

TYOLOGY IN POLLINATION BIOLOGY: LESSONS FROM AN HISTORICAL CRITIQUE

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Abstract—Typological schemes that describe putative floral adaptations for pollinators have played a central role in pollination biology. In 1882 the prominent German botanist and Darwinist Hermann Müller commented critically on a precursor of modern versions of such “pollination syndromes” that had been developed by his Italian colleague Federico Delpino. Delpino also was a self-proclaimed Darwinist, but in fact adhered to teleology—explanation beyond nature. As a consequence he viewed his typology as reflecting a deeper ideal and thus as rigidly true, and rejected as unimportant any visitors to flowers that it did not predict. Although Müller also classified flowers as to pollinators, he considered such schemes to be fallible, and pondered what diversity and variation in floral visitors might mean. Müller’s comments, which we translate here, are of interest given that appeals to teleology have resurfaced from time to time in discussions of pollination syndromes, and more importantly because his warning against taking typological schemes too literally remains valid. Typology is a useful tool in biology, including pollination biology, but care must be taken that it does not replace nature as perceived reality.

Key words: Darwinism, Federico Delpino, Hermann Müller, history, natural history, pollination syndromes, teleology, typology

INTRODUCTION

The noted evolutionary biologist Ernst Mayr (e.g. 1982, 1991) portrayed the Darwinian revolution as a replacement of typological thinking about nature by “population thinking”, the recognition and celebration of variation among individuals. Indeed, one may conclude that there is a broader ongoing tension in biology between a focus on typology and a focus on variation. Schemes for categorizing biological objects or processes perform a useful role in capturing and communicating about pattern that lurks within the complexity of nature. But it is important to recognize such schemes as fallible human constructs; as hypotheses about natural patterns that are testable and mutable in the face of new information. Risk arises when this is forgotten and typology itself becomes the perceived reality.

Our object here is to contribute an historical perspective on typological schemes that have been used to classify flowers in relation to pollination by animals, by far the dominant mode of pollination (Ollerton et al. 2011). The most widely-accepted of such schemes group together plant species, including ones that are distantly related phylogenetically, based on shared sets (syndromes) of floral traits that putatively adapt them for pollination by specific types of animals. This concept of “pollination syndromes” is a very Darwinian one of convergent evolution, and in different

manifestations it has served as a cornerstone of the study of pollination by botanists, evolutionary ecologists, cognitive behaviourists, and others—a fruitful area of study not only over the last few decades but over a longer history (Baker 1983, Waser 2006).

The clearest historical root for the modern pollination syndromes is a monograph published in 1873-1874 by the Italian botanist Federico Delpino (born 1833 near Genova, died 1905; see Fig. 1), entitled *Ulteriori osservazioni e considerazioni sulla Dicogamia nel regno vegetale (Additional observations and considerations on dichogamy in the plant kingdom; here “dichogamy” is used as a synonym for “outcrossing sexual reproduction”)*. This work laid out two schemes for classifying flowers, which, along with more recent contributions, including those of Vogel (1954) and Faegri and van der Pijl (1979), led to modern articulations of the pollination syndromes. What many pollination biologists may find surprising is Delpino’s assumption of a teleological basis for his schemes, which caused him to view them as the reality itself, precisely the danger noted above. But this fact did not escape Delpino’s contemporaries, one of whose critiques we wish to bring forward.

Serendipitous events led us to track down this critique, from the great German botanist Hermann Müller (born 1829 in Thuringia in central Germany, died 1883; see Fig. 1). Müller published important works on pollination in German and English, including *Die Befruchtung der Blumen durch Insekten* (Müller 1873), which was translated in 1883 by D’Arcy Thompson as *The fertilisation of flowers*, on the urging of Charles Darwin, who also provided the Preface.

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This influential book lays out a history of the scientific study of pollination, and general principles of floral form, insect morphology, and insect behaviour, before turning to a plant species-by-species compendium of insects and other animals observed at flowers. It was then followed by three instalments of the *Weitere Beobachtungen über Befruchtung der Blumen durch Insekten* (*Further observations on the fertilization of flowers by insects*). The third instalment in this series (Müller 1882) concerns us here. While working on an analysis of the pollination syndromes (Ollerton et al, 2009), we came across a quotation from Müller in Knuth (1898a), and a slightly different quotation of the same passage in Vogel (1954). To determine which quotation was correct we managed to find the original, which showed that *neither* was correct, and revealed the preference for natural history over teleology that caused Müller to question Delpino's classification.

We provide here an English translation of several pages from Müller (1882; Fig. 2 shows the first of the pages in question). In [square brackets] in bold, we indicate roughly where page numbers advance in the original text. The number preceding each plant species name (e.g., 232 in the case of *Solanum dulcamara*), and the page number following it (e.g., 275), refer to numbering of species and page numbers in Müller (1873), as does a reference for *Solanum nigrum* to "Fig. 91, 92". We have retained Müller's formatting of species names, which he sometimes gives in upper case and

sometimes in lower, and sometimes but not always in italics. Footnotes appear as in the original. Short of producing incomprehensible English sentences, we have attempted to retain the basic sentence structure (if not the word order) of Müller. As Samuel Clemens (1880) so humorously noted, long, tortuous sentences characterized the German of that day! Note also that Müller uses shorthand to refer to other works, as was common at the time. Thus he refers to "Sprengel", by which is meant Sprengel (1793), a key work in the history of pollination biology (Vogel 1996; Waser 2006; note the slightly incorrect abbreviation of Sprengel's name 'Christian Konrad' in the passage on *Solanum nigrum*); and to the earlier instalments of his own articles in this same series, for example as "Weitere Beob. I P. 15", by which is meant page 15 of the first article on 'Further Observations' (see above). Müller adds to his previous (1873) list of visitors for some of the species, giving dates as day/month/year and specifying the locality and/or person observing the flowers (L. = Lippstadt; N. B. = Nassau, Dr. Buddeberg; H. M. = Hermann Müller's son, who bore his same name; Tekl. Borgst. = a Mr. Borgstette Jr., a pharmacist from the city of Teklenburg). Müller also abbreviates Delpino as D. in a few places. Finally, we occasionally insert in {curly brackets} some additional words that we feel assist in understanding the meaning. We turn after the translated text to a brief further discussion of some of the points it raises.



Fig. 1. Images of Federico Delpino (left), from the frontispiece of Knuth (1899), and of Hermann Müller (right), from the frontispiece of Knuth (1898b).

THE TRANSLATION FROM MÜLLER (1882)

[20] *Solaneae* (P. 274.)

(232.) *Solanum Dulcamara* L. (P. 275.) Sprengel Tab. IX Fig. 15. Delpino¹ presents this *Solanum* species as a beautiful expression of his Borago Type. At the same time it is a good example of the inadequacy of the Delpinoist Types and the arbitrariness and unnaturalness one must unavoidably fall into, if one tries to force the almost infinite diversity of floral forms into a certain number of sharply delineated basic forms (Types).

Borago is regarded by D. with the fullest justification as adapted solely for fertilization by bees, since only bees are capable of holding themselves from below onto the downward-oriented [21] flowers and of passing their proboscis to the honey-containing base of the flower between the closely-spaced anthers that form a cone around the style; only bees were in fact observed as visitors and cross-fertilizers of Borago. It may also still be correct that bees play a substantial role in cross-fertilization of all other flowers in which the anthers sit on short, stiff filaments that form a cone surrounding the central axis formed by the style that penetrates the cone. However, Delpino does not stop with this assertion, but rather collects together into his Borago-Type such diverse flowers as Borago, Cyclamen, *Solanum*, *Galanthus*, *Leucojum*, and several genera from foreign lands as realizations of the same thought of the Creator, i.e. translated from Teleology into Nature, as adaptations of the same kind for the same crossing agent, and explains those cases in which other insects play substantial roles as agents of cross-pollination, for example the pollen-eating hoverflies at our {native} *Solanum* species, as pure chance events without any meaning. That in this way, through his preconceived opinion, he closes his mind to a deeper understanding of actual facts, can clearly be shown precisely by *Solanum dulcamara*. For the bowl-shaped blossom-base of the flowers of this plant, from which the pyramid of golden yellow anthers emerges upright on short, stiff filaments that appear dark on the outside, is blue-black in colour and as shiny as if it were covered by a thin film of liquid. The green, white-fringed, knot-shaped humps, that stand in pairs on the roots of the five blue-violet lance-shaped reflexed petals and occupy the entire rim of the bowl-shaped blossom-base, also appear moistened, and remind one immediately of the pseudo-nectaries of *Ophrys muscifera* (Weitere Beob. I P. 15). Furthermore, since direct observation reveals that flies sometimes dab with their labellum first these green humps and the blossom-base [22], then the stigma and the pollen-delivering tip of the anther cone, and by repeating this activity on different flowers act to effect crossing, so it can hardly be doubtful that we have to do here with a pronounced adaptation to flies as crossing agents, who must become of decided importance to the maintenance of the species as soon and as often as the visits of pollen-collecting bees are entirely

absent. In Delpino's Borago-Type, however, there is no space for crossing agents other than bees. D. instead explains the visits of flies to flowers of *Solanum dulcamara* as a meaningless chance event and completely ignores the adaptation {just} mentioned for these visitors.

(233.) *Solanum nigrum* L. (P. 275), Fig. 91, 92. The flowers of this common *Solanum* species, widely distributed as a garden weed, likewise lack honey, are oriented obliquely or vertically downward, with reflexed petals and a pyramid of stamens that protrudes precisely in the direction of the floral axis and is just overtopped by the stigma, and that releases pollen from the open ends of the anthers (Fig. 92) when shaken vigorously. It therefore belongs as well to Delpino's Borago-Type and is in fact also visited by pollen-collecting bees, as Chr. Conr. Sprengel had already observed. The bees "butted violently against the anthers, in order to make pollen fall out, and also carried little white pollen balls on their hind legs"². The short stiff filaments are covered with erect, somewhat frizzy hairs, which must substantially assist bees that cling from the bottom to hold on. The corolla is as a rule pure white, without offering any hint of the adaptations for flies mentioned for *S. dulcamara*. In spite of this these flowers are also sometimes visited and fertilized by pollen-eating hoverflies; [23] in addition to the two species I have mentioned previously (*Melithreptus scriptus* and *Syritta pipiens*) Dr. Buddenberg near Nassau also observed *Ascia podagrica* eating pollen on *Solanum nigrum*.

Delpino naturally denies again here any meaning to hoverfly visits, even though these act as a rule to effect crossing, and calls them a pure coincidence, and he is at least correct in this case insofar as special adaptations for these visitors are as a rule not to be recognized. And yet the visits of hoverflies are also of great meaning for this plant, since they provide the advantage of crossing with different individuals when bee visits are absent (pollen-collecting bees were not found at all at *Solanum nigrum* in Lippstadt and Nassau!). In fact, the first beginnings of adaptation to cross-fertilizing flies are perhaps even present in some cases in *Solanum nigrum*. Sometimes, namely, the tips of the petals have a blue-violet spot (which is more pronounced on the outer side than the inner); from this sometimes a narrow line of the same colour extends along the midline toward the base of the reflexed part of the petals. The unreflexed, fused basal part of the corolla is then usually orange-yellow, although far less intensively than the anthers.

Further visitors: Dr. Buddenberg found two hoverflies on blossoms in Nassau (27/7/75), *Ascia podagrica* F. and *Syritta pipiens* L., eating pollen.

[26] *Scrophulariaceae*

(239.) *Verbascum Lychnitis* L. white-flowered form (Mühlberg in Thüringen 8/7/73). In this *Verbascum* species as well, just as in {*Verbascum*} *nigrum*, the undermost petal is considerably longer and, at least toward the end of the blooming time, more strongly turned forward, than the two side ones, which for their part exceed the top two in length. At the same time, this does not serve as a landing platform; its lengthening appears to be without purpose for the plant; it

¹ Ulteriore osservazioni II, fasc. 2, p. 295.

² Das entdeckte Geheimniss, P. 129.

can therefore only be explained as an inheritance of the lineage that formerly had a purpose, if it is not simply a mechanical result of position.

In fact, as soon as the blossoms have opened, the white petals do not simply form themselves into [27] a plane, but rather bend beyond that to the back; the stiff filaments, densely covered with club-shaped hairs, stand straight out from the blossom, three in a row or triangle above, two, a bit more widely spread apart and a bit longer, below the middle of the blossom, all turning the suture of the anthers, from which orange-red pollen emanates, directly to the front. In the middle of the two lower ones, at the same level or a bit below, pointing downwards, stands the style, overtopping the anthers, fully developed and possessing a papillose, receptive stigma at the end. Following Delpino's explanation, based on direct observation of insect visits, the flowers of *Verbascum* are again adapted for crossing by pollen-collecting bees and bumble bees, which rapidly harvest the pollen issuing from the anthers as they cling to the hairs of the filaments, thereby touching the stigmas with a part of their hairy bodies, which carries pollen from previously-visited blossoms, and regularly causing cross-pollination. As satisfactory as this interpretation is in explaining most of the characteristics of *Verbascum* flowers, yet so unwarranted it is simply to ignore all those facts that do not agree with this explanation. That tiny droplets of honey and a moth that sucks them are observed in the blossoms of *Verbascum nigrum*, that many other insects take part in visits to and fertilization of all *Verbascum* species, do not accord with Delpino's *Verbascum* Type; he has simply ignored the first and has explained away the second as a "mera accidentalità priva di significato" {"mere accident lacking in significance"}.

Various small insects also act very regularly as crossing agents in *Verbascum Lychnitis*, perhaps only along with bumble bees (which I never encountered myself in the blossoms), or perhaps sometimes instead of them, in that they fly onto the protruding style and load its stigma with pollen they have brought, and then work the anthers. [28] In spite of small purple flecks at the roots of the petals, which look like nectar guides, I could find no honey.

As the stamens are spent they bend fully upward and backward and finally hide themselves between the hairs of their filaments; the style in contrast bends itself even further downward, with its stigma still facing forward, and the petals then bend themselves together in such a way that the lowest, longest one would now present a comfortable landing platform, if anything at all were still present that could induce insects to visit. But this is no longer the case after the collection of the pollen. Further visitors (7/7/73. Mühlberg in Thüringen):

A. Coleoptera: Curculionidae: 2) *Cionus hortulanus* Marsch, singly also in the blossoms. 3) *Gymnetron teter* F. the same. Malacodermata: 4) *Danacra pallipes* F., common in the blossoms, eating pollen? **B. Diptera:** Muscidae: 5) *Anthomyia* spp. eating pollen. **C Hemiptera:** 6) *Anthocoris spec.* **Hymenoptera:** Apidae: 7) *Halictus minutissimus* K. ♀. 8) *H. nitidus* Schenck ♀, both collecting pollen.

[31] (244.) *Veronica Chamaedrys* L. P. 285.
Further visitors:

A. Coleoptera: Nitidulidae: 9) *Meligethes* sp. common, pushing themselves into the blossom. 21/5/73 L. **B. Diptera:** Bombyliidae: 10) *Bombylius canescens* Mik. sucking. 6/73 N. B. Empidae: 11) *Cyrtoma spuria* Fallen sucking. 16/5/73, L. Muscidae: 12) *Anthomyia* spp. sucking, single. 21/5/73, L. Syrphidae: 1) *Rhingia rostrata* L. sucking. 25/5/73, N. B. 13) *Syritta pipiens* L. sucking. 2/6/73 in the same locality {Nassau}. **C. Hymenoptera:** Apidae: (14) *Andrena cingulata* F. ♀ ♂ sucking. 25/5, 31/5/73, N. B. 15) *A. cyanesces* Nyl. ♀ ♂ sucking. 6/73 in the same locality {Nassau} (5) *A. Gwynana* K. ♀ sucking. Jena 5/75, H. M. 16) *A. minutula* K. ♀ ♂ sucking and pollen collecting 25/5/73. N. B. 17) *A. parvula* K. ♀ pollen collecting 5/75, Jena H. M. 18) *Halictus cylindricus* F. ♀ sucking and pollen collecting 22/5/73, N. B.; Tekl. Borgst. 19) *H. villosulus* K. ♀ sucking. 25/5/73, N. B. 20) *H. zonulus* Sm. ♀ sucking. Jena 5/75, H. M. 21) *Melecta armata* Pz. ♀, sucking. Strassburg 6/76, H. M. 22) *M. luctuosa* Scop. ♂ sucking., Jena 5/75, H. M. 23) *Nomada germanica* Pz. ♂ sucking. 25/5/73, N. B. 24) *Osmia aenea* L. ♂ sucking. Jena 5/75, H. M. 25) *Sphcodes gibbus* L. ♀ sucking. 25/5/73, N. B.

It is a very striking phenomenon to see that a flower that is visited and often also crossed by so many bees and flies is equipped with such a delicate pollination mechanism, that can only be set in motion by small hoverflies and thus that can only be interpreted as an adaptation for the same. With the same justification as Delpino with *Solanum* and *Verbascum*, we could say that every other visit is a purely chance event without meaning. But the unnaturalness of such an excuse would be ever more glaringly revealed here, the more common these visits are. The only possible explanation appears to me to be, that *Veronica Chamaedrys* and the other *Veronica* species equipped with the same pollination mechanism obtained their characteristic at a time and place in which they were accorded mostly visits by hoverflies, and that they only subsequently spread to locations or entered into conditions of life that supplied them with such a diversity of other insects. [32] One may compare the arguments that I gave in my work on alpine flowers in relation to *Primula farinosa* and *Rhinanthus alpina*, as well as the conclusions in regard to the origin of certain flowers (Alpenblumen, P. 555 ff.).

DISCUSSION

An original impetus for describing what are now known as pollination syndromes was to provide a classification for a rapidly-growing body of observations on specific plant-pollinator interactions. Along with phylogenetic classification, various versions of the pollination syndromes served to supplant earlier schemes for organizing floral diversity, such as Linnaeus' (1735) method based on numbers of male and female sex organs (Mayr 1982). Pollination syndromes were adopted as a tool that could reduce the high dimensionality that characterizes floral phenotypes and that could be used to predict interactions with pollinators and to shed light on floral evolution (Fægri & van der Pijl 1979; Fenster et al. 2004). But in spite of their long evolution, the pollination

syndromes remain a work in progress; and in spite of benefits, they elicit varying levels of comfort among workers (e.g., Waser et al. 1996; Hingston & McQuillan 2000; Fenster et al. 2004; Smith et al. 2008; Ollerton et al. 2009). One source of discomfort is concern about overly-rigid typology, the same concern raised by Müller (1882).

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einnehmend, der mit einer zweilappigen Narbe endende Griffel; dicht über der Narbe, rings um dieselbe herum, stehen die nach innen aufspringenden und sich mit Pollen bedeckenden Staubgefäße. Ein in der Blütenmitte eingeführter und annähernd in der Richtung ihrer Achse in den Grund der Blüthe gesenkter Rüssel kann daher kaum vermeiden, mit einer Seite die Narbe, mit der entgegengesetzten 1 oder 2 pollenbedeckte Staubgefäße zu streifen und so bei zahlreichen Blütenbesuchen überwiegend Fremdbestäubungen zu bewirken. Bei wiederholtem Hineinstecken des Rüssels in dieselbe Blüthe, was übrigens seltener vorkommt, wird natürlich ebenso leicht Selbstbestäubung bewirkt, und bei ausbleibendem Insektenbesuche erfolgt, indem aus den über der Narbe zusammen neigenden Staubgefäßen Pollen auf diese fällt, unausbleiblich spontane Selbstbestäubung. Besucher (bei Mühlberg in Thüringen 6;7 73):

A. Hymenoptera: Apidae: 1) *Andrena nigroaenea* K. ♀ sgd., sehr lange (über ½ Miu.) an einer Blüthe verweilend. 2) *Apis mellifica* L. ♂ sgd., häufig. 3) *Halictus tetrazonius* Kl. ♀ sgd., in Mehrzahl. **B. Lepidoptera:** Rhopalocera: 4) *Lycena Aegon* S. V. ♂ sgd. **C. Thysanoptera:** 5) *Thrips*, sehr häufig in den Blüten.

Solaneae. (S. 274.)

(232.) *Solanum Dulcamara* L. (S. 275). Sprengel Taf. IX Fig. 15. Delpino¹⁾ führt diese Solanumart als schönen Ausdruck seines Borago-Typus an. Sie ist aber gleichzeitig ein gutes Beispiel der Unzulänglichkeit der Delpino'schen Typen und der Willkürlichkeit und Unnatürlichkeit, in die man unvermeidlich verfallen muss, wenn man die fast unendliche Mannigfaltigkeit der Blumenformen in eine gewisse Zahl scharf umgrenzter Grundformen (Typen) einzuzwängen versucht.

Borago wird von D. mit vollstem Rechte als nur der Befruchtung durch Bienen angepasst betrachtet; denn nur Bienen sind im Stande, sich an die nach unten gekehrten

1) Ulteriori osservazioni II, fasc. 2 p. 295.

Fig. 2. The page from Müller (1882) that begins the discussion of pollination of Solanaceae, in particular of *Solanum dulcamara*.

A rigid interpretation certainly follows automatically from a belief in teleology. The word derives from the Greek *telos* ("end"), and *logos* ("reason"). Many meanings have been attached to this concept, and a complete exploration of them lies beyond our training and ability as ecologists, and beyond the scope of this paper. However, it is sufficient here to understand the word as referring to the doctrine that observed phenomena and patterns in nature are explained not by natural mechanisms but by some deeper purpose or cause beyond nature, usually implying a deity (Pittendrigh 1958; Mayr 1961, 1982). A recurrent appeal to teleology—and opposition to it—can be identified from early observations of natural history through to the present day. Explanations that border on teleology persistently resurface in modern biology (as discussed, e.g., by Mayr 1961, 1982, 1991; Bekoff & Allen 1995; Reiss 2009). Indeed, the teleology of Delpino is

echoed in some explicitly teleological and essentialist contributions of Vogel (1954; see also Vogel 2006) to the pollination syndromes. For example, Vogel (1954) devotes pages 19–23 of his introductory section to "Die Rückkehr zur Teleologie" ("The return to teleology"), and on pp. 19–20 proposes that "Verstehen wir die teleologische Auffassung vielmehr wieder in dem weiteren, wertoffenen (Wertoffen, das heisst nicht nur Funktionswerten, sondern auch Werten nicht funktioneller Art offenstehend) und ursprünglichen Sinne, wie sie von Aristoteles in seiner Entelechienlehre gemeint war, so bietet sie sich durchaus—trotz ihrer Verrufenheit—aufs neue an." ("When we again understand the teleological concept much more in its wider original sense, open to values (that means open not only to functional values but also to values which are not functional), as it was meant by Aristotle in his entelechy doctrine, then the concept offers itself—in spite of its bad reputation—quite anew"). As with teleology, the concept of *entelechy* is difficult to express in few words, but basically refers to the idea that a pattern in nature, such as the pollination syndromes, represents the realization of an underlying perfection or order.

It is important to admit that biologists discuss different levels of causation, sometimes leading to confusion; and that evolutionary biologists often use language that suggests teleological thinking (for discussion see Pittendrigh 1958; Mayr 1961; Bekoff & Allen 1995). In proposing hypotheses to explain the phenotypes of organisms, including those of flowers, it is not uncommon to slip into language of the sort that "this feature exists for such and such a purpose". Such usage is shorthand for a proposal that natural selection has moulded the phenotype in question, and that the sources and targets of selection are of certain kinds. Surely, however, such 'apparent teleology' is not to be confused with the real thing—a recourse to higher causation beyond natural processes—even though confusion does sometimes surface (e.g., Soontiens 1991; note that Pittendrigh 1958 referred to this apparent teleology as 'teleonomy' to distinguish it from true teleology).

Hermann Müller certainly was not opposed to grouping flowers according to their putative adaptations for pollinators. At the same time, he left his mind open to many possibilities, including the existence of adaptations to multiple types of pollinators, the likelihood of geographic variation in pollinators of a given species, and the likelihood of observing pollinators not predicted by an initial deduction about floral adaptation. This openness is illustrated in the passages translated above, and in what Müller (1873, p 185) says, as just one example, of *Dianthus deltoides*: "Die Blüten geben sich hierdurch mit Bestimmtheit als Schmetterlingen angepasst zu erkennen; jedoch können ihre frei hervortretenden Staubbeutel auch von Pollen suchenden Insekten ausgebeutet werden, und diese können selbst als untergeordnete Befruchter wirken." ("The flowers thereby reveal themselves [through features Müller had just described] with certainty as adapted to butterflies; at the same time, their freely-protruding anthers can also be exploited by pollen-seeking insects, and these can act as subordinate pollinators"). Thus we see that he strongly rejects teleology, and indeed we sense that he was uncomfortable more generally with rigid adherence to typology as a substitute for direct observation of

nature. Müller himself was a careful observer, and to his own observations he could add the regular insights into tropical systems received from his brother Fritz, who had emigrated to Brazil (Schneckenburger 2009, 2010). His Darwinian world view gave him a perspective on plants and pollinators that matches what Mayr advocates in the works cited above: dynamic and flexible, full of apparent contradictions and puzzles, rather than highly orderly.

Müller's specific critique of Delpino's typology (the two referred to each other in correspondence as "Carissimo amico, leale avversario"—Dearest friend, loyal adversary) appears to be limited to the four plant species described in our translation. We have scanned his major books (Müller 1873, 1881), and the *Weitere Beobachtungen*, and do not find additional examples. We do know that Delpino had corresponded with Müller about his typology before publishing it, arguing in favour of a teleological basis for natural phenomena, as he had similarly argued to Charles Darwin (see Pancaldi 1984).

Müller (1882) raises a puzzle that persists in modern pollination ecology (Ollerton 1996): why might flowers exhibit apparent adaptations to types of insects that constitute only a fraction of their observed visitors, and lack apparent adaptations to common visitors? At times Müller invokes phylogenetic constraint, past ecological context, and mechanical or developmental constraint to explain this apparent paradox—all arguments that can be traced initially to Darwin's writings and that persist in modern discussions (e.g., Armbruster 1997; Lamborn & Ollerton 2000). Additional ideas have been advanced to resolve the paradox (e.g., Ollerton 1996; Waser 1998; Aigner 2001; Fenster et al. 2004). For example, Aigner (2001) showed how flowers might exhibit striking adaptations to only a few of their many pollinators, even to ones that are not the most common visitors, so long as the fitness tradeoffs involved exhibit a certain form. This is an idea ripe for further exploration.

The two species of *Solanum* included in the translated text are interesting because the modern view is that most flowers in this genus are "buzz" pollinated, i.e., that pollen is released from the poricidal anthers only when they are vibrated at the correct ultrasonic frequency, a feat achieved by certain bees (Proctor et al. 1996; Knapp 2010). Buchmann (1983) dates the first description of buzz pollination to the late 19th century, after Müller's time, although the passages above do hint at recognition that special behaviours of bees cause the release of pollen (even recognition on the part of Sprengel 1793). A strict view of buzz pollination therefore would call into question any role of hover flies as additional pollinators, but our recent field studies (J. Ollerton, unpublished results) indicate that these visitors do actually pollinate at least one of the two *Solanum* species. Single visits by hover flies to virgin flowers of *S. dulcamara* resulted in transfer of pollen to stigmas. Although hover flies were less frequent visitors than bumblebees at our study sites near Northampton, UK, their pollination of this species might indeed be responsible for the pseudonectaries that Müller describes, in agreement with Aigner's (2001) hypothesis of floral adaptation to minor pollinators.

Whether or not Müller is correct in each of his specific examples (as he appears correct in this one), the main points he raises, both explicitly and implicitly, remain of interest: that teleology is not an appropriate basis for understanding diversity in nature, including the diversity of floral form; more generally that an overly-strict adherence to a classification scheme such as the pollination syndromes, even if not based on any teleological assumption, is likely to miss important elements of this diversity; instead that any classification scheme should be recognized as an hypothesis subject to testing and modification; and finally that there is no substitute for careful natural history, by which, following Price and Billick (2010), we mean knowledge about the natural world gained through observation, experimentation, and any other means available.

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