and *S. melongena* L. (the aubergine) can be extremely large (Lippman and Tanksley, 2001; Passam *et al.*, 2001) and weigh up to several kilograms, but wild species also have a wide range of fruit sizes. Some of the smallest solanum fruits occur in the morelloid/dulcamaroid clade, with berries of less than 1 cm in diameter, while the largest wild solanum berry is that of the wolf-fruit, *S. lycocarpon* A. Rich. of the Brazilian cerrados, which can be up to 15 cm in diameter! Placentation patterns in the genus are also quite variable, but all are based upon the 2-carpellate, axillary condition (Nee, 1986; Symon, 1987). Placental enlargement and expansion and an increase in locule number have occurred in isolated species in all clades, not only in those taxa cultivated by humans for their fruits.

Discussion

Discussions of ecologically relevant character evolution must be framed in a phylogenetic context for testable hypotheses to be constructed. Fruit morphology, although traditionally of great importance taxonomically, is one such character of ecological importance. Fruit represent the vehicle for seed dispersal, a critically important stage of a plant's life cycle that is certainly under strong

selective pressure. It is important not only to examine the distribution of the range of fruit types in the group in question, but also to do this using a phylogeny that does not use fruit type in its construction (Bremer and Eriksson, 1992). This is not to say that fruit type and fruit characters are never features that define monophyletic groups. Fruit anatomical characters are important for recognizing generic level relationships in the Oleaceae (Rohwer, 1996) and in the dogwoods (*Cornus*, Cornaceae) the two major clades were congruent with fruit colour and the presence of particular fruit chemicals (Xiang *et al.*, 1996). Members of the family Solanaceae have a relatively restricted suite of fruit types, and homoplasy (structural similarity due to independent origin rather than common ancestry) appears to be less common than in other groups studied (Bremer and Eriksson, 1992; Clausing *et al.*, 2000). In the family, capsules are plesiomorphic, and berries—soft indehiscent fruits—have either evolved once and been lost three times, or have evolved three times independently. Distinguishing between these two hypotheses depends upon the homology of the character 'fruit a berry' in the groups concerned. As mentioned above, *Latua*, while possessing a soft berry structurally very similar to those found in the diverse berry-fruited clade (Olmstead *et al.*'s subfamily 'Solanoideae'), has traditionally been placed in the Petunia clade (Olmstead *et al.*, 1999), based on its alkaloid chemistry. Hunziker (2001), however, places *Latua* in a monotypic tribe related to *Cestrum*. The genera *Cestrum* and *Duboisia* represent berry-fruited members of clades otherwise possessing capsular fruits (Table 2), arguing for the independent (homoplastic) origin of soft, indehiscent fruits in those genera. Some species of *Cestrum* have semi-capsular fruits, where the locules appear to separate at the apex (Francey, 1935). The anatomy of these putatively transitional species will prove of interest, as will structural studies of the vasculature of the berries of *Cestrum* and *Duboisia* compared with that of their capsular-fruited close relatives. In the Melastomataceae, Clausing *et al.* (2000) showed that the anatomical origin of the fleshy portion of the fruit differed in several clades, thus showing that traditional coding of a fruit type character as 'fleshy' or 'dry' was not tenable.

The possession of berries is a synapomorphy of the large, derived clade identified as subfamily 'Solanoideae' by Olmstead *et al.* (1999). This clade (comprising the terminals between the Lycium clade and the Physalis clade; Fig. 6) represents the vast majority of species diversity within the family. Within this clade berries have been lost several times; in the Hyoscyamus clade, where fruits are pyxidia, in the genus *Datura* with capsular fruits with large seeds, and in several other genera where variously dry and modified berries have arisen (Fig. 7A, B; Table 2; Symon, 1979). Homoplastic evolution of derived fruit types in the Solanaceae has involved several losses of soft indehiscent fruits, rather than the reverse as is hypothesized to be the case in other families (Bremer and Eriksson, 1992; Clausing *et al.*, 2000).

The presence of stone cells in the berries of members of this clade is scattered on the tree (Fig. 5B). Interestingly, stone cells never occur in the berries of *Cestrum* or *Duboisia*, lending support to the independent origins of berries in those genera. In both *Lycium* (Lycium clade) and *Lycianthes* (Capsicum clade), stone cells are commonly found in fleshy fruits and a few species (*Lycianthes lycioides* (L.) Hassl., *Lycium* section *Sclerocarpellum* C. Hitchc.; Bernardello, 1986; Miller, 2002) have pyrenes, where the few (usually 2–8) seeds are completely surrounded by a hard, bony endocarp. It is tempting to suppose that the bony endocarp is derived from the stone cells, or vice versa, as suggested by Bitter (1911, 1914). His suggestion that stone cells were the remnants of the bony endocarp of an ancestral drupaceous fruit is not supported by the distribution of fruit types on the molecular phylogeny. Bernardello (1983) examined the ontogeny of fruits of *Lycium* and *Grabowskia* and found that the sclerotic granules from the mesoderm gradually enclosed the seeds, beginning at the apex and proceeding to the base. He concluded that the drupe was the most 'advanced' fruit type in the Solanaceae and that the presence of sclerotic granules (stone cells) was an indicator of fruit specialization. Although *Duckeodendron* and the members of the Goetzea clade do possess drupaceous fruits, recent evidence appears to suggest that they form a single, albeit rather poorly supported, clade (RG Olmstead, personal communication) thus suggesting that true drupes have evolved once as an autapomorphy in that clade. The structural homologies of these drupes and pyrenes have never been assessed (Carlquist, 1988), and the fibrous endocarp of *Duckeodendron* is anatomically quite distinct from the more bony endocarp of the members of the Goetzea clade. The pyrenes found in *Lycium* and *Lycianthes* most probably have an entirely separate origin to the drupes of *Duckeodendron* and *Goetzea*. In *Lycium*, section *Sclerocarpellum* has been shown to be polyphyletic, pyrenes have independently arisen at least twice in the genus (Miller, 2002), in addition to having evolved independently in *Grabowskia*. In the genus *Saracha* (Physalis clade) stone cells are abundant and usually completely enclose a few to most of the seeds in the berry (personal observation; Alvárez, 1996).

Pyrenes in *Lycium* and *Lycianthes*, both members of clades with stone cells in the berries, are derived fruit types, rather than ancestral as suggested Bitter (1911, 1914). It is tempting to speculate that a reduction in seed number coupled with accretion of stone cells around the seed led to the pyrene in all cases where it occurs in the family, but detailed anatomical and developmental studies are lacking (Bernardello, 1983). The mericarps of *Nolana* are also a fruit type probably derived from a berry (Tago-Nakazawa and Dillon, 1999). In young flowers all the

carpels are connate at the base (Di Fulvio, 1971; Bruno, 1994), and each mature mericarp represents a single carpel rather than half a carpel as is the case in Lamiaceae and Boraginaceae (Mesa, 1981). Some structures, perhaps like the stone cells of *Lycium* or the sclerites composing the endocarp of the pyrene of *Grabowskia*, may be involved in mericarp structure and development and it is clear from the sister group relationship of *Nolana* and the Lycium clade (Fig. 7B) that structural homologies should be explored.

The fossil record for Solanaceae is relatively recent, with the earliest fossil known from the Eocene (Collinson *et al.*, 1993) and no inferences can be made based on first occurrence in the Solanaceae of particular fruit types in the fossil record. This Eocene London Clay fossil *Cantisolanum daturoides* EM Reid and MEJ Chandler consists of two seeds, similar in morphology to those occurring in the berry-fruited clade, indicating that fleshy fruits had probably evolved at least by that date. Some European fossils attributable to modern genera (*Physalis*, *Solanum*) have been dated from the middle to late Miocene (Collinson *et al.*, 1993), indicating that these are at least minimum dates for the occurrence of modern fleshy fruits in the Solanaceae. Timings obtained from molecular studies indicate that the Solanales (the inclusive group including the Convolvulaceae) had an origin some 30 million years before the first fossil evidence (82–86 mya versus 53 mya; Wikström *et al.*, 2001). The genus *Nolana* has been estimated to be some 30 million years old (Eocene to Miocene; Tago-Nakazawa and Dillon, 1999), thus development of the apomorphic mericarps of that clade is concomitantly ancient. It is clear from molecular evidence and dating that rapid diversification and speciation in the family occurred in the late Cretaceous to early Tertiary, similar to the pattern of relatively recent evolution found for other species-rich derived clades of angiosperms (Magállon *et al.*, 1999; Magállon and Sanderson, 2001).

Fruit type evolution, while constrained by phylogeny, is also clearly influenced by habitat, including dispersal agents. Several broad generalizations, however, can be made. Capsular fruits, plesiomorphic in the family, are found in taxa that are generally herbaceous or shrubby inhabitants of dry areas. Species of *Nicotiana* for example, are weedy shrubs or herbs found in secondary habitats (Goodspeed, 1954) and are often in dry areas such as the southwestern USA or central Australia. In the Solanaceae, taxa with capsular fruits also tend to have very small seeds (e.g. *Nicotiana*, with thousands of seeds <0.25 mm long in a single capsule) or strongly winged seeds (e.g. *Sessea* and *Metternichia*). Small seeds and capsular fruit have been associated with dry, open habitats, while larger seeded fruits have been associated with closed forests (Eriksson *et al.*, 2000). To a certain extent this holds true for the Solanaceae, *Duckeodendron* is a large canopy tree of Amazonia, while *Schizanthus* is a herb of dry coastal Chile, but all the members of the Goetzea clade, also with drupes, occur in dry areas of the Caribbean.

Seed dispersal by animals has also been implicated in the evolution of fleshy fruits in angiosperms as a whole (Tiffney, 1984; Eriksson *et al.*, 2000). Janson (1983) suggested that fruit size, colour and morphology are adapted to the characteristics of animals that eat that fruit, but his study did not take into account the effects of phylogeny on the distribution of fruit morphologies in the forests he studied. In the Solanaceae, fleshy berries are eaten and the seeds dispersed by a wide variety of vertebrates, including birds, bats and small rodents (Symon, 1979; Cipollini and Levey, 1997*a*, *b*, *c*; Tewksbury and Nahban, 2001; Knapp, 2002*b*).

It is perhaps more illuminating to look at habitat characteristics associated with the evolution of dry, dehiscent fruits in the large berry-fruited clade than to attempt to explain the origin of fleshy fruits as an adaptation to animal dispersal. In the Hyocyamus clade, with the exception of *Atropa* with a fleshy berry (Fig. 4B), the dry fruits open within the calyx (Fig. 2). In the endemic Tibetan genus *Przewalskia*, the unit of inflated calyx plus dry fruit sometimes acts as a tumbleweed, scattering seeds as it blows through the habitat (M Gilbert, personal communication). In many species of *Hyoscyamus*, seeds are scattered by wind as the dry inflorescence is moved about, and in *Scopolia*, the entire plant dries up and falls to the ground, ripe dehiscent fruit and all (Hoare and Knapp, 1997). Species of *Nolana* all occur in arid to semi-arid habitats along the west coast of South America, and the mericarps are, in general, passively distributed. A persistent accrescent calyx serves as a cup to contain the loose mericarps, and in one annual species, the entire plant curls up at anthesis, breaks free and acts as a tumbleweed (MO Dillon, in litt.). Species of *Datura* also all occur in dry or seasonally dry habitats, where their seeds, with an oily elaiosome (Persson *et al.*, 1999) are collected by ants. All of the species of *Solanum* that possess derived, dry and dehiscent fruit types occur in dry habitats (Symon, 1984; Lester and Symon, 1989; Whalen, 1979). Members of *Solanum* section *Androceras* (Whalen, 1979) are all dispersed as tumbleweeds, and the seeds drop out of the enclosing calyx as the plant is blown about (Fig. 9E). The Australian species with censer mechanisms and the Mexican species with a splash cup fruit (Fig. 9F) all have seed dispersal assisted by knocking or rain. That all these dry and variously dehiscent fruit types derived from fleshy berries are found on species occurring in arid zone habitats suggests that environmental factors have been important in the convergent and multiple evolution of these fruit types in the Solanaceae.

Secondary chemistry of fruits is an important factor influencing seed dispersers and predators. Many ripe fleshy fruits whose primary function is to attract seed dispersers also contain unpleasant chemicals that deter consumption

by vertebrates. This apparent paradox has drawn the attention of those interested in the adaptive roles of fruit traits (Cipollini and Levey, 1997a, b, c), but this phenomenon has rarely been addressed in the light of phylogenetic constraints (Cipollini *et al.*, 2002). Theoretically, differences in seed dispersal quality should influence the evolution of fruit traits (Janson, 1983), but this has not been supported for fruit type using null phylogenetic models (Bremer and Eriksson, 1992; Herrera, 1992). In the Solanaceae, secondary chemistry has been studied in the chile peppers (*Capsicum*) and in the diverse genus *Solanum*, where wide variation exists. Chile peppers have high concentrations of the extremely pungent chemicals, capsaicinoids, in both ripe and unripe fruits (Kosuge and Furata, 1970; Contreras-Padilla and Yahia, 1998). As pepper fruits ripen, pungency decreases due to peroxidase degradation (Contreras-Padilla and Yahia, 1998), but ripe bird peppers (*Capsicum annuum* L.), although attractive to and eaten by birds, still contain enough pungent compound to deter mammals (Tewksbury and Nabhan, 2001). Tewksbury and Nabhan (2001) found that the hypothesis of directed deterrence—where chemicals in ripe fruit function selectively to discourage seed predators while not deterring seed dispersers—was supported in *Capsicum* using populations in the southwestern USA. The small mammal seed predators were put off by the pungency of pepper fruits, while dispersers, birds, were not. Selective pressures influencing the acquisition and retention of toxic chemicals in fruits are likely to be the results of trade-offs associated with differing ecological requirements at different life stages of the plant.

The directed deterrence hypothesis has also been tested in the genus *Solanum*, where fruit secondary chemistry is well known. *Solanum* fruits have widely varying concentrations of toxic steroidal glycoalkaloids such as solasodine (Carle, 1981; Cipollini *et al.*, 2002). In the morelloid clade, the concentrations of these compounds decrease dramatically as fruit matures, while in many members of the spiny solanums, concentrations remain high at fruit ripeness (Cipollini and Levey, 1997c). It has been suggested that these compounds act as antifungal defences (Cipollini and Levey, 1997b) or act to deter seed predators (as in *Capsicum* above; Cipollini and Levey, 1997a). Cipollini and Levey (1997a, b, c) found that the directed deterrence hypothesis was not supported in *Solanum*; seed predators and dispersers alike were deterred by fruit secondary chemicals. Intriguingly, Wahaj *et al.* (1998) found that alkaloids in the ripe fruits of *S. americanum* (a member of the morelloid clade) affected gut retention time of seeds, suggesting that chemicals may influence seed deposition patterns by frugivores. Amazonian maned wolves expel worms after eating the fruits of *S. lycocarpon*, suggesting they are perhaps using the secondary chemicals contained therein as a vermifuge (S Knapp, personal observation; Courtenay, 1994; Cipollini *et al.*,

2002). A multiplicity of purposes may be served by fruit secondary chemicals, some of which have simple adaptive explanations, but others are more complex. Examining the phylogenetic context in which these fruit chemistry characteristics are found led Cipollini *et al.* (2002) to conclude that phylogeny does not have an important influence on fruit chemical or morphological trait variation within the species they studied. Their preliminary data are intriguing because they suggest that rather than seeking explanations using just phylogeny or ecology, it will be more profitable to investigate the interaction of phylogeny and ecology with respect to the evolution of fruit traits. Real understanding of the evolution of a wide variety of fruit traits, however, will only come with an integration of the study of phylogeny, ecology and development, as it is their interaction that ultimately determines phenotype.

With the exception of the crucifer *Arabidopsis thaliana* (L.) Heynh., members of the Solanaceae are among the best understood of flowering plants in terms of their genomes, largely due to their importance to agriculture. The understanding of the genetic regulation of fruit shape and size in the tomato (*Solanum lycopersicum*) has benefited greatly from a comparative approach using a few closely related species (Grandillo *et al.*, 1996; Frary *et al.*, 2000; Lippman and Tanksley, 2001), but such studies are rarely put into a wider phylogenetic context. The molecular underpinnings of both fruit development (Gu *et al.*, 1998; Liljegren *et al.*, 2000; Ferrándiz *et al.*, 1999, 2000) and fruit ripening (Giovannoni, 2001) have been intensively studied in recent years, and it is clear that the commonalities of genetic control systems and regulatory mechanisms will allow new questions to be asked about the evolution of fruit types and fruit traits such as colour or secondary chemistry. Studies undertaken in tomatoes with respect to fruit size and shape (see references above; Gautier *et al.*, 2001; and for peppers, Aloni *et al.*, 1999), chemical composition (Klann *et al.*, 1996; D'Aoust *et al.*, 1999), coloration changes during ripening (Giovannoni, 2001) and locule number (Lippman and Tanksley, 2001) will all be of interest in light of the variety of fruit traits such as colour (brightly coloured to green at maturity), fruit texture (soft and juicy to hard and woody) and fruit size (small, e.g. *Solanum americanum* to extremely large, e.g. *S. lycocarpon*) that have evolved via natural selection in *Solanum*.

At the family level recent studies of the molecular regulation of fruit development will be of interest as well. The variety of dehiscence mechanisms present in the Solanaceae (septicidal and loculicidal capsules, dehiscent non-capsular fruit) may allow the elucidation of how the *SHATTERPROOF* MADS-box genes (Ferrándiz *et al.*, 2000) influence a variety of dehiscence types in closely related organisms. Lignification, perhaps like that involved in the dehiscence mechanism of *Arabidopsis* (Ferrándiz *et al.*, 2000; Liljegren *et al.*, 2000), is also involved in the

development of the hard berries found in many clades of *Solanum* (Symon, 1987), but neither developmental nor anatomical homology of these processes is well understood.

Conclusions and possible directions for future work

Because several important fruit crops are found in the family Solanaceae and molecular developmental studies on these taxa have been extensive, the family represents an ideal testing ground for the comparative study of the development and evolution of fruit traits in a phylogenetic context. Important too is the study of plants in their native environments—the selective pressures that, over time, have resulted in the huge variety of fruit types observed today had their origins in interaction with the environment, including dispersers and predators. The phylogeny of the family is currently being studied by a variety of workers, using both molecular (Olmstead *et al.*, 1999; Bohs and Olmstead, 2001; Bohs, 2002) and morphological characters (Knapp *et al.*, 1998; Estrada and Martínez, 1999; Bohs, 2001; Knapp, 2002*b*). This analysis, though a preliminary one, has suggested some areas for further investigation into fruit evolution in the Solanaceae. (1) *Cestrum* and *Duboisia* berries—do they have independent origins? Developmental trajectories of berries in the clades in which they occur may shed light on this question. (2) Drupes of *Duckeodendron* and Goetzea clade—morphology and development—are they homologous? (3) *Datura* capsules—how are they derived from berries? (4) Evolution of pyxidia—the mechanics of dehiscence mechanisms. (5) Molecular biology of rapid ripening in bat-dispersed *Solanum* berries. (6) The distribution of 'fruit ripening genes' in *Solanum*—is there a correlation with berry type?

These are by no means the only fruit traits of interest in the family, but they are clearly areas where phylogeny and development could profitably interact to shed new light on previously under-investigated problems. Such future study will require the collaborative efforts of taxonomists, developmental biologists, anatomists and molecular biologists. Using the comparative framework provided by phylogeny, insights gained from the study of fruit traits in single species important for agriculture or genomic studies will have a wider evolutionary relevance.

Acknowledgements

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