

RADIATION OF POLLINATION SYSTEMS IN THE CAPE GENUS *TRITONIOPSIS* (IRIDACEAE: CROCOIDEAE) AND THE DEVELOPMENT OF BIMODAL POLLINATION STRATEGIES

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Floral morphology and observations on insect and avian visitors to species of the southern African and largely Western Cape genus *Tritoniopsis* indicate that short-tubed pink flowers, ancestral in the genus, are pollinated by anthophorine bees foraging for nectar. Multiple shifts to more specialized pollination systems have occurred in the genus during its evolution. Four species with elongate floral tubes and a pink to red bilabiate perianth are pollinated either by sunbirds (*Nectarinia*) alone or by sunbirds and the satyrid butterfly *Aeropetes tulbaghia*. Another red-flowered species with an actinomorphic flower is inferred to be pollinated only by *Aeropetes*, while two species with pale pink flowers with red markings are pollinated by long-proboscid flies in the genus *Prosoeca* (Nemestrinidae). *Tritoniopsis parviflora* is unique in the African Iridaceae in producing floral oils as a reward to the short-tongued bee *Rediviva gigas* (Melittidae), as well as conventional sugar nectar. *Tritoniopsis nervosa* has white, sweetly scented, long-tubed flowers and is assumed to be pollinated by night-flying moths. Although relationships within *Tritoniopsis* are poorly understood, it is clear that at least five shifts in pollination strategy have occurred in this genus of just 24 species. Studies also show that bimodal pollination systems using two different pollinator groups occur in several species, using sunbirds and *Aeropetes*, anthophorine bees and nemestrinid flies, or oil-collecting *Rediviva* and nectarivorous bees. Such bimodal systems are probably important for the successful reproduction of these plants.

Keywords: sunbirds (*Nectarinia*), bees (*Amegilla*, *Anthophora*), butterflies (*Aeropetes*), long-proboscid flies (*Prosoeca*), sphinx moths (Sphingidae).

Introduction

Tritoniopsis, a genus of 24 species of Iridaceae subfamily Crocoideae, is endemic to South Africa and subendemic to the summer-dry Cape Floristic Region, with a single species extending into the summer rainfall region in Eastern Cape Province (Manning et al. 2002). The genus is taxonomically isolated in the subfamily (Goldblatt et al. 2005) and is distinguished by several autapomorphies, in particular the unusual leaves, which lack a definite midrib and instead have one or more equally developed main veins, and by the floral bracts. These are short and firm textured, with the inner bract longer than the outer, and similar in texture and shape, not bifid like the inner bracts of other genera in the subfamily. In addition, the flowers are usually spirally arranged in the mature spike rather than secund or distichous.

The genus is characteristic of acidic oligotrophic soils in winter rainfall southwestern South Africa, although a few species, notably *T. antholyza* and *T. burchellii*, also occur on clay soils, and *T. elongata* is restricted to this soil type. Most of the species are summer flowering, at which time the leaves are usually dry and withered. Flowering is generally stimulated by fire, especially in *T. parviflora*, which does not

flower in the wild unless the vegetation has been burned the previous season. All of the species have a deeply buried corm covered with tough, fibrous tunics.

Despite its taxonomic isolation and relatively uniform vegetative morphology, *Tritoniopsis* exhibits such a high degree of floral variation that the species currently placed in the genus were initially allocated to four genera depending on the form of their flowers. Three of these, *Exohebea*, *Tanaosolen*, and *Tritoniopsis* were united by Lewis (1959), but the segregation of the species with red flowers and curved, dimorphic perianth tubes into the genus *Anapalina* continued for another 30 yr until it was realized that this floral form represents an adaptation to bird pollination (Goldblatt 1990). Aside from this inference, very little data have been published on pollination of *Tritoniopsis*. Two red-flowered species, *T. lesliei* and *T. longituba* (G. J. Lewis) Goldblatt (= *T. antholyza*), were listed as conforming to the *Aeropetes tulbaghia* (Lepidoptera: Satyridae) pollination system by Johnson and Bond (1994), who characterized *Aeropetes* pollination as facultative to bird pollination in *T. triticea*. Goldblatt et al. (1999) included *T. burchellii*, *T. caffra*, and *T. triticea* in their survey of bird pollination in the Iridaceae. The only well-documented account of pollination in the genus is the discovery that *T. parviflora* secretes floral oils and is pollinated by the oil-collecting bee *Rediviva gigas* (Manning and Goldblatt 2002). This is the only record of oil secretion in subfamily Crocoideae or any African member of the Iridaceae. Clearly,

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then, the genus exhibits a diversity of pollination strategies commensurate with its floral variation. This study presents the results of pollination studies on 21 of the 24 species in the genus and confirms that the pollination biology of *Tritoniopsis* is as diverse as that found in other genera in Crocoideae in southern Africa (Goldblatt et al. 2001) of comparable size or larger.

Material and Methods

Floral Phenology and Seasonality

Flowers of selected species (tables 1, 2) were observed for timing of anthesis (i.e., opening of individual buds), anther dehiscence, expansion of stigmatic lobes, and subsequent withering of the perianth. Data on flowering time are taken from Manning et al. (2002). Plant vouchers (table 1) are deposited in NBG and/or MO.

Nectar Analysis

Nectar volume measurements were taken from unbagged flowers in the field, reflecting the balance between rates of secretion and depletion, and from spikes that had been picked and kept in water overnight. Cut stems were sampled the following morning before any change in nectar characteristics could begin (Goldblatt et al. 1998b). Nectar was withdrawn from the base of the floral tube of picked flowers with 2- μ L capillary tubes after removing the ovary. This technique is suitable in Iridaceae, where the potential for cell sap, produced by separating the ovary and perianth, to dilute the nectar is insignificant. Only fully open flowers in the male phase were sampled. We determined by sampling flowers of different ages that nectar concentration does not change over the life of a flower until fertilization (during the female phase), when sugar concentration drops and fading begins.

The percentage of sucrose equivalents in fresh nectar was measured using a Bellingham and Stanley handheld refractometer (0%–50%). Additional nectar samples were dried on Whatman no. 1 filter paper and analyzed by B.-E. van Wyk, Rand Afrikaans University, Johannesburg, using HPLC sugar analysis.

Fragrance Analysis

Presence of floral fragrance was noted with the human nose. The possible presence of scents too weak to be detected in the open air was investigated by placing several individual flowers in clean, lidded glass jars and storing them in a warm place out of direct sunlight. The contents of each jar were sniffed after 30 min.

The scent of selected species of each flower type with detectable fragrance was sampled for chemical analysis by using a vacuum pump to draw air through glass capillary tubes packed with Poropak from glass chambers containing fully open flowers on cut inflorescences placed in water. Sampling was conducted for 48 h per species so that sufficient scent compounds for measurement were accumulated. Fragrance chemistry was analyzed by R. Kaiser, Givaudan-Roure Research, Switzerland, by gas chromatography using a DB-Wax Capillary column (Kaiser 1993).

Pollinator Observations

Populations of 21 species of *Tritoniopsis*, representing all five flower types in the genus, were observed for pollinator activity. Populations were visited for several hours, either from sunset (the *T. nervosa* floral type) or midmorning to late morning (remaining floral types) (table 2). These periods have been established as the most active for nocturnal and diurnal pollinators, respectively (Goldblatt et al. 2001). All floral visitors were recorded. Insects were captured and identified by V. Whitehead, South African Museum, Cape Town. Birds and the butterfly *Aeropetes* were identified by sight. Sites of pollen deposition on the bodies of animals were observed and noted using methods described elsewhere by Goldblatt et al. (1998a, 2000a, 2000b, 2004a).

Results

Floral Phenology and Seasonality

Tritoniopsis species are seasonal, cormous geophytes of small to moderate size, typically 20–50(–150) cm high. Individuals produce a single unbranched or, less commonly, branched flowering stem annually, and flowering is synchronized in a population. Inflorescences are spikes with spirally arranged flowers except in *T. caffra*, in which the spike is distichous. The inflorescence axis is firm textured and slender or relatively thick. Flowering occurs mainly in summer and autumn, between December and April, and rarely earlier, from late September (table 2). This is later than the period of optimal growth in the Cape region, from late winter to spring (July to September), and the leaves of the plants are therefore often withered or drying at flowering.

Flowering is acropetal, with individual flowers opening sequentially in the early morning. The perianth remains open throughout the life of the flower and does not exhibit closing movements at night. Flowers of all species of *Tritoniopsis* are protandrous and markedly herkogamous (table 3). Flowers remain fresh for 4–5 d, with the stigma apparently receptive for an additional day after withering of the perianth. The male phase lasts for the first 3 d, followed by the functionally female phase. Two patterns of anther dehiscence are evident. In *T. elongata*, *T. lesliei*, and *T. ramosa*, all three anthers dehisce on day 1, but in the remaining species examined, the median anther dehisces first, on day 1, followed by the dehiscence of the lateral anthers on day 2. The anthers remain in this condition for a full day following lateral anther dehiscence. On the day following this (day 3 or 4), the filaments curve upward and diverge slightly (except in *T. caffra*, in which they lift upward to lie beneath the dorsal sepal) so that the anthers are removed from possible contact with the stigma, which descends into the position previously occupied by the anthers. On day 4 or 5, the stigmatic arms expand and appear to be receptive. The female phase lasts for 2 d, including the day on which the stigma expands. On day 5 or 6, the perianth becomes visibly wilted and partly collapsed, although the style branches remain firm and apparently receptive for a further day before withering. Thus, although the perianth remains expanded for 4 or 5 d, the functional life of the flower appears to extend for an additional day.

Table 1
Study Sites and Voucher Information for Species of *Tritoniopsis* Studied

Species	Study site; observation time	Voucher
<i>T. antholyza</i> (Poir.) Goldblatt:		
Site 1	Piekenierskloof Pass; NA	<i>Emdon 81</i>
Site 2	Clanwilliam, Pakhuis Pass; NA	<i>Taylor 11684</i>
Site 3	Near Grabouw; NA	<i>Maguire 1229</i>
Site 4	Western Cape, Redhill; NA	<i>Taylor 7662</i>
Site 5	Sir Lowry's Pass; NA	<i>Kruger 121</i>
Site 6	Villiersdorp, Stettynsberg; NA	<i>Manning s.n. no voucher</i>
<i>T. bicolor</i> J.C. Manning & Goldblatt (2 h)	Near Bredasdorp; 1230–1330	<i>Manning 2286</i>
<i>T. burchellii</i> (N.E. Br.) Goldblatt (7 h):		
Site 1	Bainskloof; NA	<i>Goldblatt & Manning 10119</i>
Site 2	Near Botrivier; 1100–1300	<i>Goldblatt & Nänni 10572</i>
Site 3	Kogelberg; NA	<i>Manning 1050</i>
Site 4	Kleinmond; midmorning	<i>Goldblatt & Nänni 11276</i>
<i>T. caffra</i> (Ker Gawl. ex Baker) Goldblatt (7 h):		
Site 1	Near George; 1100–1230	<i>Goldblatt & Porter 12271</i>
Site 2	Riversdale, Garcias Pass; midmorning	<i>Manning 2914</i>
Site 3	Near Storms River; NA	<i>Goldblatt 5241</i>
<i>T. caledonensis</i> (R. C. Foster) G. J. Lewis (2 h)	Highlands; 1030–1130	<i>Manning s.n. no voucher</i>
<i>T. dodii</i> (G.J. Lewis) G.J. Lewis (2 h):		
Site 1	Cape of Good Hope Nature Reserve; NA	<i>Goldblatt 1558</i>
Site 2	Cape Peninsula, Scarborough; 1030–1130	<i>Manning s.n. no voucher</i>
<i>T. elongata</i> (L. Bolus) G. J. Lewis (3 h)	Elandsberg Estate, Hermon; 1000–1130	<i>Goldblatt & Manning 11280</i>
<i>T. flexuosa</i> (L.f.) G.J. Lewis	Near Caledon; NA	<i>Goldblatt & Manning 10889</i>
<i>T. lata</i> (L. Bolus) G. J. Lewis (2 h):		
Site 1	Hills near Grabouw; NA	<i>Goldblatt & Nänni 11296</i>
Site 2	Highlands; 1100–1200	<i>Manning 2309</i>
<i>T. lesliei</i> L. Bolus (6 h)	Ceres, Cascades; 1100–1400	<i>Manning 2724</i>
<i>T. nemorosa</i> (E. Mey. ex Klatt) G. J. Lewis (6 h)	Near Citrusdal; 0930–1130	<i>Manning 2278</i>
<i>T. nervosa</i> (Baker) G. J. Lewis (12 h):		
Site 1	Near Citrusdal; morning and evening	<i>Manning 2306</i>
Site 2	Dasklip Pass, Porterville; NA	<i>Goldblatt 10448</i>
<i>T. parviflora</i> (Jacq.) G. J. Lewis (4 h)	Kogelberg; 1230–1300	<i>Manning 2283</i>
<i>T. pulchella</i> G. J. Lewis (4 h)	Highlands; 1100–1200	<i>Manning 2308</i>
<i>T. pulchra</i> (Baker) Goldblatt (4 h):		
Site 1	Elim; midmorning	<i>Goldblatt & Manning s.n. no voucher</i>
Site 2	Pearly Beach; NA	<i>Manning s.n. no voucher</i>
<i>T. ramosa</i> (Eckl. ex Klatt) G. J. Lewis (8 h):		
Site 1	Viljoens Pass; 1130–1300	<i>Goldblatt & Nänni 11275</i>
Site 2	Ceres, Cascades; 1100–1330	<i>Manning 2725</i>
<i>T. revoluta</i> (Burm.f.) G.J. Lewis (4 h):		
Site 1	Ladismith, Buffelskloof; 1100–1300	<i>Goldblatt & Manning 8865</i>
Site 2	Near Potberg; NA	<i>Goldblatt & Manning 10182</i>
<i>T. toximontana</i> J. C. Manning & Goldblatt (10 h)	Gifberg plateau; 1000–1500	<i>Manning 2234</i>
<i>T. triticea</i> (Burm.f.) Goldblatt (6 h):		
Site 1	Cape Peninsula, Glencairn; 1100–1230	<i>Goldblatt & Manning s.n. no voucher</i>
Site 2	Cape Town, Table Mountain; 1000–1130	<i>Manning s.n. no voucher</i>
<i>T. unguicularis</i> (Lam.) G. J. Lewis (4 h):		
Site 1	Bredasdorp; 1100–1200	<i>Manning 2287</i>
Site 2	Cape Town, Table Mountain; 1100–1200	<i>Goldblatt & Manning 9486</i>
<i>T. williamsiana</i> Goldblatt (3 h)	Hermanus, Vogelgat; 1100–1230	<i>Goldblatt 8471</i>

Note. Time of observation is given for pollinator observations but not for populations used only to obtain nectar samples, which are marked NA. All sites are in Western Cape, South Africa. Number of hours of observation for pollinator visitors is indicated after each species name (total time for pollinator observations = 96 h).

Floral Types

Five floral groups can be distinguished in *Tritoniopsis* on the basis of perianth shape, pigmentation, and attractants (table 2; figs. 1, 2). In the *T. ramosa* group (13 spp.) flowers are zygomorphic, strongly bilabiate, gullet shaped, and are held

horizontally (fig. 1A–1F). The perianth tube is funnel shaped and short, 2–10(–20) mm long. The tepals are narrowly oblanceolate, with the upper (adaxial) tepal held erect or arched. The upper laterals are directed forward proximally and spreading or recurved in the distal half, while the lower three

Table 2
Floral Characteristics of *Tritoniopsis* Species Arranged according to Flower Type

Species	Flower shape	Flower color	Tube length (mm)	Fragrance	Reward (nectar/oil)	Flowering time
<i>T. ramosa</i> group:						
<i>T. bicolor</i>	Gullet	Yellow and maroon	2–5	Sweet-acrid	Nectar	Dec.
<i>T. caledonensis</i>	Gullet	Pale yellow	Ca. 3	Acrid	Traces of nectar	Nov.
<i>T. dodii</i>	Gullet	Pink with red streaks	5–8	None	Nectar	Feb.–Apr.
<i>T. elongata</i>	Gullet	Pink with red streaks	6–8	None	Nectar	Mar.–Apr.
<i>T. flava</i>	Gullet	Yellow with maroon streaks	4–5	Unknown	Unknown	Dec.
<i>T. lata</i>	Gullet	Pink with red streaks	7–10	None	Nectar	Feb.–May
<i>T. latifolia</i>	Gullet	Pink with red streaks	8–10	Unknown	Unknown	Dec.–Jan.
<i>T. nemorosa</i>	Gullet	Yellow with maroon streaks	Ca. 8	None	Nectar	Nov.–Jan.
<i>T. parviflora</i>	Gullet	Yellow and maroon	3–5	Sweet-acrid	Nectar and oil	Nov.–Jan.
<i>T. pulchella</i>	Long-tubed gullet	Pink with red streaks	12–20	None	Nectar	Dec.–Feb.
<i>T. ramosa</i>	Gullet	Pink with red streaks	7–20	None	Nectar	Jan.–Apr.
<i>T. unguicularis</i>	Gullet	Cream with dark streaks	Ca. 3	Acrid	Nectar	Dec.–Mar.
<i>T. revoluta</i> group:						
<i>T. flexuosa</i>	Long-tubed gullet	Pink with red streaks	35–40	None	Nectar	Jan.–Feb.
<i>T. revoluta</i>	Long-tubed gullet	Pink with red streaks	(20–)40–70	None	Nectar	Mar.–May
<i>T. toximontana</i>	Long-tubed gullet	Pink with red streaks	Ca. 20	None	Nectar	Mar.–May
<i>T. nervosa</i> group:						
<i>T. nervosa</i>	Tubular	White to cream	30–40	Sweet, lily-like	Nectar	Dec.–Jan.
<i>T. lesliei</i> group:						
<i>T. lesliei</i>	Salver shaped	Red	20–25	None	Nectar	Feb.–Apr.
<i>T. triticea</i> group:						
<i>T. antholyza</i>	Cylindrical	Pink to red	25–30	None	Nectar	Nov.–Apr.
<i>T. burchellii</i>	Cylindrical	Red with black marks	30–40	None	Nectar	Feb.–Apr.
<i>T. caffra</i>	Cylindrical	Red	20–30	None	Nectar	Sept.–Dec.
<i>T. intermedia</i>	Cylindrical	Salmon to red with black marks	25–30	None	Unknown	Sept.–Dec.
<i>T. pulchra</i>	Cylindrical	Deep salmon	30–33	None	Nectar	Feb.–June
<i>T. triticea</i>	Cylindrical	Red with black marks	25–30	None	Nectar	Feb.–Apr.
<i>T. williamsiana</i>	Cylindrical	Orange-red	20–30	None	Nectar	Dec.–Jan.

(abaxial) tepals are more or less joined at the base to form a lower lip. The filaments are inserted shortly below the mouth of the tube and are unilateral and more or less arcuate, with the anthers held parallel and contiguous. The perianth color is often pink but sometimes cream colored or pale to bright yellow, sometimes with the tepals partially maroon (table 2). The lower three tepals are invariably marked with median streaks of dark red or maroon, assumed to be nectar

guides. Pink-colored flowers are always unscented, but the cream-colored or yellow flowers may have a sweet-acrid or acrid fragrance. In the *T. revoluta* group (two spp.), flowers are similar to the pink flowers of the first group but have an elongate perianth tube (20–)35–70 mm long (fig. 1G).

Flowers in the *T. nervosa* group (one sp.) are held horizontally and are zygomorphic and tubular, with oblanceolate tepals that spread or recurve from the base. The perianth tube

Table 3
Floral Phenology of *Tritoniopsis* Species

Species	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
<i>T. burchellii</i>	Pe, Am	Al	...	Ar	Sde	Pw	Sw
<i>T. caffra</i>	Pe, Am	Al	Amr, Sd	Alr, Se	...	Pw	Sw
<i>T. elongata</i>	Pe, Aml	...	Ar, Sd	Se	Pw	Sw	...
<i>T. lata</i>	Pe, Am	Al	...	Ar, Sde	Se	Pw	Sw
<i>T. lesliei</i>	Pe, Aml	...	Ar, Sd	Se	Pw	Sw	...
<i>T. nervosa</i>	Pe, Am	Al	...	Ar, Sd	Se	Pw	Sw
<i>T. pulchella</i>	Pe, Am	Al	...	Ar, Sde	Se	Pw	Sw
<i>T. ramosa</i>	Pe, Aml	...	Ar, Sd	Se	Pw	Sw	...
<i>T. triticea</i>	Pe, Am	Al	...	Ar	Sde	Pw	Sw

Note. Am = median anther dehiscence; Al = lateral anthers dehiscence; Ar = anthers recurve; Pe = perianth expands; Pw = perianth withers; Sd = stigma drops to position previously occupied by anthers; Se = stigmatic arms expand; Sw = stigma withers.

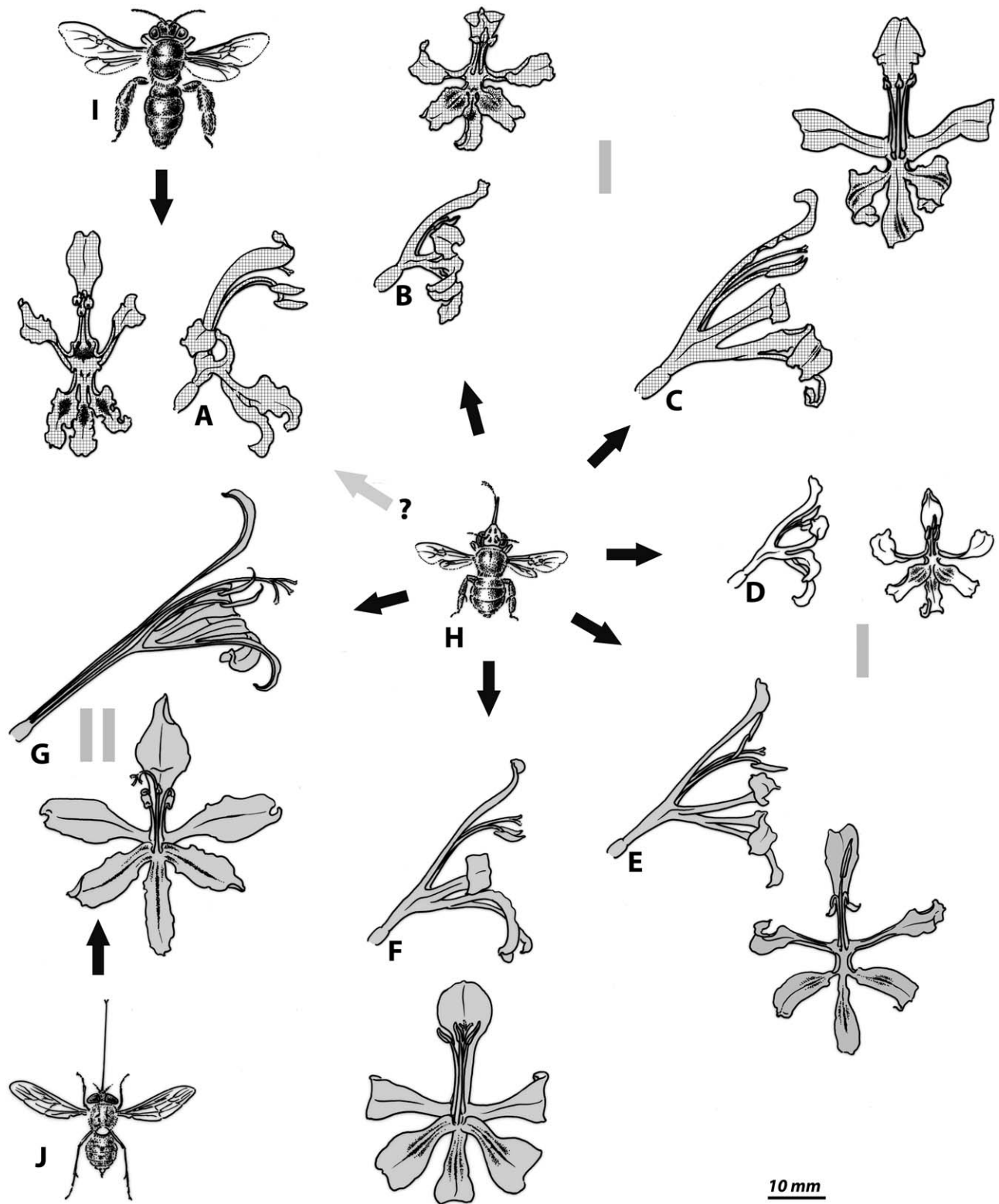


Fig. 1 Pollination systems in *Tritoniopsis*. I, *T. parviflora* flower type (A–F). II, *T. revoluta* (G) flower type. A, *T. parviflora*. B, *T. caledonensis*. C, *T. nemorosa*. D, *T. unguicularis*. E, *T. ramosa*. F, *T. lata*. G, *T. toximontana*. Pollinators: H, *Amegilla spilostoma* (Hymenoptera: Apidae). I, *Rediviva gigas* (Hymenoptera: Melittidae). J, *Prosoeca* sp. (Diptera: Nemestrinidae). Flower colors: shading = pink, cross-hatching = yellow, none = white or cream. Arrows indicate flowers visited by particular pollinators.

is narrowly cylindrical throughout and 30–40 mm long (fig. 2A). The perianth is white or cream colored without distinct nectar guides, and the flowers emit a sweet, lily-like fragrance. The filaments are inserted in the mouth of the tube and are short, unilateral, and straight, with the anthers held parallel and contiguous.

In the *T. lesliei* group (one sp.), flowers are held vertically and are actinomorphic and salver shaped, with elliptical tepals that spread horizontally from the base (fig. 2B). The narrowly cylindrical perianth tube is 20–25 mm long, with the promi-

nently displayed stamens inserted in the mouth of the tube and symmetrically arranged around the central style. The perianth is brilliant red without nectar guides and is odorless.

Last, in the *T. triticea* group (seven spp.), flowers are zygomorphic and widely cylindrical to trumpet shaped and are held horizontally (fig. 2C–2E). The perianth tube, 20–40 mm long, consists of a narrow proximal portion that widens abruptly into a broader cylindrical distal portion. The tepals are oblanceolate to oblong, and the uppermost is usually held erect (sometimes recurving later), while the other tepals are

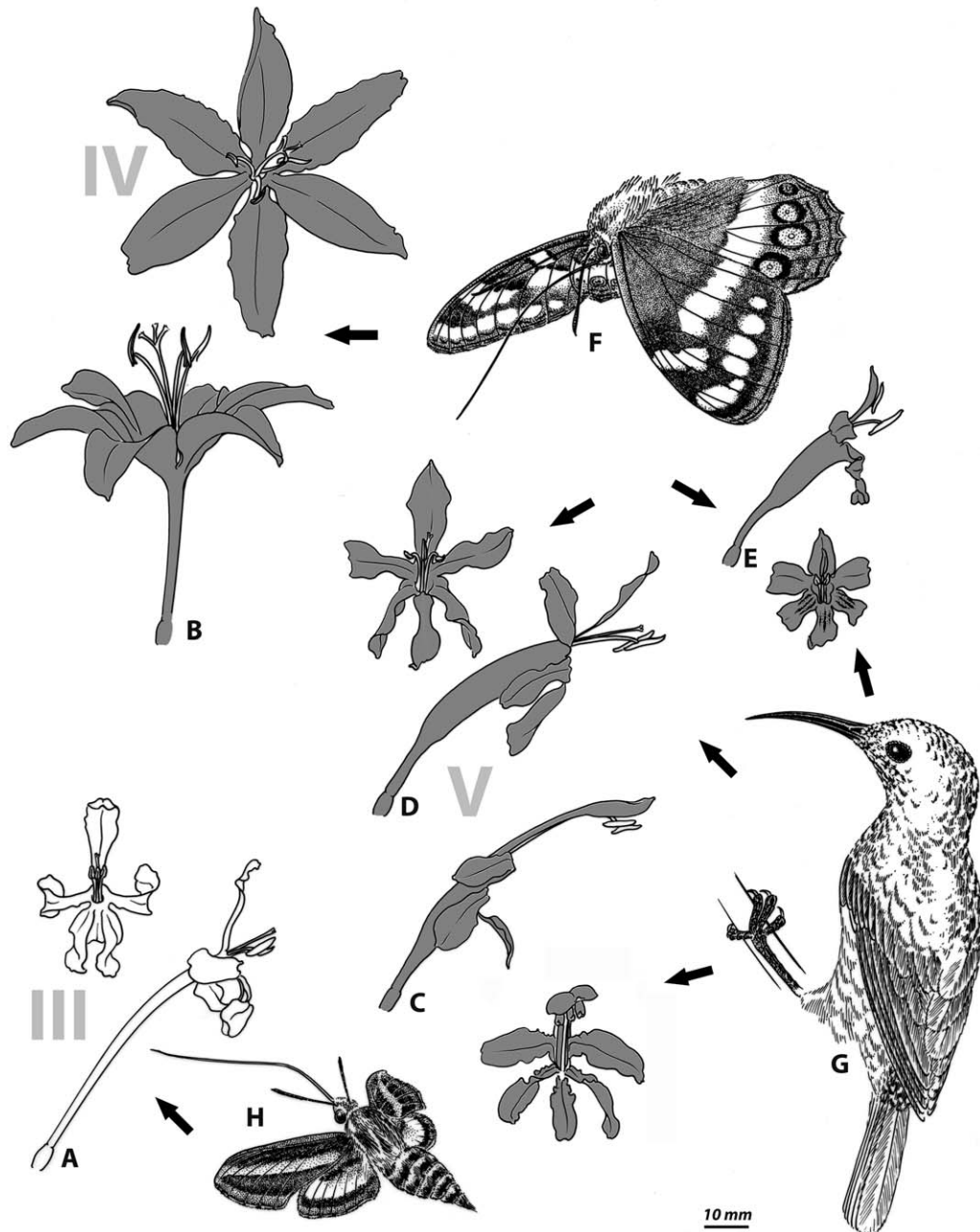


Fig. 2 Pollination systems in *Tritoniopsis*. A, *T. nervosa*. B, *T. lesliei*. C, *T. caffra*. D, *T. burchellii*. E, *T. triticea*. Pollinators: F, *Aeropetes tulbaghia* (Lepidoptera: Satyridae). G, Lesser Double-Collared Sunbird (Aves: Nectarinidae). H, *Hyles lineata* (Lepidoptera: Spingidae). Flower colors: dark shading = red, none = white or cream. Arrows indicate flowers visited by particular pollinators.

typically recurved from anthesis. The tepals are either subequal or the lower three are much smaller (*T. intermedia*). The filaments are inserted well within the perianth tube, at the junction between the lower and upper portions, and are unilateral and arcuate, with the anthers parallel and contiguous. The perianth is yellowish pink, deep salmon pink, or red, either without nectar guides or with prominent black streaks or markings on the lower tepals. The flowers are never fragrant.

Floral Fragrance

Floral fragrance was detected in only five of 21 species that were tested (table 4), and three representatives were selected for head space analysis. Fragrance is secreted throughout the day and night. Four of the fragrant species belong to the *T. ramosa* group, and the fifth is the single species of the *T. nervosa* group. The fragrance in the two groups is markedly different and dominated by different biosynthetic classes of compounds (table 4). Fragrant species in the *T. ramosa* group produce an acrid (*T. caledonensis*, *T. unguicularis*) or sweet-acrid (*T. bicolor*, *T. parviflora*) odor that is rich in benzenoid compounds. The fragrance in *T. bicolor* is dominated by the benzenoid esters methyl salicylate (55.7%), benzyl benzoate (11%), and methyl benzoate (2.2%) and the benzenoid ether o-methylanisole (5%), along with the monoterpene limonene (15.7%). In *T. parviflora*, the fragrance is dominated by the benzenoid ether 3,5-dimethoxy toluene (64%), with significant amounts of the esters benzyl benzoate (15.9%) and methyl salicylate (5.1%) and smaller amounts of the sesquiterpene caryophyllene (6.4%). *Tritoniopsis nervosa*, in contrast, produces a sweet, lily-like fragrance dominated by the monoterpene linalool (78.6%) and its oxides (2.1%), along with small amounts of caryophyllene (7%) and 2-phenylethyl alcohol (3.8%).

Floral Rewards

All species of *Tritoniopsis* examined produce nectar (table 5). The quantity secreted ranges from trace amounts in *T. unguicularis* to just less than 20 μL per flower in *T. antholyza*. Nectar is secreted from septal nectaries and accumulates in the lower portion of the perianth tube. Nectar sugar concentration ranges from 16% sucrose equivalents in *T. antholyza* to 44% in *T. unguicularis*. A single species, *T. parviflora*, secretes floral oils from epithelial elaiophores located on the proximal half of the tepals.

There is a correlation between floral types and nectar quantity and concentration (table 5). In the *T. ramosa* and *T. revoluta* groups, small volumes, 0.2–5 (–7.5) and 2.3–4.1 μL , respectively, of relatively concentrated nectar are produced, (23%–)25%–44% and 26%–34%, respectively. *Tritoniopsis lesliei* flowers produce small volumes, 0.6–1.1 μL , of less concentrated nectar, 23%–25%, while *T. nervosa*, the only species of the *T. nervosa* group, produces moderate volumes, 3–7 μL , of nectar of 25% sucrose equivalents. The species of the *T. triticea* group produce moderate to large volumes of nectar, (3–)5–16 (–19.5) μL , of moderate to relatively dilute concentration. Selected species analyzed for nectar sugar composition show either sucrose-rich or sucrose-dominant nectar.

Floral Visitors

A total of 96 h of pollinator observation showed that *Tritoniopsis* species are visited by a small range of floral visitors, and only one or two different species of floral visitors have been recorded for any population studied (table 6; figs. 1H–1J, 2F–2H). Hours spent on observation of a particular species varied depending on results. Thus, more than 12 h were spent observing *T. nervosa*, but only 2 h were sufficient to record pollinator activity and capture visitors to *T. bicolor*, *T. caledonensis*, and *T. lata*. Obviously, more time is required for some species, e.g., *T. lesliei*, for which 6 h yielded no pollinator sightings, and even *T. nervosa*, in which few sightings of the expected sphinx moths were noted and no moths were captured.

Floral visitors mostly display purposeful behavior, visiting several flowers on an inflorescence before moving to another inflorescence, where the foraging behavior is repeated. Almost all observed floral visitors contact dehisced anthers or stigmatic surfaces. They become dusted with pollen on specific places on their bodies, and pollen identity was confirmed for all insects captured. These two factors indicate that most observed visitors function as pollinators.

There is a strong correlation between floral visitors and flower type. Flowers in the first four groups are visited solely by insect species, while those of the *T. triticea* group are visited primarily by sunbirds, but most are also visited by the butterfly *Aeropetes tulbaghia*. There is a close match between the length of the floral tube and the length of the mouthparts of the insect visitors in the insect-pollinated flower types.

Flowers of the *T. ramosa* group are adapted for pollination by large-bodied bees, predominantly species of *Amegilla* (Hymenoptera: Apidae), with mouthparts 7–10 mm long. Both males and females have been recorded, though females predominate. A single species of bee is typically found in any population, but different populations of the same plant species may be visited by different species of bees. The most common bee species recorded visiting *Tritoniopsis* are *Amegilla obscuriceps* and *Amegilla spilostoma*. Species of *Amegilla* visit a variety of flower colors and sizes within the *T. ramosa* group, including flowers with and without apparent fragrance. The bees alight on the lower lip of the flowers before moving into the mouth of the flower, where they probe the tube for nectar. During probing, the head is pushed as far forward as possible until it is stopped by the base of the filaments. The mouthparts are inserted between the filaments into the lower part of the floral tube. Pollen is deposited on the dorsum of the thorax and also usually on the vertex of the head, especially in the smaller-flowered species such as *T. caledonensis* and *T. unguicularis*.

Visits to *T. parviflora* by the large oil-collecting bee *Rediviva gigas*, which probes the flower for nectar and presumably also collects oil, are described by Manning and Goldblatt (2002). The nectar, as in all Crocoideae, is secreted from septal nectaries and accumulates in the perianth tube, rising to the mouth of the tube, where it is accessible to insects with short mouthparts, including *R. gigas*. It was not possible, however, to confirm whether or not nectar was taken. The floral oils in *T. parviflora* are secreted from epithelial elaiophores located at the base of the tepals. *Redivia gigas* collects floral oils by

Table 4
Fragrance Composition of Selected *Tritoniopsis* Species

Compound (%)	<i>T. parviflora</i>	<i>T. bicolor</i>	<i>T. nervosa</i>	Compound (%)	<i>T. parviflora</i>	<i>T. bicolor</i>	<i>T. nervosa</i>
Fatty acid derivatives:				Ethers:			
Aldehydes:				o-methylanisole			
Nonanal	0.10	0.05			0.20	5.00	
Decanal		0.04		3,4-dimethoxytoluene	0.05		
Alcohols:				3,5-dimethoxytoluene			
(Z,Z,Z)-dodeca-3,6,9-trien-1-ol	0.10			3,4,5-Trimethoxytoluene	0.30	0.03	
Hexadecan-1-ol			0.10	3-methoxy-5-hydroxytoluene	0.30		
(Z)-hexadec-9-en-1-ol			1.00	Miscellaneous:			
Esters:				Phenylacetaldoxime O-methyl ether (E + Z)			
Isoamyl acetate		0.03		2-phenylacetone nitrile			1.00
Ethyl hexanoate		0.03		1-nitro-2-phenylethane			0.50
Methyl octanoate	0.10			Phenylacetaldoxime (E + Z)			0.30
Methyl decanoate	0.06			Isoprenoids:			
Methyl (Z)-dec-4-enoate	0.05			Monoterpenes:			
Methyl (E,Z)-deca-2,4-dienoate	0.06			α -pinene			
Methyl (Z,Z)-deca-2,4-dienoate	1.90						
Methyl dodecanoate	0.03			β -pinene			
Benzenoids:				Myrcene			
Hydrocarbons:				Limonene			
p-cymene		0.20		β -phellandrene			
Aldehydes:				(Z)-ocimene			
Benzylaldehyde		0.10	0.10	γ -terpinen			
Phenylacetaldehyde			0.40	(E)-ocimene			
Ketones:				trans-limonene epoxide			
Acetophenone		0.03		trans-linalool (furanoid)			
Alcohols:				cis-linalool (furanoid)			
Benzyl alcohol	0.30	0.60	0.02	Linalool	0.10	0.10	78.60
2-phenylethyl alcohol			3.80	Terpinen-4-ol		0.20	
p-cresol	0.06	0.20		Lavandulol	0.01		
Esters:				α -terpineol			
Methyl benzoate	0.40	2.20		Neral			0.10
Benzyl acetate		0.20		trans-linalool oxide (pyranoid)			0.05
Methyl salicylate	5.10	55.70		Geranial			0.10
Isobutyl benzoate		0.03		cis-linalool oxide (pyranoid)			0.10
2-phenylethyl acetate			0.02	Citronellol			0.02
Butyl benzoate		0.09		Nerol			0.03
Benzyl isovalerate	0.10	0.07		Geraniol			0.03
Amyl benzoate		0.10		2,6-dimethyl-1,7-octadien-3,6-diol			0.10
Isoprenyl benzoate	0.01	0.03		Sesquiterpenes:			
Prenyl benzoate	0.02			Isocaryophyllene			
Methyl 2-methoxybenzoate	0.08	0.08			0.03		0.10
Benzyl tiglate	0.10			Caryophyllene			
(Z)-hex-3-en-1-yl benzoate	0.03				6.50	0.80	7.00
Benzyl benzoate	15.80	11.00	0.02	Caryophyllene epoxide			
2-phenylethyl benzoate	0.05	0.02			0.40	0.20	1.50
2-phenylethyl phenylacetate			0.02	Humulene epoxide II			
Benzyl salicylate	0.06						0.08
				(E,E)-farnesal			
				Miscellaneous:			
				6-methylhept-5-en-2-one			
						0.03	0.03
				(E)-geranylacetone			
							0.03
				Total	96.7	97.7	98.7

Note. Compounds are arranged in biosynthetic classes by retention time.

rubbing both front and middle legs across the oil-secreting surface.

Single, isolated visits have been observed on flowers of the *T. ramosa* group by two other insects. The bee-fly *Anastoechus* (Bombyliidae) was observed probing *T. pulchella* flowers but did not contact the anthers and did not carry *Tritoniopsis* pollen, and therefore we do not regard it as a potential polli-

nator. The sphecid wasp *Ammophila* sp. (Sphecidae) was observed probing the small flowers of *T. unguicularis* and made contact with the anthers. Observations are insufficient to determine whether this wasp is a casual visitor or an important secondary pollinator.

Species of the *T. revoluta* group are adapted to pollination by long-proboscid flies in the genus *Prosoeca*

Table 5
Nectar Properties of *Tritoniopsis* Species

Species	Volume μL (n)	Mean sucrose equivalents (% \pm SD)	Fructose (%)	Glucose (%)	Sucrose (%)	Mean sucrose/ glucose + fructose (n)
<i>T. ramosa</i> group:						
<i>T. bicolor</i>	1.1–1.6 (5)	38.0 \pm 3.7	NA	NA	NA	NA
<i>T. caledonensis</i>	Trace	Trace	NA	NA	NA	NA
<i>T. dodii</i> site 1	1.7 (1)	31.0	NA	NA	NA	NA
<i>T. dodii</i> site 2	1.1–2.0 (4)	40.5 \pm 1.7	NA	NA	NA	NA
<i>T. elongata</i>	5–11 (5)	34.0 \pm 6.6	NA	NA	NA	NA
<i>T. lata</i> site 1	1.8–4.2 (5)	38.0 \pm 3.5	NA	NA	NA	NA
<i>T. lata</i> site 2	2.1–5.0 (5)	40.0 \pm 1.8	NA	NA	NA	NA
<i>T. nemorosa</i>	1.0–7.5 (5)	43.0 \pm 6.7	NA	NA	NA	NA
<i>T. parviflora</i>	0.2–0.4 (4)	32.0 \pm 2.5	NA	NA	NA	NA
<i>T. pulchella</i>	1.5–2.9 (5)	24.7 \pm 3.2	NA	NA	NA	NA
<i>T. ramosa</i> site 1	0.2–1.6 (10)	25.5 \pm 3.5	NA	NA	NA	NA
<i>T. ramosa</i> site 2	0.9–1.9 (3)	23.8 \pm 4.5	NA	NA	NA	NA
<i>T. unguicularis</i> site 1	0.9–1.4 (5)	44.0 \pm 5.3	NA	NA	NA	NA
<i>T. revoluta</i> group:						
<i>T. flexuosa</i>	2.8–4.1 (3)	26.5 \pm 5.3	NA	NA	NA	NA
<i>T. revoluta</i>	2.3–2.9 (2)	30.0–34.0	23	17	60	1.5 (1)
<i>T. toximontana</i>	0.7–1.6 (5)	29.0 \pm 2.9	NA	NA	NA	NA
<i>T. nervosa</i> group:						
<i>T. nervosa</i> site 1	3.0–7.3 (6)	25.2 \pm 4.2	NA	NA	NA	NA
<i>T. nervosa</i> site 2	3.8–6.5 (3)	22.3 \pm 1.5	NA	NA	NA	NA
<i>T. lesliei</i> group:						
<i>T. lesliei</i>	0.6–1.1 (4)	23.5 \pm 1.9	NA	NA	NA	NA
<i>T. triticea</i> group:						
<i>T. antholyza</i> site 1	5.4–6.7 (3)	16.1 \pm 1.3	19	23	58	1.4 (1)
<i>T. antholyza</i> site 2	7.5–9.2 (2)	16–23	NA	NA	NA	NA
<i>T. antholyza</i> site 3	14.4–19.5 (2)	27.5	3	9	88	7.33 (1)
<i>T. antholyza</i> site 4	4.7–6.9 (5)	25.9 \pm 1.9	2	6–7	90–93	10.76 (2)
<i>T. antholyza</i> site 5	2.8–9.9 (9)	27.0 \pm 4.2	NA	NA	NA	NA
<i>T. antholyza</i> site 6	7.3–10.8 (4)	25.0 \pm 2.6	NA	NA	NA	NA
<i>T. burchellii</i> site 1	5.8–8.4 (3)	18.7 \pm 1.5	16	16	68	2.13 (1)
<i>T. burchellii</i> site 2	5.3–10.4 (10)	22.7 \pm 1.0	NA	NA	NA	NA
<i>T. burchellii</i> site 3	3.9–6.2 (4)	22–26	NA	NA	NA	NA
<i>T. burchellii</i> site 4	11.9–16.6 (4)	17.5 \pm 3.5	NA	NA	NA	NA
<i>T. caffra</i> site 1	7.2–19.5 (10)	23.2 \pm 2.6	NA	NA	NA	NA
<i>T. caffra</i> site 2	7.6–18.5 (5)	15.4 \pm 4.7	NA	NA	NA	NA
<i>T. caffra</i> site 3	2.8–6.8 (2)	25.0	21	21	58	1.38 (1)
<i>T. pulchra</i>	3.7–10.9 (6)	26.3 \pm 3.7	4–6	4–7	87–92	7.63 (2)
<i>T. triticea</i> site 1	3.8–6.4 (10)	20.5 \pm 1.6	9	10	81	4.26 (1)
<i>T. triticea</i> site 2	3.1–7.8 (4)	21.3 \pm 3.2	NA	NA	NA	NA
<i>T. williamsiana</i>	6.2–7.9 (10)	24.2 \pm 1.1	NA	NA	NA	NA

Note. n = number of individuals sampled; trace = too little for measurement; NA = data not available. Nectar sugars were analyzed by B.-E. van Wyk.

(Nemestrinidae). A single fly species has been captured on each of two of the three species of *Tritoniopsis* with this pollination system, the large widespread fly *Prosoeca ganglbaueri* on flowers of *T. revoluta* and an undescribed species of *Prosoeca* on *T. toximontana*. We suspect that populations of *T. revoluta* from south of the Langeberg Mountains are pollinated by *Prosoeca longipennis*, a fly that replaces *P. ganglbaueri* in this region. The length of the floral tube is correlated with the proboscis length of the pollinating fly species (table 6). Like the *T. ramosa* group, pollen is deposited on the vertex of the head and dorsum of the thorax. The tube length in *T. revoluta* is too long to permit the nectar to be accessed by bees. *Tritoniopsis toximontana*, however, ap-

pears to be adapted for pollination by both bees and long-proboscid flies. The flowers of this species are intermediate in tube length between the *T. ramosa* and *T. revoluta* groups, with a tube rather longer than usual for bee-pollinated flowers. It is visited repeatedly by both *A. obscuriceps* and an undescribed *Prosoeca* species.

Foraging behavior of long-proboscid flies is similar to that of the bees, with the body entering the flower until prevented from further entry by the filaments, which prevent further access to the perianth tube. The mouthparts are inserted between the filaments into the lower portion of the tube. Examination of the flowers after a visit by a bee confirms that a residue of nectar remains in the lower 10 mm of the

Table 6
Avian and Insect Visitors Recorded on *Tritoniopsis* Species and Selected Characteristics

Plant species and population	Visitors (<i>n</i>)	Mouthpart or beak length (mm)	Floral tube length (mm)	Filament length	Pollen placement
<i>T. ramosa</i> group:					
<i>T. bicolor</i>	<i>Amegilla spilostoma</i> (1)	7	2–4	6–7	Vertex and dorsum
<i>T. caledonensis</i>	<i>A. spilostoma</i> (2)	7	3–5	3–5	Vertex
<i>T. dodii</i> site 2	<i>A. spilostoma</i> (2)	7	6–8	12–14	Vertex and dorsum
<i>T. elongata</i>	<i>Amegilla obscuriceps</i> (5)	7	6–8	13–16	Vertex and dorsum
	<i>Apis mellifera</i> (3)	3–4			
<i>T. lata</i> site 2	<i>A. obscuriceps</i> (8)	7	8–11	17–20	Vertex and dorsum
<i>T. nemorosa</i>	<i>A. spilostoma</i> (6)	7	7–8	12–15	Vertex and dorsum
<i>T. parviflora</i>	<i>Rediviva gigas</i> (2)	2	3–5	12–14	Vertex and dorsum
<i>T. pulchella</i>	<i>A. spilostoma</i> (4)	7	12–20	17–25	Vertex and dorsum
	<i>Anastoechus</i> sp. (1)	6			None
<i>T. ramosa</i> site 1	<i>Amegilla capensis</i> (3)	9–10	8–10	15–18	Vertex and dorsum
<i>T. ramosa</i> site 2	<i>A. spilostoma</i> (6)	7	8–9	15–18	Vertex and dorsum
<i>T. unguicularis</i> site 1	<i>A. spilostoma</i> (1)	7	2–5	5–7	Vertex
<i>T. unguicularis</i> site 2	<i>Amegilla niveata</i> (10)	7	2–5	5–7	Vertex
	<i>Ammophila</i> sp. (1)	1			Vertex and dorsum
<i>T. revoluta</i> group:					
<i>T. revoluta</i>	<i>Prosoeca ganglbaurii</i> (3)	20–25	25	15–20	Vertex and dorsum
<i>T. toximontana</i>	<i>A. obscuriceps</i> (8)	7	20	13–15	Vertex and dorsum
	<i>Prosoeca</i> sp. (6)	15			Vertex and dorsum
<i>T. nervosa</i> group:					
<i>T. nervosa</i>	<i>Hyles lineata</i> (2)	25–30	30–40	5–6	Vertex
	<i>A. spilostoma</i> (3)	7			Vertex and dorsum
<i>T. triticea</i> group:					
<i>T. burchellii</i> site 2	<i>Nectarinia chalybea</i> (3)	18–23	30–40	30–37	Head
	<i>Aeropetes tulbaghia</i> (2)	30			Wings
<i>T. burchellii</i> site 4	<i>N. chalybea</i> (2)	18–23	30–40	30–37	Head
	<i>A. tulbaghia</i> (2)	30			Wings
<i>T. caffra</i> site 1	<i>Nectarinia famosa</i> (5)	29–34	20–30	33–38	Head
<i>T. caffra</i> site 2	<i>Nectarinia violacea</i> (4)	20–23	20–30	33–38	Head
<i>T. pulchra</i>	<i>N. violacea</i> (3)	20–23	30–33	20–23	Head
<i>T. triticea</i> site 2	<i>N. violacea</i> (4)	20–23	25–30	20–23	Head
	<i>A. tulbaghia</i> (8)	30			Wings
<i>T. williamsiana</i>	<i>N. violacea</i> (3)	20–23	20–30	ca. 28	Head

Note. Hymenoptera: Apidae (*Amegilla*), Sphecidae (*Ammophila*). Diptera: Bombyliidae (*Anastoechus*), Nemestrinidae (*Prosoeca*). Lepidoptera: Satyridae (*Aeropetes*), Sphingidae (*Hyles*). Aves: Nectarinidae (*Nectarinia*). Note that the sphinx moth *Hyles lineata* was not captured; measurements of tongue length were thus measured from museum specimens.

tube, beyond the reach of the the mouthparts of the bee. The nectar in the lower 10 mm of the tube is, however, accessible to the *Prosoeca* sp., which has a proboscis 15 mm long. *Tritoniopsis toximontana* is thus adapted for two different pollinators with mouthparts of two different lengths. It is part of a guild of several plant species that have converged in their floral morphology to attract this autumn flying *Prosoeca* species. These include *Brunsvigia striata* (Jacq.) Aiton, *Strumaria salteri* W. F. Barker, *Strumaria watermeyeri* L. Bolus (Amaryllidaceae), and the long-tubed form of *Oxalis birta* L. (Oxalidaceae) (observations not previously published).

The single species of the *T. nervosa* group is apparently adapted to sphinx moth pollination. Repeated observations over five different evenings at three populations, however, produced just two sightings of the sphinx moth *Hyles lineata* visiting the flowers. These were made within an hour or two after nightfall. Both moths avoided capture. The levels of seed set observed in the study populations (which are not

self-pollinated) suggested an alternative pollinator. This appears to be the bee *A. spilostoma*, several individuals of which were observed in the early morning visiting the flowers. Observation of bagged inflorescences reveals that nectar accumulates in daily quotas of ca. 2 μ L, accumulating to a maximum of ca. 7 μ L on day 4. In unvisited flowers, the nectar accumulates to a level correspondingly nearer to the mouth of the tube each day. On day 1, nectar reaches 30 mm from the mouth of the tube, on day 2 up to 20 mm, on day 3 up to 15 mm, and on day 4 to within 6 mm from the mouth of the tube. On days 3 and 4, flowers that have not been previously visited will thus have accumulated nectar to a level where it can be reached by *A. spilostoma*.

Flowers of the *T. triticea* group are pollinated by sunbirds, *Nectarinia* species, especially *Nectarinia violacea*, the orange-breasted sunbird, and *Nectarinia chalybaea*, the lesser double-collared sunbird. The two species *T. burchellii* and *T. triticea* are also regularly visited by the large satyrid butterfly *A.*

tulbaghia. The birds probe each flower directly from the front. The beak is inserted into the upper portion of the perianth tube but cannot be pushed beyond the base of the filaments. The tongue is then inserted between the filaments to access the nectar in the lower portion of the tube. Pollen is deposited on the forehead. The critical distance for pollen placement is thus the length of the filament and not the length of the tube. There is accordingly a better match between filament and beak lengths in the bird-pollinated species than between tube and beak length.

The foraging behavior of *A. tulbaghia* is very different from that of sunbirds. The butterfly approaches a flower from the side and in this position it does not contact the anthers of the flower being probed, but pollen is picked up from other flowers in the inflorescence on the wings and body of the insect as it crawls over the inflorescence. Thus, for *Aeropetes*, the entire inflorescence is the functional pollination unit.

Tritoniopsis lesliei, the only species of its pollination group, appears to be adapted to pollination by the satyrid butterfly *A. tulbaghia* (and possibly the swallowtail *Papilio demodocus*), but no pollinator visits to the species were noted during one morning of observation.

Discussion

Tritoniopsis displays the high diversity of pollination syndromes that is now associated with many southern African genera of Crocoideae (Bernhardt and Goldblatt 2005), in particular *Gladiolus* (Goldblatt et al. 2001) and *Lapeirousia* (Goldblatt et al. 1995), and indeed many other genera, e.g., *Disa* (Orchidaceae) (Johnson et al. 1998). There is marked congruence between the pollination systems in *Tritoniopsis* and those that have been investigated in other Crocoideae (Johnson and Bond 1994; Goldblatt et al. 1998b, 1999; Goldblatt and Manning 1999, 2002), confirming the stability of the suites of morphological and phenological features that characterize these systems. This marked convergence constitutes evidence for the existence of modal optima in the pollination strategies developed in Crocoideae and the prevalence of specialized pollination systems in the family.

Nectar Considerations

Worldwide, there is substantial evidence for a general relationship between sugar ratios and principal pollinator (Baker and Baker 1983, 1990), but this may be offset by the tendency for intrafamilial similarities in the sucrose : hexose ratio of nectar (Barnes et al. 1995). Old World flowers pollinated by passerine birds typically produce hexose-dominated nectar, whereas the nectar of New World flowers pollinated by hummingbirds is usually sucrose rich. A survey of southern African sunbird-pollinated Iridaceae reveals a diversity of sucrose : hexose ratios that appears to coincide with taxonomic categories, often at the generic or infrageneric level (Goldblatt et al. 1999). The nectar of *Tritoniopsis* is invariably sucrose rich or dominant, irrespective of the pollinator type, confirming the suggestion that in African Iridaceae, at least, nectar sugar composition is primarily related to phylogeny rather than pollination biology. The higher volume and lower sugar concentration of nectar secreted by bird-

pollinated species of *Tritoniopsis* is typical of bird-pollinated Iridaceae (Goldblatt et al. 1999).

Fragrance

The bee-pollinated species of *Tritoniopsis* are unusual in several aspects compared with the typical long-tongued bee pollination system in southern African Iridaceae (Goldblatt et al. 2001). The relatively short tube, less than 10 mm long in some species, is more typical of pollen flowers or at least those visited by short-tongued bees. This may relate to the generally smaller size and shorter tongue length of *Amegilla* species compared with species of *Anthophora*, which are the primary pollinators of most other bee-pollinated Iridaceae studied. In addition, very few species are fragrant, and the acrid or sweet-acrid fragrances dominated by benzenoid compounds that are produced by the bee-pollinated species of *Tritoniopsis* are unique among southern African bee-pollinated Iridaceae, which typically produce sweet or floral fragrances dominated by the isoprenoids geraniol, geranial, and citronellol and the terpenoid ionone (Goldblatt et al. 1998b). Such acrid fragrances are more typical of oil-secreting orchids visited by oil-collecting *Rediviva* bees yet evidently do not repel polylectic nectar-feeding bees such as *Amegilla*. *Tritoniopsis parviflora* is unique among African Iridaceae in providing floral oils as a reward (Goldblatt and Manning 2002). The dominant compound in the fragrance profile of *T. parviflora*, 3,5-dimethoxytoluene, is a major component of the fragrance of the oil-producing orchid *Corycium orobanchoides* (L.f.) Sw. (R. Kaiser, personal communication), and there is a strong convergence in floral presentation and reward between *T. parviflora* and members of this oil-secreting guild (Goldblatt and Manning 2002). It is likely, therefore, that the production of benzenoid-rich fragrances among bee-pollinated species of *Tritoniopsis* was a preadaptation to the exploitation of the oil-secreting guild. Although the range of flower colors in the bee-pollinated species of *Tritoniopsis* is typical of other Iridaceae with that pollination system, the general lack of fragrance is unusual among bee-pollinated species in the Cape region. The absence of scented species is likely to be correlated with summer flowering in the genus because fragrance among Cape bee-pollinated Iridaceae is most common in spring-flowering species (Goldblatt et al. 1998b), in which its presence may be related to increased competition for pollinators at this time of the year. The linalool-rich fragrance of the moth-pollinated *T. nervosa* is typical of other sphingophilous species that have been analyzed (Knudsen and Tollsten 1993; Raguso et al. 2003), including southern African members of Iridaceae and Amaryllidaceae (Goldblatt and Manning 2002; Manning and Snijman 2002).

Bimodal Pollination Systems

A notable feature of the pollination biology of *Tritoniopsis* is the occurrence of bimodal pollination systems, also reported in four other genera of Crocoideae: *Hesperantha*, *Ixia*, *Romulea*, and *Sparaxis* (Goldblatt et al. 2000a, 2000b, 2002a, 2004b). Bimodal systems are morphologically intermediate between two syndromes and share two sets of pollinators adapted to different specialized pollination systems. They differ from generalist systems, which rely on a range of

different pollen vectors and in which the floral syndromes are not obviously intermediate between two or more specialized systems.

Two or possibly three bimodal systems can be distinguished in *Tritoniopsis*. The first combines adaptations to both bee and long-proboscid fly pollination and occurs in *T. toximontana* and probably *T. pulchella*. The flowers of these two species are intermediate in tube length between the means of the bee and long-proboscid fly systems and are visited by both bees and long-proboscid flies. Nectar sugar concentration is also compatible with both systems, unlike the higher concentration of sugar in some purely bee-pollinated species. The higher viscosity associated with high sugar concentrations prevents withdrawal of the nectar by insects with very slender mouthparts (Johnson and Bond 1994). Partitioning of the nectar resource between the two vectors is possible by a combination of tube length and foraging time. The bees forage from early morning before the flies are active but are unable to remove all of the nectar, leaving a residue in the lower part of the tube. This can be reached by the flies when they become active in late morning.

The development of this bimodal system is readily envisaged. The flower shape and coloration in the long-proboscid fly system is also developed in the bee-pollinated species, and the difference between the two is primarily the length of the floral tube. This is not the case in other long-proboscid fly systems, such as the *Prosoeca peringueyi* system (Manning and Goldblatt 1996), where the magenta or purple flower color is not part of an associated bee-pollination system. In addition, flowering in *Tritoniopsis*, unlike most Cape plant species, occurs mainly during summer and autumn, when these species can enter existing guilds of long-proboscid fly-pollinated species based on other late-flowering species, especially autumn-flowering Amaryllidaceae or summer-flowering montane Iridaceae. The morphological similarity of long-proboscid fly-pollinated flowers with bee-pollinated flowers rather than with those pollinated by butterflies, as suggested by Vogel (1954) and Johnson and Steiner (1995), was first pointed out by Manning and Goldblatt (1997). The existence of intermediates between the two systems is further evidence of the ease with which plants can shift between the two. An origin for the *P. peringueyi* guild from bee-pollinated systems was proposed by Manning and Goldblatt (1996), and it is likely that long-proboscid fly pollination has a similar origin in *Tritoniopsis*.

The second bimodal system is that between bird and butterfly pollination using *Aerpetes tulbaghia*. Two species, *T. burchellii* and *T. triticea*, are regularly visited by sunbirds as well as *Aerpetes* and represent a shared resource for these pollinators. Both pollinator groups are able to access the nectar through their long mouthparts. The relatively dilute nectar with low viscosity typical of bird-pollinated species is especially suitable for butterflies (Kingsolver and Daniel 1979), including *Aerpetes* (Johnson and Bond 1994). Although Johnson and Bond (1994) viewed *T. triticea* as a species in which pollination by *Aerpetes* is facultative to bird pollination, there are several reasons for suggesting that *T. burchellii* and *T. triticea* are not facultatively butterfly pollinated but that they adaptively exploit two kinds of pollinators. There is a very precise convergence between flower

color in *T. burchellii* and *T. triticea* and other members of the *A. tulbaghia* guild (spectral data provided by Johnson and Bond [1994]). In contrast, bird-pollinated flowers vary to some extent in color, including different shades of red, and such a close match with the *Aerpetes* guild indicates strong convergence. Notably, these two species of *Tritoniopsis*, both more abundant and widespread, serve as models for the orchid *Disa ferruginea*, which is a nectarless, deceptive mimic pollinated by *Aerpetes* (Johnson and Bond 1994). It is well documented that the evolution of this pollination strategy in the Batesian mimic *D. ferruginea* requires pollination of the models by *Aerpetes*. In addition, the form of the perianth in the two *Tritoniopsis* species is intermediate between the bird-pollinated and butterfly-pollinated types; although sharing the dimorphic tube shape of bird-pollinated Iridaceae, it closely approaches the classic- and brush-type flowers that characterize the *Aerpetes* guild rather than the obliquely tubular type that is typical of purely bird-pollinated species of *Tritoniopsis* and other Crocoideae. This morphological shift is achieved by reflexing of the dorsal tepal, thereby exposing the anthers. Johnson and Bond (1994) propose that the *Aerpetes* system developed from bird pollination systems, driven by the opportunity for exploitation of this high-volume nectar source by the butterfly.

Certainly *T. lesliei*, the single species of *Tritoniopsis* that is inferred to be pollinated solely by butterflies, including *Aerpetes*, has a floral presentation and morphology that is incompatible with bird pollination. The slender flowering stem is unable to support the weight of a perching sunbird, the flowers are radially symmetric, the floral tube is too narrow to allow a sunbird to access the nectar, and the nectar volume is less than 10% of that found in *T. burchellii* and *T. triticea*. This circumstantial reason for inferring an origin of this bimodal system from purely bird-pollinated ancestors in *T. triticea* and *T. burchellii* does not account for its origin in *T. lesliei*, which is more likely to be from an ancestor pollinated by bees or long-proboscid flies.

Existing morphological phylogenetic analysis of *Gladiolus* (Goldblatt and Manning 1998) indicates that flowers adapted to pollination by *Aerpetes* in this genus are often derived from ancestors adapted for long-proboscid fly pollination. Shifts toward radial symmetry and centrally placed stamens are common in the *Aerpetes* pollination system, and the rotate perianth and centrally placed stamens in *T. lesliei* are consistent with this trend. Confirmation of this requires more robust phylogenies, but DNA regions providing sufficient divergence for species phylogenies remain to be identified for the Iridaceae (Goldblatt et al. 2002b, 2004a).

The third apparently bimodal system involves *T. parviflora*, which secretes both nectar and oil. The species is pollinated by the oil-collecting bee *Rediviva gigas*, but indications are that it may also be visited by other bee species that do not collect oil, most likely species of *Amegilla*. First, *T. parviflora* is unique among oil-producing flowers in providing an alternative (nectar) reward, and second, the distribution of the species extends beyond that occupied by *R. gigas* (Manning and Goldblatt 2002). Populations occurring outside the range of *R. gigas* presumably rely for pollination on bees that are attracted to the flowers for their nectar reward. Further study is required to ascertain whether and how actively

T. parviflora is visited by oil- and non-oil-collecting bees, especially in that part of its range that overlaps with the distribution of *R. gigas*. Manning and Goldblatt (2002) suggest that the species is a relatively recent entrant into the *R. gigas* pollination guild. Outgroup comparison indicates that *T. parviflora* is derived from a non-oil-secreting bee-pollinated ancestor.

These bimodal systems illustrate how evolutionary transformations could proceed between bee and fly pollination and between bird and butterfly pollination while maintaining successful pollination during the transition phase. This transition in morphology is readily accompanied by shifts in nectar quality and quantity because there is already substantial overlap in ranges in nectar volume and concentration between the various pollination strategies. The bimodal systems in *Tritoniopsis* furnish examples of how this might be achieved. Such bimodal systems are also likely to be highly labile and prone to shift in either direction in response to changes in the pollinator environment. Their prevalence in *Tritoniopsis* compared with other genera of Crocoideae may be related to a relative paucity of floral visitors in the Cape in the summer and, conversely, the paucity of plants then in bloom. Comparative studies on numbers of insects active in spring versus summer are, however, lacking. The labile nature of specialized pollination syndromes has been demonstrated in *Dalechampia* by Armbruster and Baldwin (1998), where they interpret a shift from highly specialized resin secretion to more generalist pollination strategies to have been driven by the absence of suitable pollinating bees in more recently colonized geographical regions. Similarly, in *Tritoniopsis*, we interpret a shift from a strictly (unimodal) specialist system to a bimodal one to be driven by a relative seasonal shortage of suitable pollinators.

Pollination in *T. nervosa* is not typical of the bimodal systems discussed above. Although visited by both the sphinx moth *Hyles lineata* and the bee *Amegilla spilostoma*, the floral morphology in this species is not intermediate between two systems and is typical in all respects of sphingophilous species. This includes the elongate floral tube, pale pigmentation without nectar guides, and linalool-rich fragrance. Despite the fact that the flowers of *T. nervosa* appear to be primarily adapted to moth pollination according to the criteria of Faegri and van der Pijl (1979), observations indicate that populations are poorly visited by sphinx moths and that the nectar-collecting bee *A. spilostoma* plays an important role as a secondary pollinator. It may, in fact, assume the role of primary pollinator in certain seasons or populations. This situation differs from the other bimodal systems, however, in that the nectar reward is available to the bee only in the absence, over several successive days, of visits to the flowers by moths, by which time the nectar may accumulate in the floral tube to a level where it may be reached by the bee. We interpret this to indicate that *T. nervosa* is only facultatively bee pollinated and not a true bimodal pollination system.

Bimodal pollination systems such those found in *Tritoniopsis* occupy a paradoxical position along the specialist-generalist continuum. In *Delphinium*, they have been interpreted as evidence for doubting the existence of specialized systems (Waser et al. 1996), but an alternative interpretation may be more appropriate in *Tritoniopsis*. Structurally and function-

ally, the bimodal systems in *Tritoniopsis* are specialized systems that combine the distinct adaptive features of two different systems. They also function as independent specialist systems when being utilized by individuals of the two different pollination classes, providing the same benefits of dedicated pollen transfer as other specialized systems. The two classes of visitors may thus be considered to be complementary, and these systems differ, essentially, from other specialist systems only in extending their appeal to more than one functionally analogous group of pollinators. The selective pressures driving the evolution of these systems, however, are apparently those that normally favor the development of more generalized systems, but in this case, they have resulted in a modified specialist system instead. Detailed studies of pollinator effectiveness (Schemske and Horvitz 1984) are required to assess this.

The identification of distinct pollination syndromes in *Tritoniopsis* provides additional evidence for the predominance of specialist pollination in the Iridaceae and the close relationship between floral presentation and one or a limited number of specialist pollinators. Although there is a close correlation between floral morphology and pollinator type in most Iridaceae, the relationship between single species of plant and pollinator is seldom exclusive. Pollinators are almost invariably polylectic, while in most cases the plant species are visited by a small group of pollinator species, at least across their total range. Among species of *Tritoniopsis*, it is usual that two or three different but functionally analogous or, in the case of the bimodal species, functionally complementary pollinator species are involved. This has significant implications for the long-term survival of the plant species in the case of extinction of part of the pollinator spectrum. Specialized pollination systems are most likely to develop under conditions when appropriate pollinators are predictably present (Stebbins 1970), whereas generalization is favored when pollinator availability is unpredictable (Waser et al. 1996). Several factors determine the relative prevalence of these two ends of the pollination continuum, including plant life history, successional status, abundance, and breeding system (Baker 1965; Feinsinger 1983; Schemske 1983; Bond 1994; Johnson and Steiner 2000). The relatively long-lived nature of cormous Iridaceae, their propensity for vegetative reproduction, and the relatively dispersed nature of flowering plants among the vegetation accord with three of the conditions that have been proposed to favor the development of specialist pollination strategies (Bond 1994; Johnson and Bond 1994; Waser et al. 1996). The distribution of specialist versus generalist pollination systems is also taxonomically linked, with families such as Asteraceae and Ranunculaceae occupying the generalist end of the continuum and Apocynaceae and Orchidaceae occupying the specialist end (Johnson and Steiner 2000).

Iridaceae are among the families dominated by specialist pollination systems. Reduction in anther number or agglomeration of pollen grains or both are characteristic of the taxa in which specialized pollination systems are most prevalent, and Iridaceae, with three anthers in most genera but functionally just one in each partial flower in the genera *Iris*, *Moraea*, and *Dietes*, are no exception. In addition, recent work in the species-rich temperate flora of South Africa has revealed the existence of numerous highly specialized

Table 7
Relative Proportion of Pollination Systems among the Larger Zygomorphic-Flowered Genera of Crocoideae in the Cape Region

Genus	No. species	% species with each pollination system					
		Bee	Long-proboscid fly	Sunbird	Butterfly	Moth	Beetle
<i>Babiana</i>	49	67	12	4	0	6	14
<i>Gladiolus</i>	110	52	20	16	5	10	1
<i>Lapeirousia</i>	15	53	40	0	0	13	0
<i>Sparaxis</i>	15	60	13	0	0	0	26
<i>Tritonia</i>	18	50	33	0	0	0	22
<i>Tritoniopsis</i>	24	52	11	25	8	4	0
<i>Watsonia</i>	33	18	18	70	0	0	0
Mean		50	21	16	2	5	9

pollination systems (Steiner and Whitehead 1990; Johnson and Bond 1994; Johnson 1996; Manning and Goldblatt 1997; Johnson and Steiner 2000). Iridaceae are among the families that have their center of diversity in temperate southern Africa (Goldblatt and Manning 2000b), and there are thus several determinants for the prevalence of specialized pollination systems in the family.

Pollinator Specialization

The pollination systems among the southern African Iridaceae are now sufficiently well established for comparison of their representation within and among genera (Goldblatt et al. 1995, 1998a, 1998b, 2000a, 2000b, 2001; Manning and Goldblatt 1996, 1997; Goldblatt and Manning 1999, 2000b). Ancestrally actinomorphic genera, such as *Ixia* and *Romulea*, are relatively conservative in their pollination systems compared with the zygomorphic genera (Goldblatt et al. 2002a). Comparisons between genera are thus only appropriate within each type of floral symmetry. A comparison of the proportional representation of different pollination systems in the Cape species of the larger, zygomorphic-flowered genera of Crocoideae reveals some significant anomalies (table 7).

Tritoniopsis is typical among comparable Cape genera of Iridaceae in the relative proportions of species pollinated by bees and long-proboscid flies, which are the two most common pollination systems, and in moth-pollinated species. It is, however, overrepresented in species pollinated by birds and butterflies (only *A. tulgahia*) and underrepresented in beetle-pollinated species. The explanation for this skewed pollination profile is almost certainly the unusual flowering time of the genus. Flowering in beetle-pollinated species in the Cape Region is restricted to spring and early summer, before *Tritoniopsis* species bloom. The emergence of adults of *Aeropetes* between January and April, however, coincides with the peak flowering time in the genus, while sunbirds are active throughout the year. Different bee faunas are also active throughout the year, with the genus *Anthophora* active in spring and *Amegilla* most active in summer and autumn, while several species of long-proboscid flies are on the wing at different times of the year.

Various strategies for the separation of the vegetative and reproductive phases of growth (hysteranthly) have originated in some genera of Iridaceae, notably *Gladiolus*, to permit flowering to take place outside of the spring maximum, but summer flowering in *Tritoniopsis* has predisposed this genus to exploiting summer- and autumn-specific pollination systems. The atypical flowering season for species of the Cape Region, between summer and autumn, in *Tritoniopsis* appears to be the single most significant determinant of its pollination profile, in particular the relative overrepresentation of bird- and butterfly-pollinated taxa. A similar diversification of unusual pollination systems has occurred in *Gladiolus* section *Linearifolius*, many species of which also flower during the summer (Goldblatt and Manning 1998). In this case, we hypothesized that section *Linearifolius* entered the Cape Region relatively recently through its ability to flower at a time when many other Cape geophytes were dormant. A similar interpretation for *Tritoniopsis* is unlikely in light of its basal position within Crocoideae. Summer flowering is characteristic of several paleoendemic shrubs in the Cape Region (Goldblatt and Manning 2000a) and has been interpreted as a historical legacy of their origin before the establishment of a summer-dry climate in the Cape. These taxa are typically restricted to higher-altitude sandstone slopes that receive some moisture during summer fog and clouds. The genus *Tritoniopsis* is well represented in similar habitats, possibly for similar historical reasons, but the development of hysteranthly has presumably enabled it to occupy drier habitats as well. This scenario is supported by a proposed date for the divergence of the genus ca. 20 Ma (Goldblatt et al. 2002b), well before the estimated inception of a Mediterranean climate in southern Africa at no more than 5–8 Ma.

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