Discovering The Floral Biology of Aristolochia

How German botanists unraveled the intricacies of these remarkable flowers; in their own words.

Selected, Edited and Translated
By

Richard Edward Rintz

Dedicated to the memory of my father, EDWARD J. RINTZ, whose financial generosity made this work possible.

Title page shows a photo of *Aristolochia fimbriata* taken by the author in 2007 of a cultivated plant.

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Introduction

In August of 2005 I was walking along a trail in Big Bend National Park when I glanced down and noticed a cushion of dark green, heart-shaped leaves, poking out of which were a few funnel-shaped flowers with yellow, brown-spotted throats. My first reaction was that it looked like a *Ceropegia,* even though I knew that this genus did not occur in North America. As I examined the plant, I noted the alternate, raher than opposite, leaves and the bilaterally, rather than radially, symmetrical flowers. It was definitely not a *Ceropegia*. What then? For some reason *Aristolochia* came into my mind, despite my never having seen a live plant of this genus and despite my thinking that it was restricted to the tropics. The next day I looked up *Aristolochia* in the Peterson wildflower guide and was surprised to find that there were four species, known locally as pipevines, in the Southwest, two of them right there in the Big Bend area. Later, I found more blooming plants of *A. coryi* in another area and a few days later I came upon plants of *A. wrightii* in bloom. I was fascinated by them.

When I searched the literature on *Aristolochia*, I found that all of the seminal work and many of the most important papers had been published in German. As I translated them I also noticed that they were splendidly done and, when read in chronological order, presented a remarkable picture of how the intricacies of this flower were unraveled. Yet, there they were buried, so to speak, in German journals held in certain select libraries; at best, the interested layman would be fortunate if he found even an English summary of a few of these papers. I think the public should have access to this material, so I have put together this collection of important German papers.

Aristolochias (often called birthworts in English) have been known medicinally for several thousand years around the Mediterranean. They were mentioned by THEOPHRASTUS (c. 300 B.C.E.) and dealt with by DIOSCORIDES (c. 0065) and PLINY THE ELDER (c 0070). they were described in all of the medieval herbals and widely planted in European herb gardens. When Europeans arrived in North America, a local species, *A. serpentaria*, was being used medicinally by Native Americans. The flowers, however, were not investigated until the development of the magnifying glass and the formal birth of taxonomy in the 1700s. Even so, it wasn't until SPRENGEL gave them his attention in 1793 and revealed some of their intricate details that we got our first accurate look at these strangely constructed flowers. SPRENGEL was the father of floral biology, the first to note that certain flowers had developed in such a way that they manipulated, rather than just attracted, insects. Unfortunately, he did not understand that these developments favored cross-pollination rather than self-pollination and, initially, his work was largely disregarded.

I am including here two paragraphs from a book on Asclepiads written in Latin by one of Europe's leading botanists at that time. When writing of SPRENGEL in 1811, JACQUIN referred to the former's work on *Aristolochia* and expressed his incredulity that Nature would waste time making flowers so unnecessarily complicated just to get self-pollinated. JACQUIN was expressing the sentiment of his day and so there is this long gap of 74 years between SPRENGEL and his successor, HILDEBRAND.

During this period, however, botanical knowledge was expanding greatly, thanks in good part to improvements in optics and then to DARWIN's views regarding speciation by natural selection in 1859. Botanists were coming to understand that such seemingly overcomplicated flowers could actually have been naturally selected for over long periods of time to ensure cross-pollination. Indeed, DARWIN mentions SPRENGEL's work several times in THE ORIGIN OF SPECIES. And so, in 1867 HILDEBRAND took up where SPRENGEL left off, corrected a few of his errors, and added considerable detail, in particular the structure and function of the tube hairs and the proterogynous dichogamy of the flowers. HILDEBRAND also translated and published the work of the Italian botanist, DELPINO, adding the latter's insights to his own, insights that might have been overlooked otherwise.

However, HILDEBRAND did make some errors and these were largely dealt with 24 years later by CORRENS. Notably, CORRENS discovered the nectary on the roof of the kettle, thereby providing a food source for the captive flies, and he explored the various trichomes in great detail. He also dismisses BURCK's objections to HILDEBRAND's interpretation of the flower as serving for cross-pollination.

In complicated situations like this one, someone always seems to come forward to play Devil's Advocate, to challenge the accepted view no matter how well-reasoned it is; in this case it was BURCK. He regarded the *Aristolochia* flower, as did SPRENGEL, as adapted for self-pollination and insisted that the captive flies died within the flower. His views were disputed by all subsequent authors, especially CAMMERLOHER, and disregarded.

Next are three interesting papers by ULE, including two dealing with Brazilian Aristolochias in their native habitats. He seems to be the first one to have attempted to cross different species and produce hybrids, indicating that these outwardly distinct flowers are really quite closely related.

The first of CAMMERLOHER's three papers explores a fascinating problem in floral biology, namely, how the delayed opening of a flower can lead to sterility and to the eventual natural extinction of a species. Not all recent extinctions are the result of human activity.

CAMMERLOHER's second paper is a detailed exploration of the remarkable *A. grandiflora* and a careful repudiation of BURCK's views. His work definitively established the proterogynous dichogamy of the *Aristolochia* flower.

In 1928 LINDNER reported on another remarkable *Aristolochia* that he had recently discovered in Bolivia. He seems to be the first person to have noted the change in the pigmentation inside of the flower and its relationship to the temporary captivity and release of the insect visitors. This was an important new observation and added a new dimension to our understanding of these amazing flowers.

I am including here KNOLL's short account on "slide-trap flowers" because it is frequently cited by subsequent authors and readers should know what they are referring to. It is not a formal paper but is the synopsis of a lecture he gave at a botanical meeting.

In CAMMERLOHER's third paper he directs his attention to LINDNER's new species examining it thoroughly from a botanical perspective. LINDNER was an entomologist and he did his work at the discovery site in Bolivia; as a consequence he missed some of the more subtle aspects of the flower. CAMMERLOHER, working with cultivated plants in Vienna, had much more time and better working conditions for his very comprehensive investigation.

We then have two papers by DAUMANN. The first one gives his results from a thorough investigation of the kettle hairs in several species and provides some remarkable new information about them and the nutrition available to the captive insects. His second paper investigates the flower's attractive effect on small flies and provides still more new information.

The last two papers compliment two previous papers and provide a proper conclusion to this collection. In the first one, IBISCH brings us up to date on *A. lindneri* in Bolivia and in the second one, HEINHUIS, ROTH and BARTHLOT provide a splendid update on *A. arborea*.

Since many of these papers do not have habit illustrations of the various species that they discuss, I have included some illustrations that I collected from other sources so the reader can see what these plants actually look like. Taking these illustrations in chronological order, one can see how the emphasis gradually shifts from roots and habits in pre-Linnaean times to predominantly flowers in the 19th and 20th centuries.

If the reader is not entirely satisfied with this collection and would like to read some non-German authors, there are papers in English, Spanish and Portuguese that deal with many of these same species and others as well. The oldest English paper that I know of is by PETCH (1924) who worked in Ceylon. His paper is 109 pages long discussing many unusual species with illustrations. PFEIFER (1966 and 1970) has revised the taxonomy of the North and Central American species in two works and has good illustrations, especially in the latter one. CROSSWHITE and CROSSWHITE (1984) have a good discussion of *A. watsonii* in Arizona and CHEATUM, JOHNSON and MARSHALL (1995) discuss and illustrate the 6 Texas species in their remarkable book on useful wild plants. A number of foreign authors have also written in English and are cited in the bibliographies of most recent papers.

The plant that started it all in 1790.

Aristolochia clematitis L. Osterluzei

Illustration from: Thomé, O. W. 1885. Flora von Deutschland, sterreich und der Schweiz. Gera-Untermhaus. E. Kohler. **Osterluzei** is German for Aristolochia.

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I owe a debt of gratitude to MISSOURI BOTANICAL GARDEN for the unrestricted use of their fine botanical library from which the German originals of these papers were obtained; to librarian VICTORIA McMICHAEL for her unstinting assistance; and to KAREN D. SMITH for her invaluable help in formatting this work.

Sprengel, C. K. 1793. Das Entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. Berlin. Pp. 418-429.

Nature's Mystery Revealed in the Structure and Fertilization of Flowers.

By
Christian Konrad Sprengel.

Aristolochia.

Aristolochia Clematitis. Common Birthwort. Frontispiece Fig. XXI. The flowers standing upright, reduced a little in size, still not fertilized. Fig. XXIII. The flowers hanging down, already fertilized. Plate VI. 13-15, 23, 30, 31, 34.

13. The enlarged, unfertilized flower from which the front half of the corolla has been cut away, in natural position.

23. Refer to the preceding Figure. The body on which the stigma and the anthers are situated, seen from above.

14. The fertilized flower from which the front half of the corolla has also been cut away, in natural position.

15. Taken from Fig. 14. That body seen from below.

30. The portion, abcd Fig. 13, of the corolla of the unfertilized flower, seen from below.

34. The same portion of the corolla of the fertilized flower, Fig. 14, seen from above. Both are enlarged the same as the following Figure.

31. A small fly or gnat of the same species which is encountered most often in the unfertilized flowers. It is enlarged 10X in diameter, therefore actually 1000X. There is some anther dust on its breastplate.

This flower has the attention, I hesitate to say, of flower lovers probably because of its ugly appearance and its simple structure ----- since its mostly foul and completely unnatural taste does not deserve to be taken into consideration ----- but botanists have not taken much interest in it. And yet it is, in my opinion, just because of the simplicity of its structure, and because of the unique artistry which Nature has shown in the arrangements made for its fertilization, the best of all those flowers whose mysterious arrangement has so far been successfully revealed to me. I have examined it many times over several years, and pondered its arrangement. But only just last summer have I been so fortunate as to solve the mystery which it had been for me until then. Accordingly, I will relate how I have gradually come to this understanding.

The first thing which I discovered some years ago was that Linnaeus had been mistaken in regard to the stigma. Namely, he had taken for the stigma the entire body located in the enlarged base of the corolla, which I will call for the sake of brevity the kettle. He must then, as becomes clear from his description, have taken it from such a flower which still occurred in the first stage when it does not yet have a stigma, but first makes arrangements for producing it. It has then the form depicted in Figs. 13 and 23. Then as little a stigma as there initially is, just as little have the anthers, situated on the side of this body, already opened; on the contrary, they are still closed. After some time, however, this body acquires a cylindrical shape where it formerly had a more spherical one. Then the stigma occurs in the center on its uppermost base, which can not be seen in Fig. 14, but can definitely be seen in Fig. 15 where it is stippled. Then the anthers, which are seen in both Figures, have also opened and show their pollen. After that, then, is just the moment when the flower can be fertilized. Linnaeus' conception, according to which the anthers sit on the stigma itself, would certainly seem likely to some for this reason, because in such a manner the fertilization must inevitably occur in each individual as reliably as possible. Except that in the first place no other flower is known, at least to me, in which the anthers sit directly on the stigma. And, in the second place, I also suspect that no flower of this arrangement may be found in the entire world, and for this reason, because otherwise I would have to think that the creator would also have created such flowers in which absolutely no artistry could be found. For, as I have already said in *Serapias*, even the simplest person, if he should be inspired to design the ideal of a flower, would first of all decide to place the anthers directly on the stigma, because he would think that in such a way the fertilization could never fail.

The anthers, in this case, occur at some distance from the stigma, and one may then either accept that the flower should be fertilized when it stands erect, or that such should take place later when it hangs down: thus one sees that in neither case can the pollen come by itself onto the stigma. If one thinks the pollen could possibly be loosened from the anthers and brought to the stigma by vibration in which the wind shakes the plants, and consequently the flowers as well, then one errs. For, in the first case the pollen falls onto the base of the kettle, and in the second onto the uppermost portion of this kettle, which then is the reason that only the smallest part of it falls on the stigma. That the wind, however, should be able to blow the pollen directly onto the stigma, would seem to be possible to absolutely no one, when not the slightest breath of air can steal into the kettle through the narrow, long and closed-up-with-threads tube of the corolla.

Hence, it also follows that, if insects surely do not fertilize the flower, it can never be fertilized; which, however, is contrary to experience, since the plants, although only very sparingly, bring forth full seed capsules with good grains of seed.

The first time when I examined the flowers, I selected, as I saw from the drawing made of it at that time, either fairly old flowers which hung downward, or, which is more likely, I found the plants in the autumn when they had some pendant flowers, but no more upright ones.

Partly this circumstance, partly that at that time I still knew nothing of flowers with false nectaries, led me astray. That is, I thought that the flower might be a nectar flower whose nectar gland and nectar holder would be the body situated at the base of the kettle. I thought that I erred so much less in this regard because this body is fleshy, smooth and white. I certainly did not find nectar in it; yet I thought that the nectar could be imagined as a film with which it might be covered, and that in spite of its extremely small quantity, on account of which it might be invisible to the unaided eye, yet very small insects, such as thrips and even smaller ones, could obtain an ample nourishment from it. This, I thought, would be so much more likely because, if it were present in larger quantities, it would submerge the anthers and make their pollen utterly useless. Moreover, the thread-like hairs in the corolla tube (Fig. 13), in so far as I had observed them at that time, had strengthened me in this opinion; for I had, of course, considered them as nectar covers.

In this case I had now overtaken myself in more than one way. Firstly, I gave analogy preference over experience when I imagined that, although I had found no nectar in the flower, it still must have nectar because up to now I had always noticed that all flowers that were not fertilized in a mechanical way, but by insects, are nectar flowers. However, I should have proceeded from experience, placed the analogy aside for this abnormal flower, and ought to have considered that the infinitely wise creator can achieve each one of his objectives by more than a single means. Moreover, before I made a decision concerning the arrangement of this flower, I should have first sought to learn whether it is fertilized by insects and by which insects. Finally, if I had examined the thread-like hairs in the corolla tube quite carefully, I would have found that they could not be nectar covers. For at any time for those hairs to serve as hindrances to the rain, they must turn their tips toward the opening of the flower; but in this case they turn them toward the base of the flower, Fig. 13.

In the summer of 1790 I had found small flies in the kettle of the corolla. This experience caused me, in the following winter as I pondered the arrangement of this flower, to record the following.

"3. Although the flower stands upright, nevertheless, not only the nectar gland, but the entire enlarged base of the corolla tube, are completely protected against the rain, because the tube is very narrow and, moreover, is covered with hairs."

"4. The flowers catch the eyes of insects even from afar. For there are 8 or 9 of them together, and they bloom at the same time. The lip, which most of all catches the eyes of insects, is yellow; the remaining portion of the corolla, however, is more green-yellow and is unattractive."

"5. Examination shows that fertilization can not occur in a mechanical manner, for the pollen of the anthers comes to the stigma neither unassisted, nor can it be brought to it by the wind. I have encountered thrips and small flies in the enlarged base of the corolla tube, and of the latter sometimes 6 or 10 and even more. Hence, one can imagine how small these insects must be. If one cuts that base of the corolla tube, then they fly out of it with haste, as though out of a prison from which they could not have come by themselves. I found a flower beetle of the smallest sort in the opening of the corolla tube, which made every effort to crawl into it, but in vain, for it was too large. It is more than likely that the flower is fertilized by these small animalcules. I could sometimes see very clearly that the small flies had anther dust on their bodies. Even the remarkable situation, that very few flowers produce fruits, demonstrates this. For if fertilization occurs in a mechanical manner, then it would have taken place in most of the flowers. But if it is executed by these small insects, then it must not occur often, because not all flowers are fertilized by them. Because the manner by which this flower is fertilized by these small insects is very different from the way other flowers are fertilized by other insects. If, for example, a bumble bee fertilizes the wild sage, then it sits on the upper lip of the corolla, extends its proboscis into the nectar holder and extracts the nectar found in it. All this is done in a few seconds. Then it flies from this flower to another one and does it again. In such a way the bumble bee visits and fertilizes a few hundred flowers in a quarter of an hour. It is, therefore, completely natural that such flowers almost always produce seeds. Or, supposing an umbel, for example, *Angelica sylvestris*, is visited by 10 or even more flies and other insects: then the time which they need in order to use up the nectar of each flower amounts to a few seconds. The insects, therefore, run to and fro on the umbel and from one flower to another. Each flower receives such a visit not once or twice, but often. It is no marvel, then, that umbel flowers rarely abort, but are richly supplied with seeds. With our birthwort the situation is completely different."

"The more I ponder the peculiar structure of this flower, the more likely it becomes to me that Nature may have made an entirely different mechanism in it. But before I express my speculation, I must first show that the flower may be specific solely for these small insects, but not at all suitable for larger ones such as, for example, bees and bumble bees. These would be unable to reach the nectar otherwise than by inserting their proboscises into the corolla tube. For if they approached in a violent manner and bit a hole in the enlarged base of the corolla tube (I have actually found such holes), then this would be a proof that the flower is not specific for them. Now if one examines all of those flowers which are actually visited and fertilized by those large insects, then one will always find that the insects can stand conveniently on a part of them while they draw forth the nectar. This part, for example, in two-lipped flowers, is the lower lip. But in our flower such a part is absent; it definitely has an upper lip, but no lower lip. Secondly, larger insects also need a lot of nourishment and such flowers which they visit likewise usually have a large supply of nectar. But in the birthwort one can see no nectar with the naked eye. Accordingly, if nectar is actually present, then it is in so small a quantity there that it can be of absolutely no use to large insects. Thirdly, I have never encountered such large insects on this flower."

"Therefore, I imagine the matter to be thus. Since small flies actually creep down into the flower, then it must have something in itself whereby they are enticed to do such a thing. This probably consists, in addition to the yellow color of the lip and the tubular shape of the flower, since flies know from experience that flowers so shaped tend to contain nectar, in a fragrance agreeable to insects, which is certainly too faint for the scent apparatus of humans, but can be strong enough for the scent apparatus of such small animalcules. Enticed by this means, one of these flies proceeds into the opening of the corolla tube. This is wide and bare at first (Fig. 13), but becomes progressively narrower and is covered with hairs, the former probably in order that the creeping-in may be made comfortable for the insect and it does not lose heart at the outset, but the latter is probably for the purpose that no rain drops may enter into the enlarged part of the corolla tube. If it has now worked through the narrow part of the corolla tube, then it comes into the wide base of the flower which is almost a spacious chamber to it. And in such a way yet more flies gradually creep in, because this part is undoubtedly so wide solely for this reason, so that many of these flies have room in it. Now the flower ought to be fertilized by this small group, that is, the pollen of the anthers ought to be taken to the stigma. This can not occur other than accidentally, so namely, that, while the flies creep about on all sides, they first get on the anthers, remove the pollen with their bodies, and later get on the stigma and in that place remove once more the pollen stuck on their bodies. The uncertainty which is associated with this chance occurrence must, as I have already mentioned in *Parnassia*, be compensated for by the length of time. Hence, it is appropriate that the flies stay here as long as possible. And this is accomplished most definitely when they cannot go out again. That they are, then, actually confined here, I conclude partly due to the quantity in which I have encountered them in different flowers, partly out of the impatience with which they left and flew away from it when I cut the flower apart. Perhaps the base of the corolla tube is so smooth that they cannot creep upwards on it and creep into the tube. Now if that is actually the case, then nectar is superfluous here. Since, however, Nature does nothing superfluously, then the flower can contain no nectar. That the structure, which I have up to now taken for the nectar gland, may secrete no nectar is probable, because the anthers, which sit directly on it, would be submerged by an ever-so-small quantity of nectar and made useless. Now if the flower has no nectar, then Nature misleads the small flies in order to allow the flower to be fertilized by them, and if the flies cannot come out of the flower again, then Nature sacrifices their welfare to that purpose."

"I have already recounted in *Asclepias* that insects are held fast by it so that they either die or must maintain life by losing a leg, and that this is probably related to the fertilization of the flower. In *Orchis latifolia* and some other species I have seen, they definitely have a nectar holder and a nectar spot, but no nectar; that, consequently, the insects which visit them are actually deceived and fertilize the flowers with loss of their lives."

"Now, if the matter stands as I have shown, then one understands how it is that very few flowers are fertilized and set fruit. For, since insects visit other flowers in such fashion that they fly from one to another, consequently just one insect can visit and fertilize very many flowers of the very same species in a short time: however, in this case each fly that has gone inside a flower remains confined and can, consequently, fertilize only this single flower."

"Nevertheless, since flies, when Nature's purpose is to be achieved, must remain only until they have actually brought the pollen of the anthers onto the stigma, and if they, after they have done this, still remain confined and must die of hunger: then one would have no choice but to find their fate too hard and Nature rather ruthless. Contrary to this view, Nature vindicates itself by the fact that it allows the flowers to bend down after they have stood upright as long as was needed for their fertilization. Hence, the flies, which could not creep upwards into the inner opening of the narrower part of the corolla tube in the former position of the flowers, now fall down into this opening in this position of the flowers, creep into the narrower part of the tube and creep out of its outer opening again. They will, however, probably take care not to creep into another flower, since the first visit went so badly for them. Consequently, in this way then only one flower can be fertilized by one fly."

After I had written this, I anxiously anticipated the time when the flowers would begin to bloom. When I found the plants in bloom the following May, I fell upon the flowers with great enthusiasm and, after I had examined them, had a pleasant surprise, since I had been convinced by the examination that, just as I had imagined, the great author of Nature confined the small flies first in this flower so that they fertilize it, but later, when this purpose has been achieved, they are freed again from their confinement; hence, by the marvelous arrangement of this flower, he shows just as much his goodness as he does his wisdom.

I first cut off the kettles of various erect flowers and almost every time found in them a number of small flies which seemed to be quite happy that they had been freed from their confinement, and gamely flew from it. Afterwards, I cut off the kettles from some pendant flowers and found not a single fly in them. In order to fully convince myself, I continued this investigation with both types of flowers and every time found exactly the same thing. Hence, if I could no longer doubt that the flies are held captive in the flowers while they stand erect, but as soon as they have dipped down are allowed out again; then I would also wish to know whether this occurs in just the manner as I have imagined; namely, that the kettle is smooth inside. Hence, I turned over a stem and expected that then the flies would come out of the erect flowers which now hung down. A small beetle actually fell out of a flower, but out of not one did a fly appear. After I had held the stem in this position for a while, I then thought that perhaps there must be no flies in its young flowers. Accordingly, I cut them open, but found the kettles full of flies. Hence, I saw that the flies were not held captive by the smoothness of the kettle as I had supposed, but in another way. I was not led astray by the small beetle. For this one had, like the one which I have mentioned above, been willing to creep into the flower, but had not been able to come out. It went only up to the upper, wider opening of the corolla tube and must then, when I inverted the flower, consequently fallen out of it. I cut lengthwise both an erect and a pendant flower from it and made a discovery that delighted me.

Namely, I saw that the corolla tube of the erect flower was covered with stiff, thread-like, white hairs which begin about in its middle, and these stand separately, gradually get more numerous, but at its end stand most numerous of all; that these hairs were not turned with their tips toward the opening, but rather toward the kettle; hence, there, where the tube sits on the kettle, they formed a small weir-basket, which means that the flies can easily creep downward through the tube and into the kettle, but when they have crept into the kettle, cannot creep out of it again into the tube and then out of the flower again. One will realize this when one examines Figs. 13 and 30. But with regard to the pendant flower, I saw that in this flower these threads have withered and shrunk together, and appear as dark points. See Figs. 14 and 34. Hence, if the prison has thereby been opened, then the flies have not hesitated to proceed out of it again and go free. In order to be certain of my facts, I cut open more flowers and found the same thing.

Figs. 30 and 34 show that I have not entirely erred in my presumption that the kettle might be smooth inside. For, it is definitely lined as it were in large part with a tissue of thread-like hairs, but has a circular smooth place above directly beneath the weir-basket.

The flower occurs, while it grows, in three different stages. After it attains its specific size and has opened, then it definitely appears to bloom, but actually it is not yet blooming, i.e., it is not yet able to be fertilized because neither has an anther reached its proper maturity, nor has the stigma reached its full development, Figs. 13 and 23. During this first stage the flower must trap a number of flies by which it should be fertilized in the second stage. But now since, as soon as the flower has opened, the flies do not immediately come flying as though summoned, but are gradually led to it by chance; then this stage must be of somewhat longer duration. I have found that it lasts 6 days. During this time chance leads one fly today, two or three tomorrow, onto the flower which each fly creeps into, deceived by the appearance. In such a way, a fairly large community of these animalcules ultimately arrives there, for whom a so-unexpected gathering in a very narrow chamber, and a so-undeserved confinement in a very well closed prison would seem strange enough. But they still have none of its pollen on their bodies, because the anthers have not yet opened. Therein follows the second stage in which the flower has ripened the anther dust, has a developed stigma, and enough flies to bring the one onto the other. This definitely cannot happen frequently because in this case everything is also by chance, but it must also sometimes happen easily. For, of course, the flies, since they have already been confined so long and have gotten nothing to eat (1), have become impatient in the process and run about angrily in the kettle. Moreover, strife cannot be easily avoided in such an atmosphere, and in this small prison into which the human eye cannot gaze, it may sometimes get rather warlike. In such a case, however, they must, among other things, also get on the anthers, strip off their pollen, haul it about everywhere, and among other things also bring it to the stigma. This stage, then, may be of no long duration (2). Therefore it happens that one seldom encounters a flower standing erect in this stage; most of them which one cuts open are in the first stage. In this second stage one often finds that the flies, which are dark, have something on their backs, Fig. 31. This is anther dust consisting of grains, which I have found with the use of a magnifying glass. Now, as soon as Nature has attained its purpose, it then places the flower in the third stage, wherein it turns it upside down and allows the small weir-basket to wither and vanish; so that now finally the wretched flies can once again come out of its prison and regain their freedom.

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(1) That insects can fast a long time without starving to death is well-known.

(2) That this stage cannot be of long duration follows from the fact that such extremely small anthers and a stigma which is definitely far larger than those, but is nevertheless very small, cannot possibly retain their active and passive fertilizability for long, but must soon wither and become useless. The stigma in this case, however, is very large proportionately for just that purpose for which it is very large in *Asclepias fruticosa* and probably in *Nymphaea lutea* as well, i.e., with this the ovary would be fertilized all the more certainly; while the insects in this case do not bring the pollen onto the stigma in as precise and essential manner as, e.g., in *Didynamia*, but in a very imprecise and random manner. A bumble bee, which visits *Lamium purpureum* or *Stachys sylvatica*, must by all means strip the pollen from the anthers of the younger flowers, must by all means strip it off onto the stigma of the older flowers; but in the birthwort a fly can linger a long while without touching the anthers or the stigma.

The flies which creep into the flower are certainly very small collectively, as goes without saying, but are of different shapes. That kind which I have sketched is the commonest. It is dark, and is distinguishable by its unusually formed antennae which, seen through the magnifying glass, appear not singly, but tufted (3). In order to catch the flies, I knew how to devise no other means, due to their extraordinary smallness, than this, that I covered a little piece of paper with gum Arabic, made a hole in the kettle and held the paper before it. Now, as soon as one fly after another crept out of it, it got on the gum and remained stuck.

The flowers produce very few mature seed pods filled with good seeds. Many remain unfertilized, which one recognizes by the fact that, after blooming is finished, when the corolla has dropped off, the ovary has not grown, but has withered. Even this shows that the flowers are fertilized by the small flies, and that the anthers are in no way, as Linnaeus had thought, adherent to the stigma. For, if only the matter was such, then all flowers would be fertilized, since the rain can not impede this, for a raindrop cannot possibly get into the kettle and wash away and spoil the pollen. But it is natural, both that not all flowers are visited by flies, and that those in which flies have actually crept in, nevertheless, sometimes remain unfertilized; although the fertilization business is certainly left to these insects, yet, nevertheless, it is still subject to chance. But of those ovaries which have actually been fertilized, the fewest develop. Most develop a long time and have a good appearance, but after that they wither. The reason for this is unknown to me.

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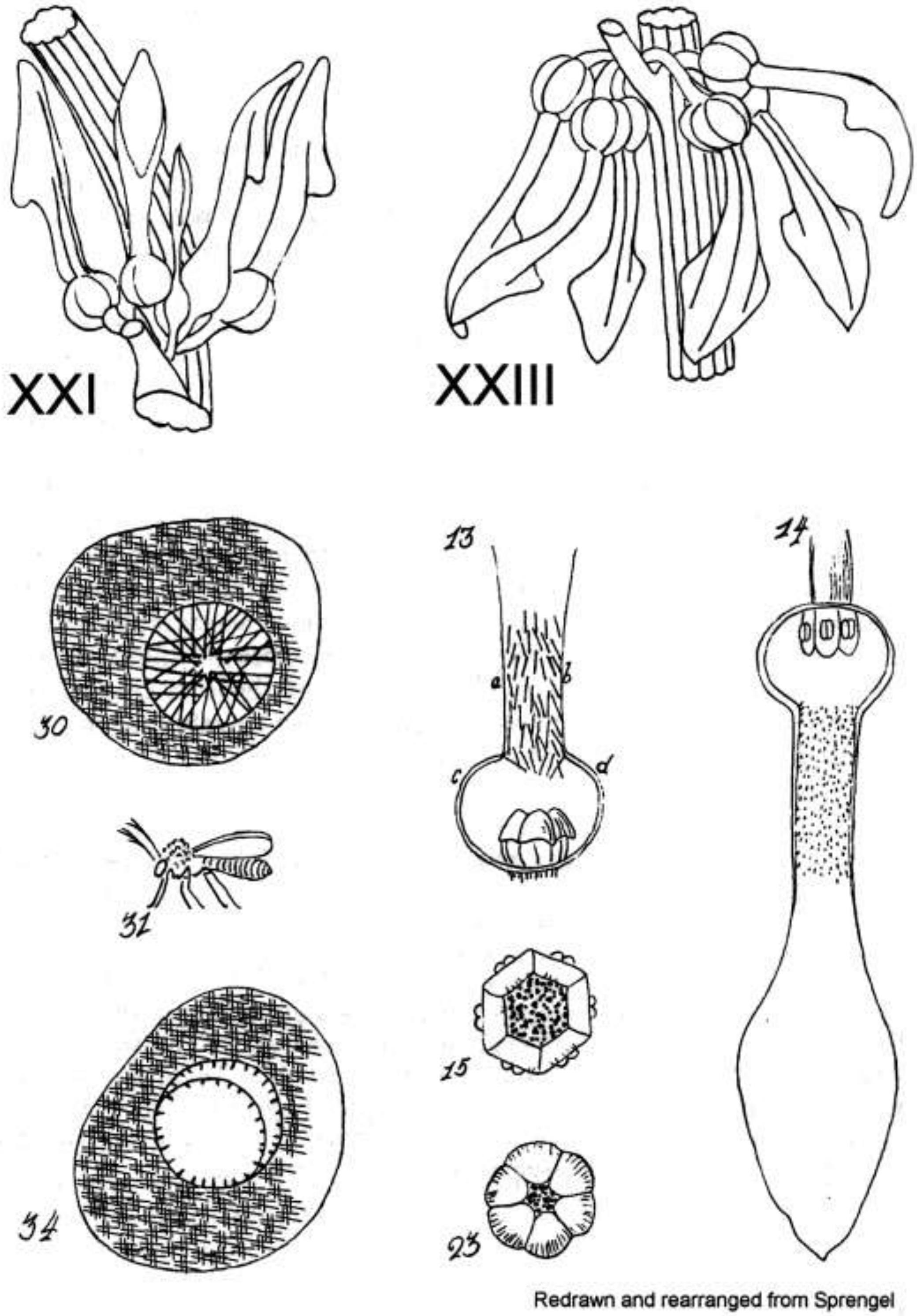
(3) At that time as I made this investigation, none of the entomological works of [Johann Christian] Fabricius was yet known to me. But this year when I had acquired them for myself, I found a place in them which I read with great astonishment. He said of *Tipula pennicornis* (In: Species Insectorum. 1781. Vol. II. P. 412, as well as in: Philosophia Entomologica. 1778. P. 177.), which he may have observed often at Leipzig, that it stays in the flowers of the birthwort and assists its fertilization. I wished that he had explained more precisely about this. Moreover, I think that the insect, which I have sketched, is just this *Tipula pennicornis*. The antennae must certainly, according to his description, be even more clustered; but perhaps the fault is that I may not have had at hand as good a magnifying glass as he had. The color, however, corresponds with his description.



Redrawn and rearranged from Sprengel

FLORA BRASÍLICA

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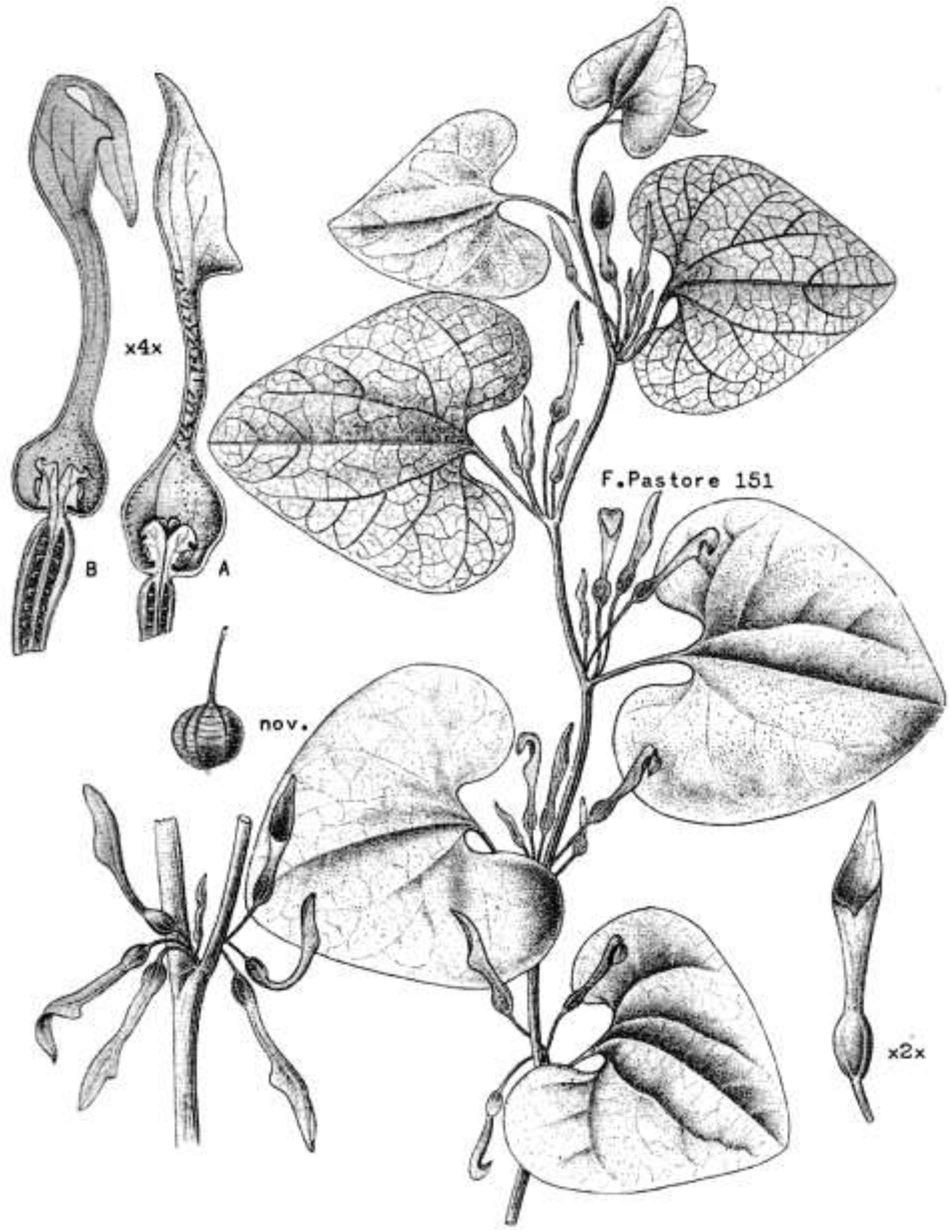

Aristolochia clematitis L.

Illustration from: Hoehne, F. C. 1942. Flora Brasílica. Vol. XV, II. São Paulo, Brazil.