Discovering
The Floral Biology of
Ceropegia

How German botanists revealed 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.

Cover shows a photo of *Ceropegia langkawiensis* Rintz taken by the author along the beach on Pulau Langkawi, Malaysia in November, 1975.

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Federigo Delpino's Further Observations Concerning Dichogamy in the Plant Kingdom

Friedrich Hildebrand

d. *Ceropegia elegans.*

In his first paper on the fertilization of phanerogams, DELPINO presumed, after examining an individual flower of *Ceropegia elegans*, that with the tubular shape of the corolla on this Asclepiad, the pollinating insects must be butterflies; however, when he later observed the olive-colored and spotted flowers in the illustrations of species of this genus, he immediately realized that this coloration pointed to flies as pollinators — and sometime later he was actually able to establish the accuracy of his supposition on the first blooming flower, and here to examine an additional case, similar to the Aristolochias, of the occurrence of a temporary prison. No less than 14 flies (*Gymnopa opaca*) belonging to the tribe Chaetoloxae crawled out of the bulging, expanded kettle of that one first flower; to them clung the pollinia of that same flower. On additional blooming flowers he was subsequently able to make the following careful observations: with *Ceropegia elegans*, exactly as with *Aristolochia*, one can distinguish three regions on the corolla; below, an inflated swelling, the kettle, in whose middle the sexual component lies at the bottom; in the middle, a tube; and above, a large wier apparatus, the latter with five wide entryways, different from the ones in *Aristolochia*. Whereas with the latter the tube is entirely full of the hairs that cause the confinement of the insects, indeed, here they occur only in a ring in the kettle at the entryway out of the tube; but they nonetheless imprison the insects. Initially they are entirely rigid; later, when the insects must be freed, they become ribbon-like, flat, and curl up. The flowers of *Ceropegia elegans* bloom for two days and the captivity of the insects is limited to the first day. During this time the flower is entirely upright and the confining hairs are rigid and cylindrical; the flies come this way and have on their proboscises pollinia out of the previously visited flowers, from which they, after crawling into the flower, insert some into the slots leading to the stigma and at the same time are newly confined. On the

second day the flower tilts very quickly and becomes almost pendant, the confining hairs curl up and the flies now crawl outside burdened with pollinia, about to crawl into another flower.

As DELPINO combines these observations on *Ceropegia*, *Aristolochia*, *Heterotropa*, and *Arum*, he makes use of them for a further proof that in Nature the most morphologically-distinct elements are often changed into entirely the same contrivances in order to achieve one and the same purpose; i.e., the form of the element is subordinated to the purposes to which they are put[1]. In the present case, of course, the end result is the same, in that insects are temporarily held captive in a flower kettle so as to carry out the pollination, whereas the morphological significance of the element comprising the prison in the different genera is an extremely distinct one; whereas the prison in *Arum* is formed from the sheath leaf of an inflorescence, this is done in *Aristolochia* and *Ceropegia* using a simple corolla; with *Arum* the entrance to the prison is formed from vestigial stamens, with both other genera it is by means of single hairs. With *Arum* the unlocking of the prison is caused by the wilting of the parastemons;[2] with *Aristolochia* through shriveling; and with *Ceropegia* through curling of the hairs forming the lock.

Yet with some other flower arrangements in which the insects are held captive for the purpose of pollination, they are, however, partly not so complicated and complete as with the just-mentioned plants, in some cases not yet precisely examined. To the former belong the Cypripedeae, in whose shoe-shaped lower lip HERMANN MÜLLER, who precisely and completely described the pollination mechanism of *Cypripedium calceolus*, found small bees (*Andrena tibialis* and *A. fulvicrus*); DELPINO observed flies on the stigma lip of a different Cypripediae, i.e. on *C. barbatum*; the captivity here was produced in the same way as with *Aristolochia sipho*, in that the horizontally-situated, shoe-shaped organ has entirely smooth walls. With the Rafflesiaceae a similar situation probably occurs and one can accept with considerable certainty, considering the sordid color and the evil odor of these flowers, that here the insects will be blowflies which carry out the pollination in captivity. It is also evident here again, as it should be desirable that, when traveling, botanists not merely collect and dry plants but they should observe them closer in their habits.

DELPINO classified the insects very accurately into those which actually assist the pollination in the above-mentioned plants, and those which occur only inci-

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[1] The expression of Delpino, who has teleological opinions for the development of species, can be translated precisely as follows: "...type and purpose are the permanent and dominant elements, form and matter are the variable, subordinate elements."

[2] "Parastemons" are the rows of stamens. [Ed.]

dentally or for other reasons in the kettles. He observed some insects waiting in ambush on the vexillum of the Aristolochias so as to sieze the visitors crawling out of the kettle.

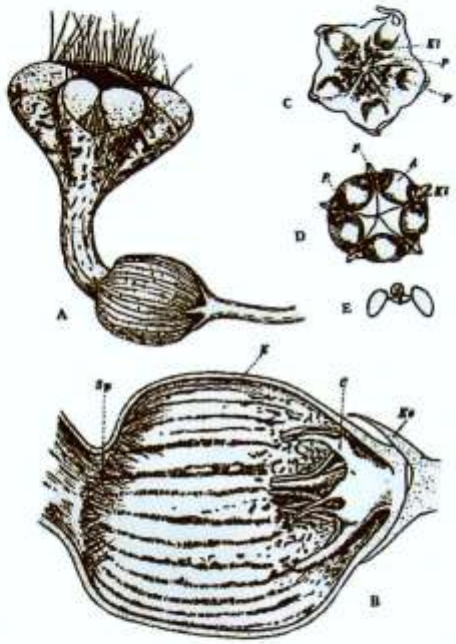

Fig. 86. *Ceropegia elegans.*

A Flower from outside; enlarged 2X. B Kettle of flower, longitudinal section, containing the corona; 6X. C Corona & sexual organs from above; 6X. D Sexual column after removal of the corona from above; 12X. E Clamp body with 2 pollinia; 20X. Ke Calyx. K Corolla. C Corona. Sp Barrier hairs. Kl Clamp body. P Pollinium. A Anther. F Its wing-like appendage

Illustration from: Kirchner, Oskar von. 1911. *Blumen und Insekten: Ihre Anpassungen und ihre gegenseitige Abhängigkeit.*

Painting by W. Fitch from 1862. *Curtis's Botanical Magazine*. Vol. 88.

Painting from nature at the Versailles Gardens by P. Stroobant. 1864.
L'illustration horticole. Vol. II. *C. gardneri* is now *C. elegans*.

Painting from nature at the Versailles Gardens by P. Stroobant. 1864.
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Schumann, K. 1897. Ceropegia. In: Engler & Prantl's Die Natürlichen Pflanzenfamilien. Vol. 4, 2; Pp. 203, 270. Mit Tafeln 50 und 51.

Ceropegia L.

Karl Schumann

Page 203. The genus *Ceropegia* shows a further complication of the intricate situation, as in it the elongated flower corolla tube is inflated ventricose at the base; the relatively small sexual apparatus then finds its place in the sphere. This situation is similar to *Aristolochia*, and one can actually even follow the agreement in this respect, when here weir-trap-like hairs with the tips directed downwards are found, that definitely allow entrance into the spherical space, but prevent smaller insects the exit. Only one day after blooming, the hairs curl up and open the way. Then soon afterwards the corolla folds up and thus after pollination has occurred prevents further entry into the flower space.

Page 270. Sepals short, seldom reaching the flower corolla tube in size, mostly small, tapered, with 5 glands. Flower corolla elongated, tubular, frequently expanded globose at the base, sometimes curved, the tips valvate, either free, erect or folded back, in the early stage or even later frequently united only at the upper portion; the throat expanded uniformly or like an inverted cone. Corona attached to the stamen tube, either formed solely of 5 lobes, usually greatly exceeding the stigma, that usually bear larger or smaller auricles laterally at the base of each one, or between those membranes, which form honey pockets; or in addition to the large lobes, an outer, cup-shaped, more or less deeply 10-cleft corona, with which those lobes are attached by means of tissue strands. Anthers without appendages, erect, bent over the stigma. Stamen tube attached to the base of the flower corolla tube, very short, so that the anthers fit closely, or less often elongated. Stigma flat or shallowly conical. Follicle slender or thicker, smooth, round. — Erect, very seldom leafless, mostly leafy, slender twining perennials or undershrubs, often from tuberous rhizomes, with narrow or usually wider, herbaceous, less often fleshy, leaves. The flowers in few or many-flowered, single-axis corymbs or stalked umbels.

80 species from western through tropical and southern Africa, through Arabia to China and Australia; is unknown to me from Oceania, although BAILLON reported it from there.

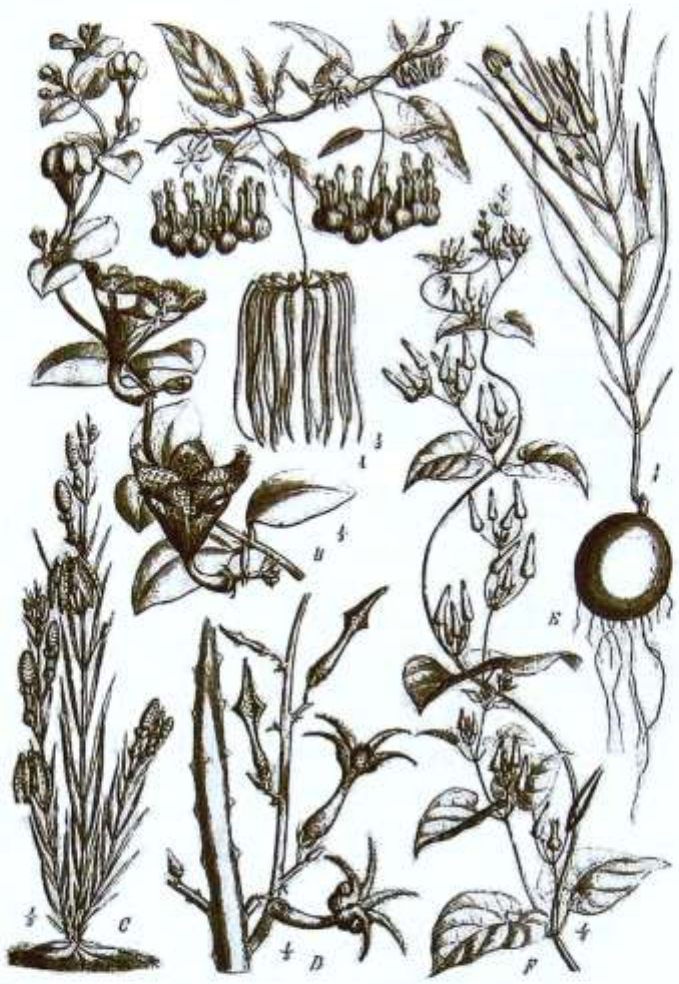


Fig. 50. A *C. candelabrum* L. --B *C. sandersonii* Decne. --C *C. bowkeri* Harv. --D *C. stapeliaeformis* Harv. --E *C. vigualdiana* Rich. --F *Riocreuzia torulosa* (E. May) Decne. E original; others after Delessert and C.B.M.

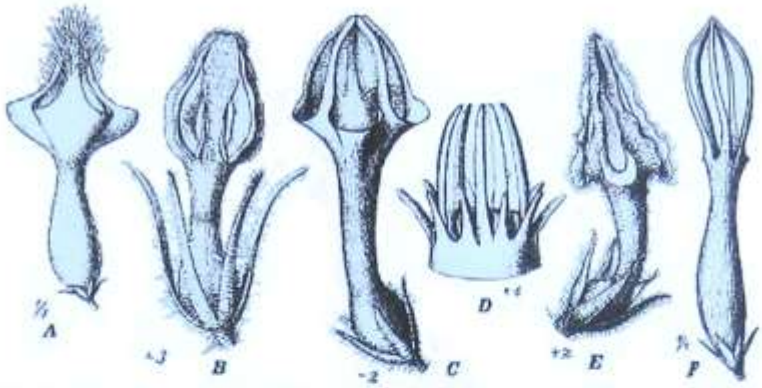
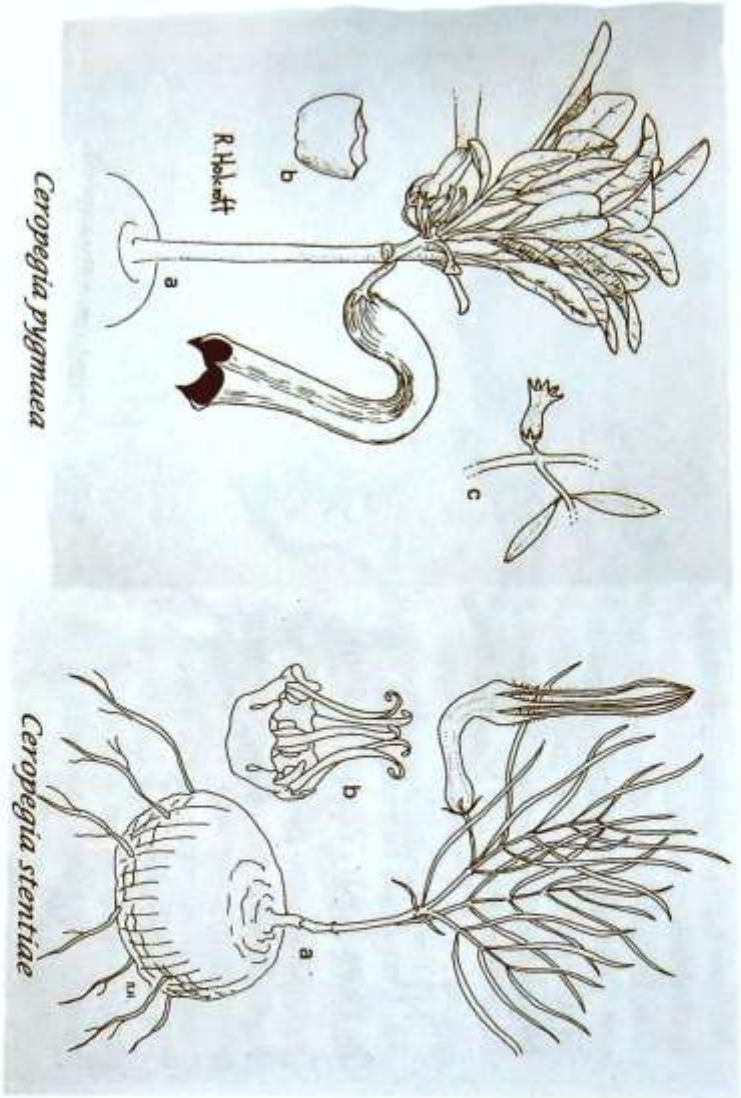


Fig. 31. Flowers of *Ceropegia*: A *C. denticulata* K.Sch.; B *C. leucotaenia* K.Sch.; C *C. meyeri johannis* Engl.; D corona of *C. filipendula* K.Sch.; E *C. ringens* A.Rich.; F *C. umbraticola* K.Sch. (original).

In 1914 RUDOLF SCHLECHTER estimated the number of *Ceropegia* species at 160 in: *Asclepiadaceae Africanae*. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie. Vol. 51, P. 151. Below: **W.C. Africa**.



Two drawings by Rosemary Holcroft from Robert Allen Dyer. 1983. *Ceropegia, Brachystelma and Riocreuxia in Southern Africa.*

Müller, L. 1926. Zur biologischen Anatomie der Blüte von *Ceropegia Woodii* Schlechter. Biologia Generalis, Bd. 2, 799-814. Mit Tafel XLV und XLVI und 1 Textfigur. (Aus dem botanischen Institute der Universitat Wein.)

On the Biological Anatomy of the Flower of *Ceropegia Woodii* Schlechter.

Leopoldine Müller
(Vienna)

At three different places in the plant kingdom the form of the kettle-trap flower is repeated, in the *Araceae*, the *Aristolochiaceae* and the *Asclepiadaceae*. In the first case the kettle is formed, as is well known, by a spathe that wraps around the club-shaped inflorescence. In the *Aristolochiaceae* the simple perianth [calyx] produces the kettle; in the *Asclepiadaceae* with the double perianth, only the corolla forms the kettle.

As is well known, DELPINO (1869, P. 218) was the first to point out the exceptional convergence between the 3 mentioned cases. In all 3 the same result is obtained ultimately by various means.

In particular, the biologically-interesting findings of KNOLL (1913a, Pp. 828-830; 1913b, P. 77; 1913c, Pp. 629-630; 1914, P. 487; 1923, Pp. 246-254), CORRENS (1891, P. 161) and CAMMERLOHER (1923, Pp. 180-198) in *Arum* and *Aristolochia* suggested also submitting the *Ceropegia* flowers among the Asclepiadaceae, so far not sufficiently studied anatomically, to a careful examination in this regard; for with respect to the epidermis of the corolla really thorough investigations are lacking for *Ceropegia* species. Only the barrier hairs and the hairs on the purple top-portion of the flower are known.

DELPINO, the first one who has interpreted the flower of *Ceropegia elegans* in the biological sense. assigned it to the *Aristolochia*-type, i.e., to the same micromyiophilous form. (KNUTH, 1898, P. 18). His remarks also relied upon the assertions of other authors. According to KNUTH (1898, P. 157), *Ceropegia* species constitute a transitional form from the kettle-trap to the clamp-trap flowers; according to KIRCHNER (1911, P.220), they are a "combination of kettle-trap and clamp-trap insofar as the entire flower represents a kettle-trap that at its base yet conceals a clamp-trap." SCHUMANN (1895, P. 203) agrees with the foregoing conceptions.

The object of my investigations was mainly *Ceropegia Woodii* Schlechter, as well as *Ceropegia debilis* N. E. Brown. Both plants were at my disposal in the glass house of the Vienna Botanical Institute.

The previous illustrations of *Ceropegia Woodii* Schlechter (Gardener's Chronicle, 1897, vol. XXII, pp. 357-358, fig. 104; Curtis's Botanical Magazine, 1900, vol. LVI, Third Series 7692-7751, t. 7704; Gartenflora, 1901, t. 1486) do not render the shape, position and color of the flower sufficiently; moreover, the descriptions of the flower (ENGLER, Botanischer Jahrbuch, 1894, vol. XVIII, Beibl. Nr. 45, P. 34 and 1895, vol. XX, Beibl. Nr. 51, P. 49; Flora Capensis, 1909, vol. IV, Sect. 1, p. 823) leave a good deal out [see Appendix]. Accordingly, it would be necessary first of all to describe more completely the flower with the aid of some colored illustrations [see photo at end].

The flower (Plate XLV, Fig. 1) of *Ceropegia Woodii* Schlechter can be differentiated into three parts that are distinctly different from one another: the purple-colored top (a) that is formed by the lobes of the corolla attached at the tips; the bright red, sometimes colored somewhat greenish and white, narrow tubular portion (b) that is darker downwards; and the still-darker reddish-colored kettle (c) that at its base distinctly appears demarcated white (kettle window, d). The tip of the calyx reaches up to the upper edge of this window. The kettle encloses the so-called corona with the sexual organs (Plate XLVI, Fig. 1).

In the development of the flower three main stages can be distinguished:

Initially, the flower bud hangs downwards; soon it rights itself and in this position the bud opens in a curious way. The 5 crown lobes forming the apex become free solely in their middle and lower parts due to loosening of the interconnection, while they remain united at the ends. Thus, only 5 openings that are slit-like at the top and wider downwards furnish the visiting insects access into the flower. In the manner of accesses that offer the flower to the visitor, it agrees with the flower type that GOEBEL designates as "window flowers," because they do not open at the apex, but rather offer the insects only lateral entry (windows) into the flower. As is apparent from the previous account, I understand by "window" another portion of the corolla, ie, the bright, white, but closed portion of the kettle wall (d). In the same sense one speaks also in *Cypripedilum calceolus* L. of a window in contrast to the two actual openings located above the window.

At the climax of anthesis, the flower is arranged vertically upwards (Pl. XLV, Fig. 2). One to two days later, rarely after several days, the flower begins to slowly bend downwards so that it comprises with the vertical an angle that becomes continually larger (Pl. XLV, Fig. 3). The color difference of the flower parts during the blooming period is also noteworthy.

At the time of the full bloom, the apex is colored dark red-purple and is opened at its widest. The lobes of the corolla forming it are papillose and in addition are yet beset with dark purple hairs that from now on I would like to designate as "purple-hairs." The papillae are short, cylindrical, at this time rigid and also colored purple. The purple-hairs stand erect. Each epidermal cell becomes either a papilla or a hair. The opening of the tube portion (b) is formed by a funnel-shaped expansion whose 5 sinuses, standing wide open at the time of full blooming, form the continuation of longitudinal slits (e). From the flowers at this time, especially on sunny days, a scarsely-noticable scent, hence also not more precisely definable, is to be perceived. I noticed the scent at the strongest when I opened a young flower, being just before anthesis with still-closed apex, or the kettle portion of a flower, being at the beginning of full bloom. DELPINO, and after him HILDEBRAND (1867, P. 269), described the *Ceropegia* species as scented and came, therefore, to the false conclusion of assuming butterflies as pollinator, as DELPINO himself realized from later observations.

On the flower, tilted further downwards, the purple color of the apex assumes a reddish-gray tint. The purple hairs become shrivelled; their color, as well as that of the papillae, fades and thereby causes the discoloration of the entire apex. The arched lobes wilt and shrivel together. Also, the coloration of the tube portion and kettle fades. Thereby the wilting of the flower procedes from the top downwards.

The flowers at this stage usually fell off, unless there was to be fruit formation. Yet the plant can produce fruits even in the glass house of our region. Hence, I obtained a fruit of *Ceropegia Woodii* from Mr. J. DLOUHY, head gardener at the Vienna Botanical Garden at Bruck an der Leitha. Now and then I was also able, in accordance with SCHUMANN'S (1895, p. 203) assertion, both in *Ceropegia Woodii* and in *Ceropegia debilis* to observe a sealing of the tube due to bending of the uppermost portion of the tube.

No assertions occur in the literature about whether the flower of *Ceropegia Woodii* is dichogamous, just like the *Arum* and *Aristolochia* flowers, or perhaps is homogamous. For the present even my own investigations in this regard still lead to no certain conclusion. Yet the fact that the full-blooming generally lasts only one day and the pollen are already at this time easy to remove, speaks more likely for a homogamy of the flower.

The investigation of the inner epidermis of the flower tube of *Ceropegia Woodii* had the following result:

The expanded, funnel-shaped entrance into the tube (e) is accentuated outside by a small, whitish fringe about the sinuses. From it proceed tooth-shaped papillae, whose tips are turned downwards towards the inside of the tube (Pl. XLV,