

FURTHER NOTES ON RETZIACEAE: ITS CHEMICAL CONTENTS AND AFFINITIES

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ABSTRACT

Retziaceae is a taxonomically isolated monotypic family of the Cape Region of South Africa. It has been related in the past to Convolvulaceae, Solanaceae, and most recently to Loganiaceae (Gentianiflorae), especially Buddlejaceae. The iridoid compounds of Retziaceae, identified here, are distinctive and suggest that the family is unrelated to Gentianiflorae, but is probably allied to Lamiiflorae, including Verbenaceae, Scrophulariaceae, and the endemic Cape family Stilbaceae. There is a remarkable similarity between the iridoids of *Stilbe ericoides* and Retziaceae. A detailed review of morphology, anatomy, biology, and other characteristics of Retziaceae is presented. The suggestion of a relationship between Retziaceae and Stilbaceae appears to find considerable support from morphological as well as chemical considerations.

Retziaceae is a monotypic family consisting of *Retzia capensis* Thunb. This is a conspicuous member of the Cape fynbos or Cape macchia flora in South Africa, where it has a restricted distribution. Its isolated systematic position is undoubted and various efforts have been made to place it taxonomically and to clarify its most likely affinity. Recently evidence was presented on its pollen morphology and chromosome number by Goldblatt & Keating (1976). Further information is given here on its morphology, anatomy, and especially its iridoid glucosides.

THE HISTORY OF *RETZIA* IN LITERATURE

The literature concerning *Retzia* has been surveyed extensively by several workers including Marloth (1932: 540), Leeuwenberg (1964), and Goldblatt & Keating (1976). A review is given below.

Retzia was described by Thunberg in 1776 and named in honor of Anders Jahan Retzius (1742–1821), Botanical Demonstrator and Professor in Natural History in Lund, colleague and contemporary of Thunberg. Among Retzius's botanical contributions should be mentioned *Observationes Botanicae* and *Florae Scandinaviae Prodrromus*. His herbarium in Lund contains many duplicates of Thunberg's South African collections.

The family Retziaceae was first described, in a somewhat ambiguous way, by Bartling (1830: 192) as "genera desciscentia (Retzionaceae)" under Convolvulaceae. *Retzia* was accompanied by *Lonchostoma* (now in Bruniaceae), with

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which it was often associated during the following decades. *Retzia* was also placed in Convolvulaceae by Harvey (1838) in his *Genera of South African Flowering Plants*. Retziaceae was regarded as a distinct family next to Apocynaceae by Lindley (1836), and by Agardh (1858), while Endlicher (1836) included *Retzia* in Solanaceae, as did de Candolle (1852). Bentham & Hooker (1876) found an acceptable position for *Retzia* in Solanaceae-Cestreae, within which some taxa undoubtedly resemble *Retzia* superficially, except that they do not have verticillate leaves. This solanaceous affinity gained some support, and *Retzia* continuously appeared in this family in the works of Wettstein (1895), Wright (1904), and Phillips (1926). Retziaceae was still retained in Solanales by Hutchinson as late as 1973.

Fedde (1896) in an anatomical analysis of Solanaceae found *Retzia* to be aberrant in lacking intraxylary phloem, and Solereder (1899) came to the same conclusion. On this evidence Fedde referred *Retzia* to Loganiaceae-Buddlejoideae, and since then several botanists have been inclined to accept a loganiaceous affinity. The fact that Buddlejaceae, like *Retzia*, lacks intraxylary phloem seems to have encouraged this idea, but the placing of *Buddleja* in Loganiaceae has been challenged, for example by Takhtajan (1969), who placed the families Buddlejaceae and Retziaceae in his Scrophulariales, an alternative which gains some support from the data presented here. Leeuwenberg (1964) in his treatment of Loganiaceae distinguishes Buddlejeae and Retzieae as tribes.

Airy Shaw (1973) is representative in expressing great doubts on the affinity of *Retzia*; he places the genus in a separate family with the remark that it is isolated and possibly has connections with Solanaceae, Scrophulariaceae, or families of the order Loganiales, differing from all the latter except Buddlejaceae in the absence of intraxylary phloem.

More recently, Thorne (1976) has placed *Retzia* in a separate subfamily of Loganiaceae, and Buddlejaceae as a separate and adjacent family. Dahlgren (1975) treated Retziaceae and Buddlejaceae as separate families next to Loganiaceae, but admits an alternative position of Buddlejaceae in Scrophulariales with due consideration to the absence of internal phloem and the presence of different (non-seco) types of iridoids. At that time the iridoids in *Retzia* had not been analyzed in detail, though their presence had been confirmed (Jensen et al., 1975). Goldblatt & Keating (1976) in a study of chromosome cytology and pollen microstructure found no evidence for removing Retziaceae from the vicinity of Loganiaceae, although they did not consider the relationship to be close or that it was possible to relate *Retzia* to any particular group in that family.

New evidence presented here suggests an affinity between *Retzia* and the genera of Stilbaceae, the latter often treated as a tribe, Stilbeae, or as a subfamily, Stilboideae, of the Verbenaceae. This alternative, to our knowledge, was first suggested in Dyer (1975), where it was mentioned that "there seems to be some affinity between *Retzia* and the family Stilbaceae which deserves investigation."

The arguments for this possible affinity and the problems involved in the taxonomic groupings will be further discussed below.

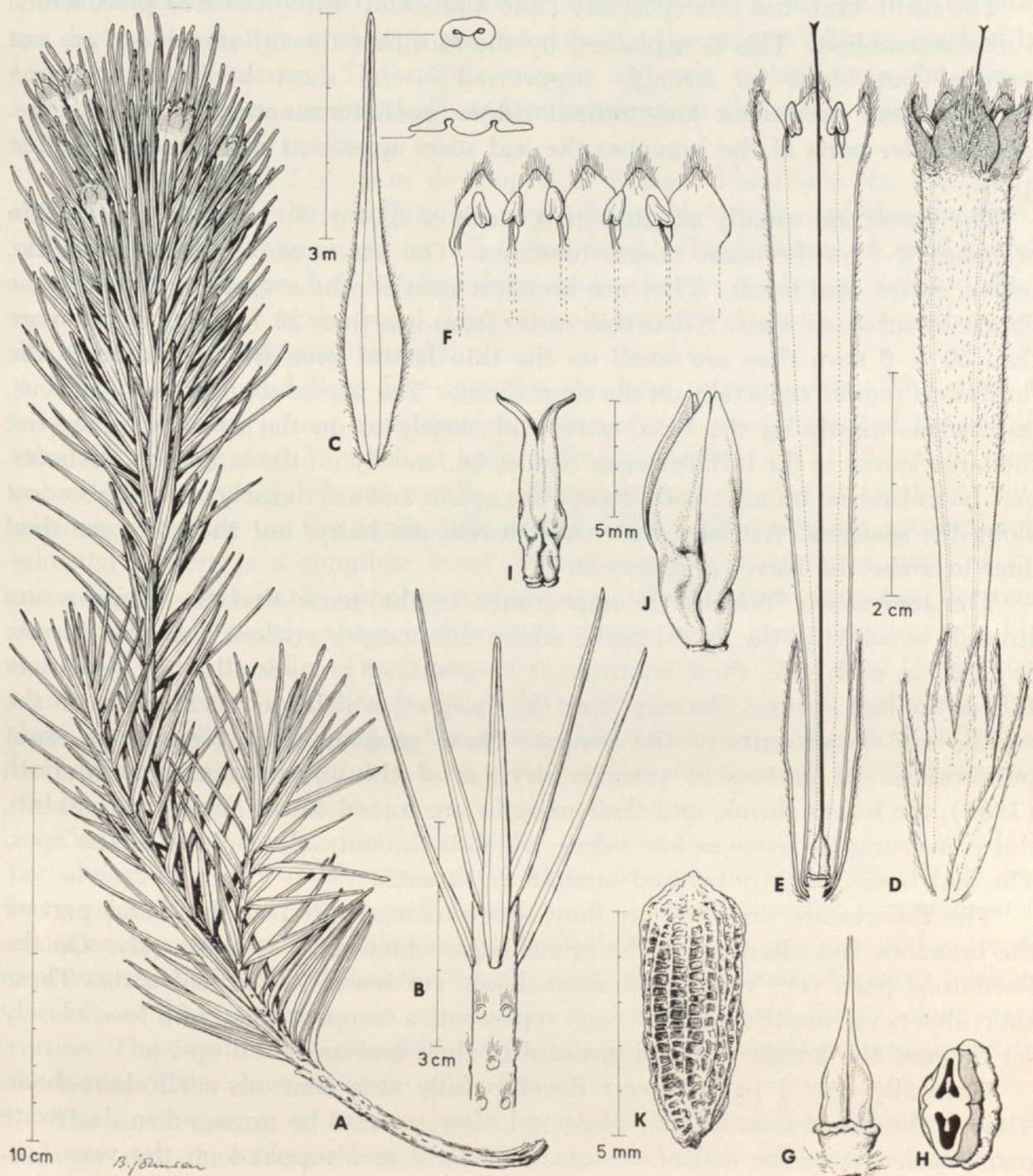


FIGURE 1. *Retzia capensis* Thunb.—Raven & Raven 26127 from slopes near Betty's Bay, Caledon District, South Africa, 1973.—A. Flowering branch.—B. Section of branch with whorls of 4 leaves.—C. Floral bract.—D. Flower with the 2 bracteoles.—E. Longitudinal section of a flower.—F. Upper part of corolla tube with stamens.—G. Ovary with the surrounding thin disc.—H. Transection of an ovary seen from above.—I-J. Capsules, showing septicidal as well as loculicidal dehiscence.—K. Seed.—Del. Bent Johnsen.

MORPHOLOGY (FIG. 1)

Retzia capensis is a sparingly branched shrub, generally 60–130 cm tall with stiff, coarse and strong branches, which are densely villous or at least tomentose on the young parts. There seems to be great variation in length and density of pubescence.

The shrub branches monopodially (like a juvenile, little-branched pine, which it also resembles). This is explained by the fact that the inflorescences are not terminal but borne on strongly suppressed lateral short-shoots. The young branches bear prominent longitudinal ridges, each terminating at a leaf base. On the older parts of the branches the leaf scars appear as more or less distinct spots.

The leaves are usually situated in verticels of 3, 4 or 5; 3 mainly on the thin branches, 4-5 on the main, coarse branches. The leaves are exstipulate, simple, sessile, entire, and linear. They are broadest near the base tapering towards the obtuse or subacute apex. Their size varies from less than 30×3 mm up to more than 50×6 mm; they are small on the thin lateral branches but large in the floriferous region, especially on the short shoots. The leaves are often subglabrous, puberulous mostly on the basal parts and closely so on the basal margins, but the large leaves in the inflorescence region, i.e., mostly on the lateral short-shoots, may be pubescent on most parts except the apices and are densely white-pubescent along the margins. Actually, the young leaves are hairy, but the hairs are shed later to make the leaves glabrescent.

The leaves are "ericoid" in appearance in the sense that the margins are strongly revolute in the apical parts, where the margins enclose a narrow furrow or canal on each side; these continue as longitudinal grooves all along the lower side of the leaf at some distance from the margins, which are not revolute on the middle and basal parts of the leaves. These grooves often carry some short pubescence. In periods of extreme dryness of the air, according to Marloth (1932), the leaves shrink, and their margins are forced closer against the midrib, this converting the grooves into tubes, which is the normal condition at the apex. The leaf base is tightly pressed against the branch.

The flowers are crowded on short-shoots concentrated at the distal part of the branches, but often not at the branch tips, which grow continuously. On the floriferous part, very contracted short-shoots are borne in the leaf axils. These short-shoots are multifoliate and each represents a compact spike of a few, closely set flowers, the lowest often suppressed in their leaf axils.

Generally only 1 or 2 flowers develop fully at a time on each short-shoot. Though the flowers are densely clustered, they seem to be arranged in decussate pairs, each one in the axil of a large, hairy leaf and supplied on the very (ca. 1 mm) short, white pubescent pedicel with 2 bracteoles. These are similar to but smaller than the leaves: linear, puberulous, varying in size between the flowers but frequently reaching about as far as the calyx lobes. (This "compound" nature of the inflorescence region rarely seems to have been understood by previous investigators.)

The flowers are most conspicuous. The calyx is tubular and slightly tapering at the base; the tube is pale, ca. 10-13 mm long, glabrous towards the base, puberulous in the middle and distal parts; and the lobes are linear-lanceolate, ca. 8-12 mm long, pointed, puberulous to short-sericeous but with denser and longer white hairs on the margins.

The corolla is tubular, ca. 6-7 mm wide, and 55-65 mm long including the 5 triangular-ovate, ca. 8-11 mm long lobes, which have a valvate to reduplicate-

valvate aestivation. While the corolla tube is brightly red to orange red, the lobes are dark, (bluish) black, though the color on the tips of the lobes is masked by long white pubescence. The corolla tube is diffusely ribbed from the sinuses (where the stamens are inserted) and puberulous on the outer side, becoming subglabrous towards the base.

There are always 5 stamens developed in *Retzia*. The filaments, inserted in the sinuses between the corolla lobes, are 4–5 mm in length, and the dorsifixed, versatile, introrse anthers are ca. 2.5–3 mm long. The 2 thecae of each anther are fused in the upper half but free from each other in the lower half and often more or less distant at the base. They are obtuse at both ends (the anthers are not sagittate as sometimes stated).

An annular, undulating disc encircles the base of the ovary. The pistil is bicarpellate. It has a long, very slender, glabrous style reaching out of the corolla tube and greatly exceeding this at early anthesis, pointing up to 10 mm or more out of the yet mostly closed corolla. The style apex is shortly bilobate, with stigmatic papillae on the inner side of the lobes. The ovary is incompletely bilocular. There is a complete basal septum reaching to about a third of the ovary height, while in the upper part of the ovary there is free connection between the locules and merely along each carpel margin a rib projecting towards but not fused in the middle. The 2 placentae are situated at the top of the septum center; each bears 1 or 2 closely situated pendulous ovules and 1 ascending; thus there are usually 4–6 ovules in the ovary. (Some of the ovules in a collection studied were transformed into a long, winding, threadlike strand growing towards the base of the stylar canal.)

The fruit is a longitudinally dehiscent capsule, the construction of which is not always correctly understood. It is often strongly folded (Figs. 1I–1J) but has a smooth surface. When well matured it is 7–9 mm long, but sometimes it is considerably smaller. The dehiscence starts *loculicidally* at the apex and proceeds downwards to about a third of the length; each valve apex often becomes bilobate or cleft as it often breaks up *septicidally* by a longitudinal fissure along each suture. The capsule is enclosed in the long-persistent perianth and enveloped by the leaves of the short shoots.

The seeds are up to 6 mm long, elongate-triangular and somewhat crested, strongly reticulate from the thickened lateral and inner walls of the epidermis cells of the testa. The embryo is surrounded by mealy endosperm; it is straight, cylindric and almost as long as the endosperm (Leeuwenberg, 1964).

ANATOMY

The anatomy is described in detail in a still unpublished thesis by Herbst (1972) and therefore has not been included in this study. A few observations may be given, however. The stomata of the leaves are anomocytic and are not particularly sunken below the epidermis surface. There are two hair types: (1) ordinary filiform hairs consisting of 1, 2, or 3 cells, the terminal cell being the longest, and (2) small, stalked glandular hairs with a head consisting of a few cells standing parallel to the longitudinal axis of the hair. According to Herbst's

(1972) profound study, most of the vessels in the stem were observed to have scalariform perforation plates.

EMBRYOLOGY

The embryology seems to be entirely unknown and deserves being studied, especially with respect to endosperm formation and endosperm haustoria. (It is expected that the ovules are unitegmic and tenuinucellate, and that the endosperm formation is cellular; most likely terminal endosperm haustoria may be present.) The seeds are reported to contain endosperm.

POLLEN

Pollen of *Retzia* is tricolporate with an obscurely delimited aperture and a microreticulate exine as reported by Punt & Leenhouts (1967) and by Goldblatt & Keating (1976). As reported by Goldblatt and Keating, the grains are spheroid equatorially, circular-semiangular in polar view and in size $P = 35 \mu\text{m}$, $E = 30 \mu\text{m}$. This type of pollen corresponds reasonably with Buddlejaceae, but not with most Loganiaceae. The large families Scrophulariaceae and Verbenaceae have a wide variety of pollen types, and grains similar to those of *Retzia* occur in several genera not otherwise related to *Retzia*. Pollen of Stilbaceae has not been much studied, but Erdtman's (1952) illustration of pollen of *Stilbe ericoides* is worth comparing with *Retzia*. Erdtman describes this as tricolporate, and prolate spheroidal, and in size, $18.5 \times 17 \mu\text{m}$. Pollen of *Retzia* and *Stilbe ericoides* can thus be said to be generally similar in morphology, though differing greatly in size.

CYTOLOGY

Cytology is of little value in assessing the affinities of *Retzia*, which has $n = 14$, since almost all of the groups with which it has been allied are cytologically heterogeneous. In Lamiiflorae, with which *Retzia* exhibits strong chemical as well as morphological similarities, both Scrophulariales and Lamiales are cytologically diverse. In Scrophulariaceae, for which Raven (1975) tentatively postulated a base number of $x = 7$, there are numerous taxa that are fundamentally tetraploid with a frequent number of $n = 14$ and 12. Verbenaceae have an even wider range of chromosome number than Scrophulariaceae, both at diploid and tetraploid levels, with $n = 5, 6, 7, 9, 11-18$ well represented in various genera. Stilbaceae, believed to be very closely related to Verbenaceae, are cytologically unknown. Buddlejaceae, with which *Retzia* is often associated, is, in contrast, cytologically uniform with $x = 19$ in all genera so far examined, making this an unlikely ally.

CHEMISTRY (IRIDOID GLUCOSIDES)

The presence of iridoids in *Retzia capensis* was demonstrated by Jensen et al. (1975), but, owing to scarcity of material, it was not possible at that time to identify any of the components.

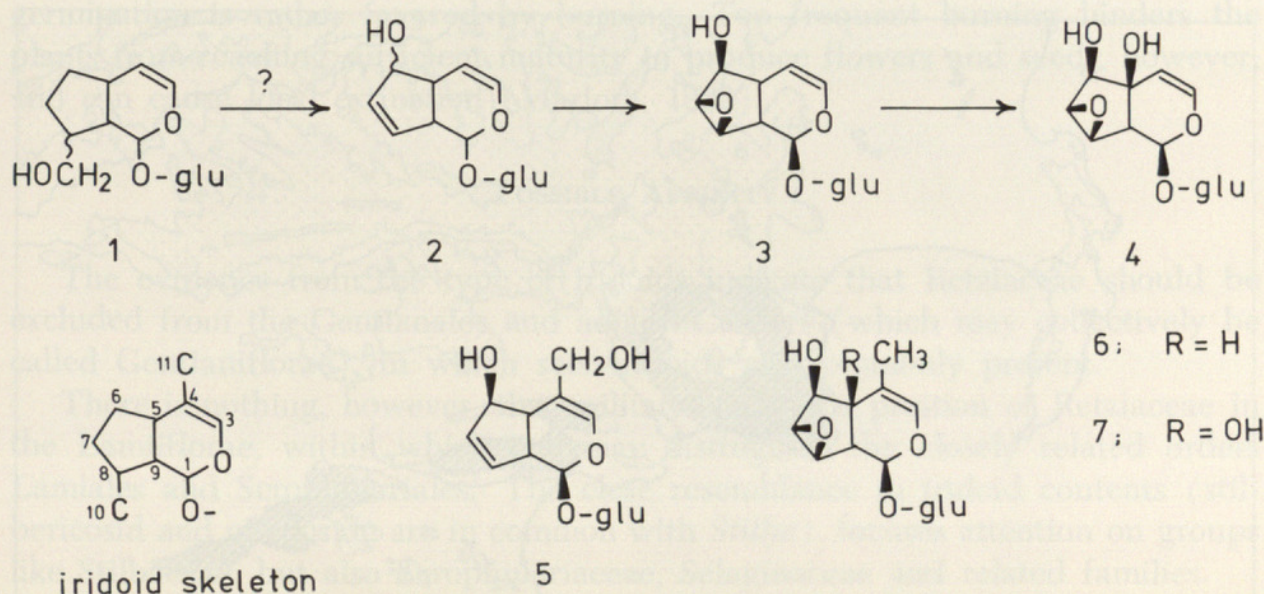


FIGURE 2. Upper row: Structures of the four iridoids occurring in *Retzia capensis*.—Lower row: Some biogenetically related iridoids, which as 2–4 in the upper row have lost C-10, but which have C-11 intact. They occur in Cornales and Loasales, which are no doubt related—though more distantly—to the Lamiales-Scrophulariales complex.

More material of the species has since become available and has been examined. Four iridoid glucosides have been isolated. Two of these have been identified, viz., unedoside (Fig. 2: 3) (mp, optical rotation and PMR-spectra of glucoside and its pentaacetate) and stilbericoside (Fig. 2: 4) (PMR-spectra and optical rotation of glucoside and pentaacetate, mp of pentaacetate). Tentative structures (Fig. 2: 1–2: 2) for the other two compounds are proposed on the basis of PMR-spectra and decoupling experiments. To our knowledge these two compounds have not been reported before as occurring in nature. Unedoside is known from *Arbutus unedo*, Ericaceae (Geissman et al., 1966) and from *Stilbe ericoides*, Stilbaceae (Rimpler, 1972), where it occurs together with stilbericoside (Rimpler & Pistor, 1974).

The compounds shown in Figs. 2: 2–2: 4 can be arranged in a very probable biosynthetic sequence, after which epoxidation of the 7, 8-double bond in compound 2 leads to 3, which is transformed into 4 by allylic oxidation at C-5. Whether 1 fits into this scheme is not easy to say, as nothing is known about the way in which C-10 is lost.

The compounds shown in Figs. 2: 5–2: 7 form a group of biogenetically related compounds, which like the *Retzia* compounds 2–4 have lost C-10, but in which C-11 is intact. It includes decaloside (5) in *Mentzelia* (Loasaceae), deutzioside (6) in *Mentzelia* and *Deutzia* (Hydrangeaceae), and scabroside (7) in *Deutzia*.

Details about the structure of the iridoids of *Retzia* will be published later.

A preliminary investigation of material of *Xeroplana gymnopharyngia* (Stilbaceae) indicates that this species also has quantities of stilbericoside as judging from the PMR-spectra.

POLLINATION

Retzia capensis is, at least to a great extent, bird pollinated. It has been

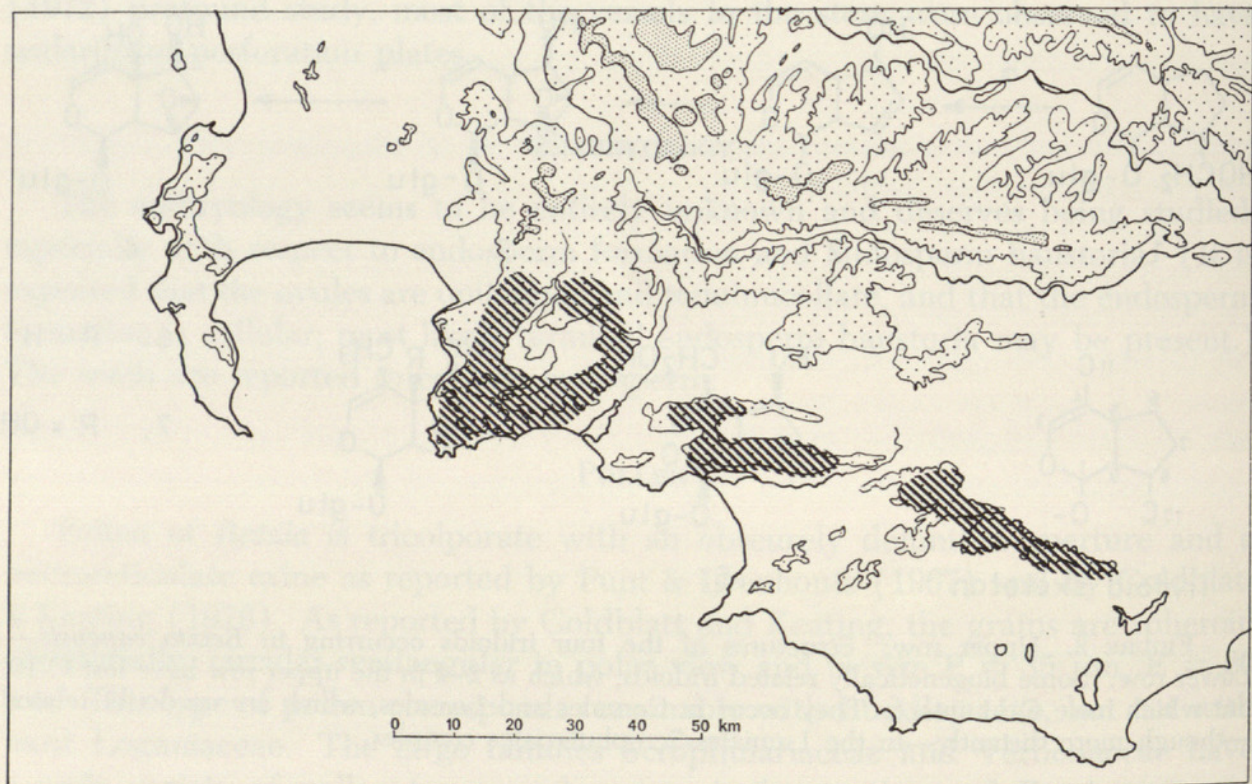


FIGURE 3. Approximate distribution of *Retzia capensis*. Based on information in Herbst's (1972) unpublished study on the species.

observed on several occasions to be visited by the orange breasted sunbird (*Anthobaphes violacea*) at Betty's Bay, Caledon District. The long tubular flowers also suggest bird or possibly advanced insect pollination. The flowers are protogynous. A noticeable detail is that the style, in the material studied by the authors, elongates more rapidly than the corolla tube. Therefore, in early flowering stage, the style reaches up to more than 10 mm out of the flower, while the corolla lobes are still mostly closed. Thus when sucking nectar a visiting bird or insect has great chances to touch the very minute stigmatic lobes. In a later flowering stage the introrse anthers stand well out of the floral tube between the lobes.

DISTRIBUTION AND ECOLOGY

Retzia capensis (according to Herbst, 1972) is restricted in its distribution to the Somerset West, Caledon and Bredasdorp districts, occurring from the Hottentots Holland Mountains (Sir Lowry's Pass-Elgin area) in the west and northwest, then along the Klein River, Houw Hoek Pass, and Babylons Tower Mountains, continuing eastwards along the Elandskloof Mountains to the Bredasdorp Mountain in the east (Fig. 3).

It grows on slopes of the Table Mountain sandstone, in sand or gravelly sand, often among rocks. It is fairly common locally in the Caledon and Bredasdorp districts. In certain areas it is threatened by repeated veld fires. Normally, veld fires at long intervals cause little harm, as *Retzia* withstands burning down to the root crown, from which branches can regenerate. It is also likely that seed

germination is rather favored by burning. Too frequent burning hinders the plants from reaching sufficient maturity to produce flowers and seeds, however, and can cause local extinction (Marloth, 1932).

POSSIBLE AFFINITY

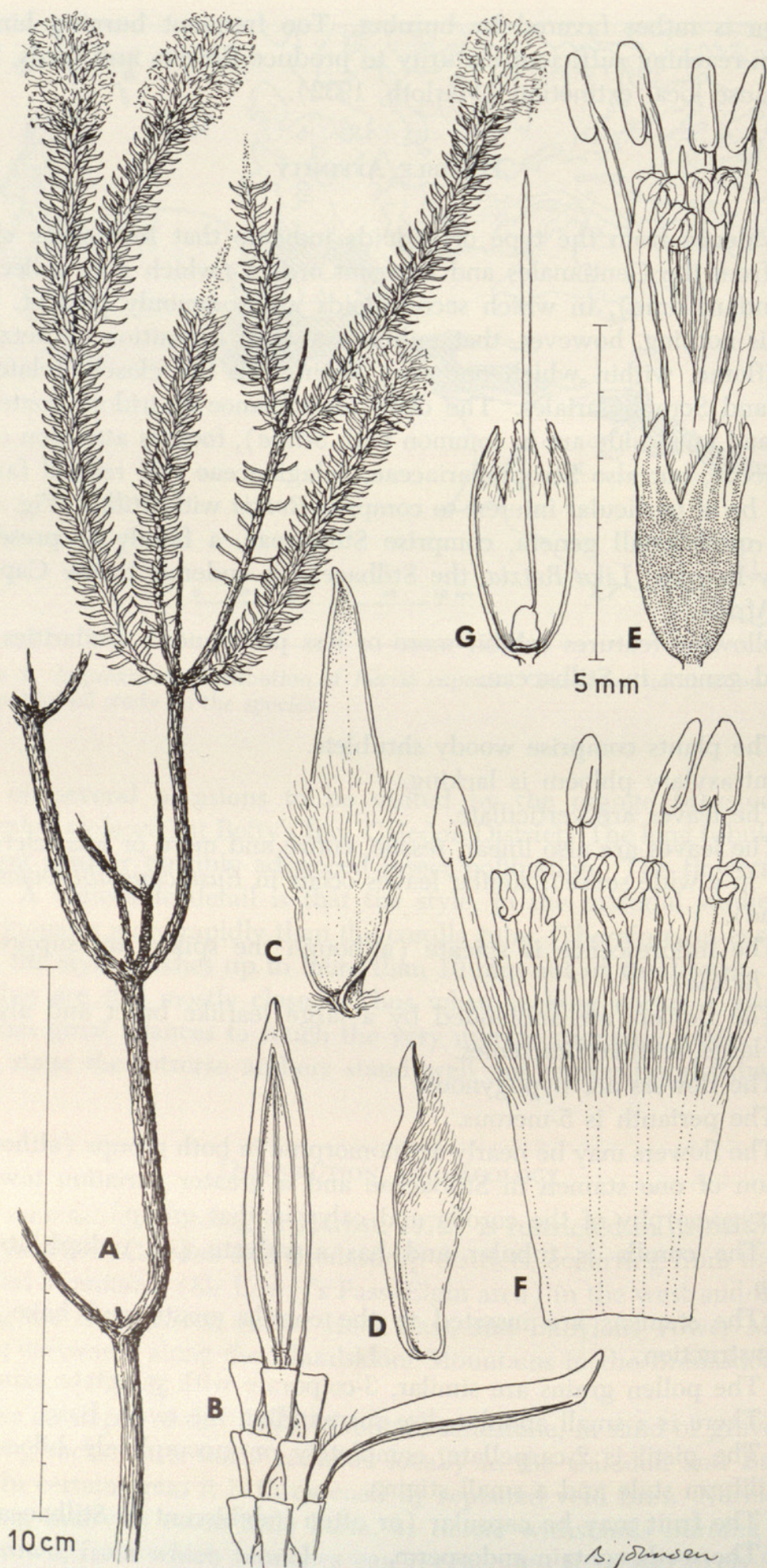
The evidence from the type of iridoids indicate that Retziaceae should be excluded from the Gentianales and adjacent orders (which may collectively be called Gentianiflorae), in which seco-iridoids are commonly present.

There is nothing, however, that militates against a position of Retziaceae in the Lamiiflorae, within which one may distinguish the closely related orders Lamiales and Scrophulariales. The close resemblance in iridoid contents (stilbericosid and unedoside are in common with *Stilbe*), focuses attention on groups like Stilbaceae, but also Scrophulariaceae, Selaginaceae and related families.

It may be of particular interest to compare *Retzia* with *Stilbe* (Fig. 4). This, with four more small genera, comprise Stilbaceae, a family at present being studied by Rourke. Like *Retzia*, the Stilbaceae is endemic to the Cape Region of South Africa.

The following features exhibit more or less pronounced similarities between *Retzia* and genera in Stilbaceae:

- (1) The plants comprise woody shrublets.
- (2) Intraxylary phloem is lacking.
- (3) The leaves are verticillate.
- (4) The leaves are also linear, sessile, entire and more or less sclerophyllous ("ericoid" in a wide sense); similar leaves occur in *Eustachys abbreviata* A. DC. (Stilbaceae).
- (5) The inflorescence is spicate (although the spikes are suppressed and lateral in *Retzia*).
- (6) The flowers are subtended by a large leaflike bract and also have 2 relatively large, leaflike bracteoles.
- (7) The flowers are hypogynous.
- (8) The perianth is 5-merous.
- (9) The flowers may be nearly actinomorphic in both groups (although there is reduction of one stamen in Stilbaceae and a greater variation towards pronounced zygomorphy of the corolla and calyx in that group).
- (10) The corolla is tubular and has a valvate (or reduplicate-valvate) aestivation.
- (11) The stamens are inserted in the corolla mouth and have a similar anther construction.
- (12) The pollen grains are similar, 3-colporate with punctate exine.
- (13) There is a small annular disc surrounding the ovary base.
- (14) The pistil is 2-carpellate, completely or incompletely bilocular, with a single filiform style and a small stigma.
- (15) The fruit may be capsular (or often indehiscent in Stilbaceae).
- (16) The seeds contain endosperm.



- (17) The iridoid compounds present are similar.
- (18) The distribution is similar.

This list may seem impressive, but several differences may also be noted, such as:

- (1) The more reduced and lateral spikes of *Retzia*.
- (2) The much smaller flowers with weaker petals in Stilbaceae.
- (3) The 4 instead of 5 stamens in Stilbaceae.
- (4) The greater tendency for floral zygomorphy, sometimes also reduction, in number of petal lobes, in Stilbaceae.
- (5) The few to solitary ovules in Stilbaceae, where one locule of the ovary may be empty. In this family the typical, pendulous ovules found beside the ascending ones in *Retzia* are lacking.
- (6) The punctate stigma in Stilbaceae.

These differences in the authors' opinions seem rather insignificant relative to the similarities enumerated above. The affinity between Stilbaceae and Verbenaceae also needs to be further investigated. Stilbaceae certainly appears to be distinct from other Verbenaceae and thus merits family rank.

Poetically enough, *Retzia* was described by Marloth (1932) as "a living witness of the relic nature" of the Cape flora. There is no doubt that it is primitive in some characters, such as the scalariform perforation of the vessels and the ovules which are of both the ascending and the pendulous kind. This type by reduction of either the ascending or the pendulous kind could result in the ascending ones only (as in Stilbaceae) or the erect only (as in Selaginaceae). Another primitive state is the isomorous unreduced androecium and the nearly actinomorphic calyx and corolla.

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FIGURE 4. *Stilbe vestita* Berg.—*Dahlstrand 1015* from the Cape of Good Hope Nature Reserve, Cape Peninsula, South Africa, 1966.—A. Branch in the flowering stage.—B. Section of branch showing a leaf and also the subverticillate leaf insertion and the prominent stem ridges.—C. Bract, adaxial side.—D. Bracteole, adaxial side.—E. Flower, bracteoles removed.—F. Corolla opened, seen from the inside; notice that there are only 4 stamens.—G. Calyx in longitudinal section and the somewhat unsymmetrical pistil.—Del. Bent Johnsen.



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