

**TELEOLOGY AT THE ROOT OF “POLLINATION SYNDROMES”: A CRITIQUE FROM THE
PAST**

Nickolas M. Waser¹, Jeff Ollerton², and Andreas Erhardt³,

¹ School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA.

² Landscape and Biodiversity Research Group, School of Applied Sciences, University of Northampton, Northampton, NN2 7AL, UK.

³ Institut für Natur-, Landschafts- und Umweltschutz, Universität Basel, St. Johannis-Vorstadt 10, 4056 Basel, Switzerland.

Abstract.

Here we provide, and discuss, a translation of several pages from an 1882 paper by Hermann Müller. In it, the prominent German Darwinist uses several plant species to criticise the floral classification schemes of his Italian contemporary Federico Delpino. Delpino also was a self-proclaimed Darwinist, but in fact adhered to teleology—explanation beyond nature. Müller’s comments seem especially àpropos given later teleological and essentialist contributions to “pollination syndromes”—the modern version of Delpino’s classifications. Müller’s comments also seem àpropos given the recent interest in revisiting (and improving) the syndromes as a central concept in an important area of ecology, the study of pollination.

Key words: Darwinism, Essentialism, Delpino, History, Müller, Pollination, Teleology

Introduction

Our object in this unusual paper is to bring forward an historical critique of some of the teleological roots that nourished the concept of “pollination syndromes”. The pollination syndromes describe suites of floral traits that putatively adapt distantly-related plants for pollination by specific types of animals. This concept, a very Darwinian one of convergent evolution, has served as a cornerstone of the study of pollination by botanists, evolutionary ecologists, cognitive behaviorists, *et al.*—a solid pocket of fruitful scientific activity over the last several decades.

The pollination syndromes date to the Italian botanist Federico Delpino (born 1833 near Genoa, died 1905; see Figure 1, left). In 1873-1874, Delpino published a monograph whose title is translated as *Additional observations and considerations on dichogamy in the plant kingdom* (with “dichogamy” used as a synonym for “outcrossing sexual reproduction”). This work laid out two functional schemes for classifying flowers, which were modified over subsequent decades by other workers. These early contributions, and more recent ones, including those of Vogel (1954) and Faegri and van der Pijl (1979), led to modern articulations of the pollination syndromes.

An original impetus for describing syndromes was to provide a non-taxonomic classification for a rapidly-growing body of observations on specific pollination interactions. Viewed equivalently but in retrospect, such classification served as a working tool to reduce the high dimensionality that so strikingly characterizes floral form in the angiosperms, as well as to predict pollination interactions and to interpret floral evolution (Faegri and van der Pijl 1979, Fenster *et al.* 2004). But the pollination syndromes remain even today somewhat elusive and vague, with no single universally-

accepted version. And the syndromes elicit varying levels of comfort among workers (e.g., Waser *et al.* 1996, Hingston and McQuillan 2000, Fenster *et al.* 2004, Smith *et al.* 2008, Ollerton *et al.* 2009). Inherent scepticism about overly-orderly classification may play a role in any discomfort.

Although many proponents of syndromes have stressed that the intended classification is a loose one, others, including Delpino, adopted a more rigid view. It is intriguing to recognize that some of Delpino's rigidity derived from a teleological perspective on the natural world, rather than from a true Darwinian perspective.

During the long gestation of an analysis of the pollination syndromes that has now appeared in print (Ollerton *et al.* 2009), serendipitous events led us to track down one early argument against too rigid a classification, that of the great German botanist, pollination biologist, and Darwinist Hermann Müller (born 1829 in Thuringia in central Germany, died 1883; see Figure 1, right). Müller published important works on pollination in German and English, including an influential book, *Die Befruchtung der Blumen durch Insekten* (Müller 1873), that was translated by D'Arcy Thompson in 1883 as *The fertilisation of flowers*, at Charles Darwin's suggestion. This book lays out a history of the scientific study of pollination, and general principles of floral form, insect morphology, and insect behavior, before turning to a plant species-by-species compendium of insects and other animals observed to visit flowers.

Müller's 1873 book was followed by three instalments of further observations, logically enough entitled in German *Weitere Beobachtungen über Befruchtung der Blumen durch Insekten* (*Further observations on the fertilization of flowers by insects*). It is the third instalment in this series (Müller 1882) that concerns us here. The obscurity of

this article to most modern pollination biologists might have persisted, except for the strange fact that Müller had been quoted both by Knuth (1898a) and by Vogel (1954), but quoted *slightly differently*. 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 floral classification.

We concluded that it would be of interest to provide an English translation of several pages (see Figure 2) from Müller (1882), and this appears below. In **[square brackets]** in bold, we show 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 italicizes.

Footnotes from the original text appear as endnotes at the end of this contribution. Short of producing incomprehensible English sentences, we have attempted to retain the basic sentence structure (if not the word order) of Müller. As Clemens (1880) so humorously noted, long, tortuous sentences characterized especially 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 “Sprenkel”, 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, in modern context.

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 color 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 color 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 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) *Danacaca 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) *Syrirta 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. cyanescens* 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) *Sphecodes 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

The word *teleology* derives from the Greek *telos* (“end”), and *logos* (“reason”). Many meanings that have been attached to this word, and we readily acknowledge that to truly explore this conceptual territory lies beyond our training and ability as ecologists, and beyond the scope of this paper. However, we also feel that it is sufficient to understand the word in a basic sense, as referring to an explanation in terms of a perceived deeper purpose or plan, usually (even if only implicitly) that of an entity beyond nature, such as a deity (Pittendrigh 1958, Mayr 1961). A recurrent appeal to teleology—and opposition to it—can be identified from early observations of natural history through to the present day. As early as 1790, for example, Goethe railed that for “...centuries...we have been retarded in our philosophic views of natural phenomena by the idea that living organisms are created and shaped to certain ends by a teleological life force” (quoted in Gould 2002). Yet explanations that border on teleology persistently resurface in modern biology (as discussed, e.g., by Mayr 1961, Bekoff and Allen 1995, Reiss 2009). Indeed, the teleology of Delpino is echoed in much more recent contributions of Stefan Vogel (1954, 2006) to the pollination syndromes, which are explicitly teleological and essentialist. For example, Vogel (1954) devotes almost four pages (his pages 19–23) to “Die Rückkehr zur Teleologie” (“The return to teleology”). In arguing for this return he proposes, for example, 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 Entelechie 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 (which means open not only to functional values but also to values which are not functional), as it was meant by Aristotle in his *Entelechy*, then [the concept] offers itself—in spite of its bad reputation—quite anew”).

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 and 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 phenotypic expression exists for such and such a purpose”. Such usage is at best an innocent shorthand for an hypothesis that natural selection has molded the phenotype in question, and that the sources and targets of selection are of certain kinds. At worst it indicates vague thinking about the evolutionary process, a sort of open-and-shut invocation of a “just –so story”, with neither clear recognition of the hypothetical nature of the proposition nor clear intent at closer examination. 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., Soontjens 1991). What is clear is that most scientists, including evolutionary biologists, soundly reject teleological explanations for natural phenomena (e.g., Reiss 2009).

Hermann Müller exemplifies these latter scientists. He certainly was not opposed to inferring floral adaptation to pollinating animals. This 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”). He was, however, scathing in his condemnation of teleology as a substitute for Darwinian thinking. We infer, from the writings of Müller, that he weighed direct observation of nature first, and any typological classification scheme second. It is certain that he was a careful observer of nature, and to his own observations he could add the regular insights into tropical systems received from his brother Fritz, who had emigrated to Brazil. His Darwinian worldview gave him a perspective on plants and pollinators that was dynamic and flexible, full of apparent contradictions and puzzles, rather than a perspective that was highly orderly. In these characteristics Müller was an intellectual forefather of recent workers who have used versions of the pollination syndromes as a rough guide, while warning against interpreting them too literally (e.g., Baker and Hurd 1968).

Müller’s specific critique of Delpino’s floral classification appears to be limited to the four plant species described in our translation. We have scanned Müller’s major books (Müller 1873, 1881), as well as the three instalments of the *Weitere Beobachtungen*, and do not find obvious additional examples (his death just one year after publication of the 1882 instalment may have forestalled any further commentary). We do know that Delpino had corresponded with Müller about his classification of

flowers before publishing it, arguing in favor 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, as recently emphasized by 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 and Ollerton 2000). Additional ideas to resolve the apparent paradox have been put forward (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 specific form. This is an idea that is 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 that vibrate their flight muscles appropriately (Proctor *et al.* 1996). Buchmann (1983) gives a good historical review of buzz pollination, dating its recognition to the late 19th century (after Müller’s time), and specifically discussing *Solanum*. The passages above do hint at a recognition that special behaviors of bees were needed to release the pollen (even recognition on the part of

Sprengel 1793!), but it is uncertain whether Müller fully understood the system. It is also uncertain whether hover flies, which do not buzz the flowers, actually pollinate these *Solanum* species.

Regardless of such details, which further study of specific systems should clarify, Müller's main points remain: that teleology and essentialism are not an appropriate basis for understanding diversity in nature (see also Mayr 1961), including the diversity of floral form; that overly-strict typologies are unlikely to capture essential elements of this diversity; and 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.

Acknowledgements. We thank James Cresswell, Mary Price, and Stacey Smith for encouragement and comments, and Alta L. Price for translating parts of Delpino (1873-1874) from the Italian.

References

- Armbruster WS. 1997.** Exaptations link evolution of plant-herbivore and plant-pollinator interactions: A phylogenetic inquiry. *Ecology* **78**: 1661–1672.
- Baker HG, Hurd PDJ. 1968.** Intrafloral ecology. *Annual Review of Entomology* **13**: 385–414.
- Bekoff M, Allen C. 1995.** Teleology, function, design and the evolution of animal behaviour. *Trends in Ecology and Evolution* **10**: 253–255.
- Buchmann SL 1983.** Buzz pollination in angiosperms. In: Jones CE, Little RJ, eds. *Handbook of experimental pollination biology*. New York, Van Nostrand Reinhold, 73–113.
- Clemens S. 1880.** *A tramp abroad, Appendix D: The awful German language*. Hartford, Connecticut, American Publishing Company.
- Delpino F. 1873–1874.** Ulteriori osservazioni e considerazioni sulla dicogamia nel regno vegetale. *Atti della Società Italiana di Scienze Naturali* **16**: 151–349, **17**: 266–407.
- Faegri K, van der Pijl L. 1979.** *The principles of pollination ecology*, 3rd revised edition. Oxford, Pergamon Press.
- Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD. 2004.** Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* **35**: 375–403.
- Gould SJ. 2002.** *The structure of evolutionary theory*. Cambridge, Belknap Press of Harvard University Press.

- Hingston AB, McQuillan PB. 2000.** Are pollination syndromes useful predictors of floral visitors in Tasmania? *Austral Ecology* **25**: 600–609.
- Knuth P. 1898a.** *Handbuch der Blütenbiologie. I. Band: Einleitung und Litteratur.* Leipzig, Wilhelm Engelmann.
- Knuth P. 1898b.** *Handbuch der Blütenbiologie. II. Band: Die bisher in Europa und im arktischen Gebiet gemachten blütenbiologischen Beobachtungen. 1. Teil: Ranunculaceae bis Compositae.* Leipzig, Wilhelm Engelmann.
- Knuth P. 1899.** *Handbuch der Blütenbiologie. II. Band: Die bisher in Europa und im arktischen Gebiet gemachten blütenbiologischen Beobachtungen. 2. Teil: Lobeliaceae bis Gnetaceae.* Leipzig, Wilhelm Engelmann.
- Lamborn E, Ollerton J. 2000.** Experimental assessment of the functional morphology of inflorescences of *Daucus carota* (Apiaceae): Testing the "fly catcher effect". *Functional Ecology* **14**: 445–454.
- Mayr E. 1961.** Cause and effect in biology. *Science* **134**: 1502–1506
- Müller H. 1873.** *Die Befruchtung der Blumen durch Insekten, und die gegenseitigen Anpassungen beider.* Leipzig, Wilhelm Engelmann.
- Müller H. 1881.** *Die Alpenblumen, ihre Befruchtung durch Insekten und ihre Anpassungen an dieselben.* Leipzig, Wilhelm Engelmann.
- Müller H. 1882.** Weitere Beobachtungen über Befruchtung der Blumen durch Insekten, Teil III. *Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande und Westfalens*, Neununddreissigster Jahrgang. Vierte Folge: 9. Jahrgang, 1–104.

- Ollerton J.** 1996. Reconciling ecological processes with phylogenetic patterns: The apparent paradox of plant-pollinator systems. *Journal of Ecology* **84**: 767–769.
- Ollerton J, Alarcón R, Waser NM, Price MV, Watts S, Cranmer L, Hingston A, Peter CI, Rotenberry J.** 2009. A global test of the pollination syndrome hypothesis. *Annals of Botany* **103**: 1471–1480.
- Pancaldi G.** 1984. *Teleologia e Darwinismo. la corrispondenza tra Charles Darwin e Federico Delpino*. Bologna: Cooperativa Libreria Editrice.
- Pittendrigh, CS.** 1958. Adaptation, natural selection, and behavior. In: Roe A, Simpson GG, eds. *Behavior and evolution*. New Haven, Yale University Press, 390–416.
- Price MV, Billick I.** 2010. Introductory remarks to Section 3. In: Billick I, Price MV, eds. *The ecology of place: Contributions of place-based research to ecological understanding*. Chicago, The University of Chicago Press, in press.
- Proctor M, Yeo P, Lack A.** 1996. *The natural history of pollination*. London, HarperCollins.
- Reiss JO.** 2009. *Not by design: Retiring Darwin's watchmaker*. Berkeley, University of California Press.
- Smith S, Ané C, Baum DA.** 2008. The role of pollinator shifts in the floral diversification of *Iochroma* (Solanaceae). *Evolution* **62**: 793–806.
- Soontiëns FJK.** 1991. Evolution: Teleology or chance? *Journal for General Philosophy of Science* **22**: 133–141.
- Sprengel CK.** 1793. *Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen*. Berlin, Friedrich Vieweg der aeltern.

- Vogel S. 1954.** Blütenbiologische Typen als Elemente der Sippengliederung, dargestellt anhand der Flora Südafrikas. *Botanische Studien* **1**: 1–338.
- Vogel, S. 1996.** Christian Konrad Sprengel's theory of the flower: The cradle of floral ecology. In: Lloyd DG, Barrett SCH, eds. *Floral ecology: Studies on floral evolution in animal-pollinated plants*. New York, Chapman and Hall, 44–62.
- Vogel S. 2006.** Floral syndromes: Empiricism versus typology. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **127**: 5–11.
- Waser NM. 1998.** Pollination, angiosperm speciation, and the nature of species boundaries. *Oikos* **82**: 198–201.
- Waser NM. 2006.** Specialization and generalization in plant-pollinator interactions: An historical perspective. In: Waser NM, Ollerton J, eds. *Plant-pollinator interactions: From specialization to generalization*. Chicago, University of Chicago Press, 3–17.
- Waser NM, Chittka L, Price MV, Williams NM, Ollerton J. 1996.** Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043–1060.

Figure Legends.

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

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

Figure 1

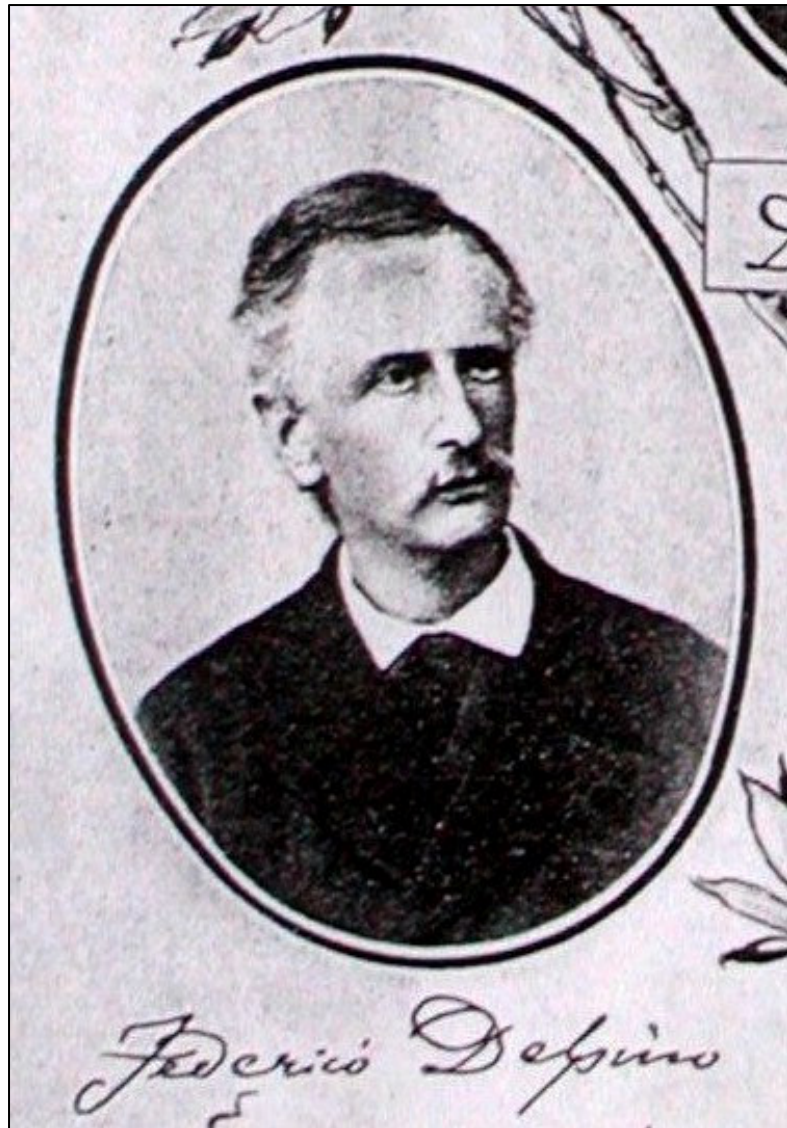


Figure 20

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 Blüte 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 Blüte, 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 $\frac{1}{2}$ Min.) an einer Blüte verweilend. 2) *Apis mellifica* L. ♀ sgd., häufig. 3) *Halictus tetrazonius* Kl. ♀ sgd., in Mehrzahl. B. Lepidoptera: Rhopalocera: 4) *Lycaena 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.

Blumen von unten anzuklammern und zwischen den eng zusammenliegenden, den Griffel in Kegelform umschliessenden Staubgefäßen hindurch den Rüssel in den honighaltigen Blüthengrund zu führen; nur Bienen wurden tatsächlich als Besucher und Kreuzungsvermittler von Borago beobachtet. Es mag auch noch richtig sein, dass an allen anderen Blumen, bei denen die Staubgefäße auf kurzen steifen Filamenten sitzen und den als Achse hindurchgehenden Griffel in Kegelform umschliessen, die Bienen als Kreuzungsvermittler wesentlich mitbetheiligt sind. Delpino begnügt sich aber nicht mit dieser Feststellung, sondern fasst so verschiedenartige Blumen wie Borago, Cyclamen, Solanum, Galanthus, Leucojum und mehrere fremdländische Gattungen als Verwirklichungen desselben Schöpfergedankens, d. h. aus dem Teleologischen ins Natürliche übersetzt, als gleichartige Anpassungen an dieselben Kreuzungsvermittler, in seinen Borago-Typus zusammen und erklärt in denjenigen Fällen, in welchen andere Insekten, wie z. B. bei unseren Solanumarten pollenfressende Schwebfliegen, als Kreuzungsvermittler wesentlich mitwirken, deren Besuch als reine Zufälligkeit ohne Bedeutung. Dass er sich auf diese Weise durch seine vorgefasste Meinung einem eingehenderen Verständnisse tatsächlich vorliegender Verhältnisse verschliesst, lässt sich gerade an *Solanum Dulcamara* recht deutlich zeigen. Denn an den Blumen dieser Pflanze ist der napfförmige Blüthengrund, aus welchem die goldgelbe Staubbeutelpyramide auf kurzen, steifen, aussen dunkeln Filamenten senkrecht hervorsteht, von blauschwarzer Farbe und so glänzend, als wenn er mit einer dünnen Flüssigkeitsschicht überzogen wäre. Die grünen, weiss umsäumten, knopfförmigen Höcker, welche paarweise auf den Wurzeln der fünf violettblauen, lanzettlichen, zurückgeschlagenen Blumenblätter stehen und den Rand des napfförmigen Blüthengrundes ringsum besetzen, sehen ebenfalls wie besetzt aus und erinnern unmittelbar an die Scheinnektarien von *Ophrys muscifera* (Weitere Beob. I S. 16). Da nun überdies die directe Beobachtung ergibt, dass bisweilen Fliegen erst diese grünen Höcker und den Blüthengrund,

Footnotes from the text of Müller (1882).

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

² Das entdeckte Geheimniss, P. 129.