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# ON THE INTERRELATIONSHIPS OF CERTAIN SPECIES OF PETUNIA

## 1. TAXONOMIC NOTES ON THE PARENTAL SPECIES OF PETUNIA HYBRIDA

H. J. W. WIJSMAN

Genetisch Instituut, Kruislaan 318, 1098 SM Amsterdam

## SUMMARY

On the basis of a study of herbarium sheets of the described species *Petunia axillaris, P. integrifolia, P. propinqua, P. inflata, P. occidentalis,* and *P. parodii,* it is concluded that only two biological species are involved, the white-flowered *P. axillaris* (with subspecies *axillaris* and *parodii*) and the purple-flowered *P. integrifolia* (with subspecies *integrifolia, inflata* comb. nov., and *occidentalis* comb. nov.). The name *P. violacea* is rejected as a synonym of *P. integrifolia.* Possible relations of *P. axillaris* with an isolated population from Peru of an undescribed species of *Petunia* are discussed. The geographical distribution of the characters separating the species and subspecies is given.

## 1. INTRODUCTION

Several authors have traced the history of the introduction into Europe of *Petunia axillaris* (Lam.) B.S.P. (grown in the Jardin des Plantes, Paris, in 1820) and *P. integrifolia* (Hook.) Schinz & Thellung (in 1831) to cultivation of the wild species and the first attempts at crossing them (1834, 1835), resulting in the Garden Petunia, *P. hybrida* (Bailey 1896, Skan, 1918, Stout 1952).

In his taxonomic review of the genus *Petunia* Fries (1911) made a distinction between two subgenera, *Pseudonicotiana* and *Eupetunia;* the first flowering white and the second purple. From the point of view of the many biologists interested in *Petunia hybrida* (cf. Hanson 1980) such a division is impractical, separating as it does both that hybrid's ancestries. Rather, the purple and the white parental species and their relatives with 14 chromosomes in the nucleus apparently form a natural array, in view of the intercrossability (Sink 1975, Lamprecht 1966, Mather & Edwards 1943, Wijsman, in prep.).

Natarella & Sink (1974) and Sink (1975) have raised the question whether genes of *P. parodii* Steere and *P. inflata* R.E. Fries were also introduced into *P. hybrida. P. inflata* was described by Fries in 1911, but has recently been synonymized with *P. integrifolia* by Smith & Downs (1966). A third species, also described by Fries in 1911, and apparently related to *P. integrifolia/inflata,* is *P. occidentalis.*

As to the white-flowered species contributing genes to *P. hybrida,* recently Cabrera (1977) has proposed to consider *P. axillaris* and *P. parodii* conspecific, a conclusion that is in accordance with the data presented below.

The present paper deals with the taxonomy of the putative parent taxa of *Petunia hybrida* (on the one hand *P. axillaris* and *P. parodii,* and on the other *P. integrifolia, P. inflata,* and *P. occidentalis*) on the basis of herbarium studies. Predictions are being made as to the possibility of testing experimentally the implicit hypothesis that infraspecific taxa share genes and can freely intercross. Results of crossing experiments will be dealt with in a forthcoming paper.

## 2. MATERIAL, METHODS, AND NAMES

### 2.1 Material

The following herbaria were visited for study of their *Petunia* material: Leiden (L), Utrecht (U), Kew (K), British Museum (BM). Specimen localities are indicated in *fig. 3.* A full list of specimens is not provided because most of the material concerns incompletely labelled sheets dating from the 19th century, of limited value to a study based on geographical distribution of specific characters. In addition, the inbred lines S12 and S13 of *P. integrifolia* from the Institute of Genetics (University of Amsterdam) and an excellent voucher specimen of S13 (leg.T.M.Pedersen 12564, herb. Wijsman) have been inspected; from *P. axillaris* inbred line S2 (from Uruguay). All three lines originated from seed collected in the wild.

The material in Berlin, studied by R. E. Fries, was destroyed during the second world war. Material from Stockholm (Regnell herbarium, S) was not received on loan though requested.

### 2.2 Methods

Tube length in *P. axillaris* s.l. was measured from the lower end of the calyx to the point or zone separating tube and limb. Total flower length in *P. integrifolia* s.l. was measured from the lower end of the calyx to the farthest end of the flower limb.

### 2.3 List of names

The sources of the relevant names used in the text are given below. For the synonymy in general I refer to the review of Fries (1911).
*Petunia* Jussieu, Ann. Mus. Hist. Nat. 2(1803) 215–216, Pl. XLVII.
Type of genus: *P. parviflora* Jussieu, op. cit.

*P. axillaris* (Lam.) Britton, Stern & Poggenburg, Preliminary catalogue (1888) 38
*Nicotiana axillaris* Lamarck, Tableau encycl. méthod. botan. 2 (1793) 7; as to the type, see text.
*P. propinqua* Miers, Lond. J. Bot. 5 (1846) 185.
Type: Miers s.n., Barrancas Buenos Aires, BM.
*P. integrifolia* (Hook.) Schinz & Thellung, Vierteljahrschr. Nat. Ges. Zürich 60 (1915) 361.
*Salpiglosis integrifolia* Hook., Curt. Bot. Mag. t. 3113 (1831).

Type: no type specimen is present; the figure should serve as the type; in K a specimen has been labelled type, but it dates from 1837.

*P. integrifolia* (Hook.) Schinz & Thellung var. *depauperata* (R.E. Fries) Smith & Downs, Flora Ilustrada Catarinense, Solanaceas (1966) 266.

*P. violacea* ssp. *depauperata* R. E. Fries, Kungl. Svensk. Akad. Handl. 45(5) (1911) 34.

Type: of the three syntypes, after the loss of the Berlin material only one sheet remains (Lindman A. 831, S). This is necessarily the lectotype, though the Stockholm material was not received on loan. However, I could study a specimen from the same locality (Vieira) in K(Archer 4302).

*P. inflata* R. E. Fries, op. cit., 35.

Type: after the loss of the Berlin material the following syntypes remain: Paraguay: Anisitis 109, S, Asuncion; Hassler 6146, herb. Hassler & W, Tobaty; Hassler 816, 817, 3922, herb, Hassler & W, San Bernardino; Hassler 3091, herb. Hassler, Ypacarai.

Argentina: Ekman s.n., 22-11-1907 and 12-1-1908, S, Posadas, (Misiones).

The following isosyntypes have been inspected: Hassler 6146, K, BM; Hassler 3922, K. Moreover, from the same localities as some syntypes the following specimens could be inspected:Hassler 12331, K, L, BM, Ypacarai; Balansa 2169, K, Asuncion. In K a specimen (Hassler 18604) is labelled as "Type", but it is not one of the syntypes.

*P. occidentalis* R.E. Fries, op. cit., 37.

Type: after the loss of the Berlin material the following syntypes remain: Bolivia: Fiebrig 2135 and 2200, "Herb. Monac.", Bermejo; Argentina: R. E. Fries 472, S, Piquete (Jujuy).

The following isosyntypes have been inspected: Fiebrig 2135 and 2200, L, K, BM.

*P. parodii* Steere, Pap. Mich. Acad. Sci., Arts & Lett. 13 (1931) 213.

Type: Steere 202–1, MICH; from cultivation.

## 3. RESULTS

### 3.1 The white-flowered species: *P. axillaris* s.l.

Measurements of flower tube lengths of *P. parodii* and *P. axillaris* do not overlap (*fig. 1*), the first having a tube(generally much) longer than 46 mm, the latter having one shorter (see *table 1*). Moreover, from living material it can be deduced that the ratio of tube length to corolla diameter is $<1$ in *P. axillaris* and $>1$ in *P. parodii* (WIJSMAN, in prep., where also figures are given of the relevant tubes). In general, the taxon with a long flower tube (*parodii*) occurs from Bolivia along the eastern slopes of the Andes south to Patagonia, and from there to the province of Buenos Aires. From Buenos Aires northwestward (in Uruguay and, sparse, in Rio Grande do Sul), the taxon *axillaris* with a short tube is resident. Among the mounted material from the *parodii* region a very few exceptional flowers have also a short tube, but this may relate to their overall small size.

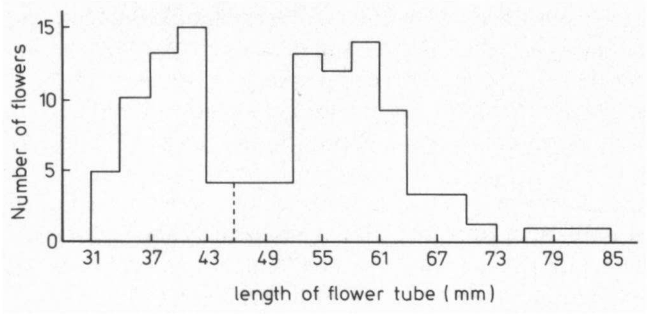

Fig. 1. Frequency of flower tube lengths in *P. axillaris* ssp. *axillaris* (left) and *P. axillaris* ssp. *parodii*. All specimens smaller than 46 mm came from the ssp. *axillaris* area (see *fig. 3*) and all those exceeding 46 mm from the ssp. *parodii* territory. The specimens in the transitional classes (43–49 mm) are specified in *table 1*. The three flowers with extremely long tube all come from Choreti, Bolivia; see text.

Table 1. Specimens of *P. axillaris* ssp. *axillaris* and ssp. *parodii* from the transitional frequency classes of *fig. 1*.

| Tube length | Herbarium collections |
|---|---|
| 43 | – |
| 44 | Tweedie s.n., don. Cunningham, K; Parana (river or town), Argentina. |
| 45 | Gibert 2034, anno 1839, K; Montevideo, Uruguay. Univ. Calif. exp. 23201 (anno 1938), K; Magdalena, prov. Buenos Aires, Argentina.<br>Rosengurtt e.a., s.n., anno 1936, U; dep. Soriano, Uruguay. |
| 46 | Schreiter, s.n., anno 1932, U; Valle de Tafi, alt. 2000 m, Argentina. |
| 47 | – |
| 48 | Lossen, s.n., K; Cordoba (3 flowers). |

However, short-tubed plants have been collected at the Argentinian side of the Rio de la Plata by Miers (1843) and Tweedie (Buenos Aires and the borders of the river Uruguay). From both areas extremely long-tubed plants have also been collected. It seems as if in this region secondary intergradation has created a hybrid swarm with a wide range of measures.

From the data presented above it is concluded that geographical subspecies are involved. This has already been recognized by CABRERA (1977).

The type of *P. propinqua* Miers originates from the above-mentioned region of secondary introgression. Since its tube was described as 2 inches long, and its stamina as of the 4 + 1 type (see discussion), this could have been an older synonym of *P. parodii*. However, the type specimen in the British Museum has a tube of only 42 mm. The specific epithet *propinqua* can safely be assumed a synonym of *axillaris*.

As to the provenance of the types for both subspecies, *P. axillaris* ssp. *axillaris* has been collected by Philibert Commerson during a stay in the La Plata region of 29th July till 14th November, 1767, on the expedition of "La Boudeuse" and "L'Etoile" (BOUGAINVILLE 1772). Fries traced typical material collected by Commerson as described by Lamarck in 1793. Its provenance was Montevideo, which must be regarded as the restricted type locality. Fries stated that the plant was identical to *P. nyctaginiflora* Jussieu. A clear figure of the latter allows taking measurements falling well within the range of *P. axillaris* (tube length 33 mm).

On the figure in the original description of *P. parodi* by Steere, on the contrary, tube lengths are 60 and 62 mm. The type was reported to originate from the central part of Formosa Province, Argentina. Dr T.M. Pedersen (in litt.) writes that as far as he knows no *Petunia* can be found in the extremely inhospitable area.

Northwards from the Argentinian plains, *P. axillaris* ssp. *parodii* tends to grow at higher elevation. Around Jujuy and Salta it can be found at 1200, 1300 m; around Tarija (South Bolivia) around 1900 m; at Choreti at at least 900 m, and at its most northern station, Cochabamba, up to 2800 m (Univ. of Calif. Exped., 1938, 24932, K). In Peru in Huamachuco Province at 1900 m altitude, 1700 km north-west of Cochabamba, the University of California Expedition 1963/64 collected a white-flowering plant (6222) with an extremely long flower tube, labelled by L.B. Smith as "Petunia spec., surely undescribed". On duplicates in K and L, I measured 5 tube lengths, which varied from 77–108 mm; the flower diameter cannot be measured but seems to be small. Because the longest tube in *P. axillaris* ssp. *parodii* has been found in Bolivia (not so much Cochabamba with 54–61 mm in 6 specimens, as well Choreti, on Rio Parapeti, leg. Brooke 5446:78–82 mm), the Peruvian material might represent the extreme of *parodii* variation. Fries gives 75 mm as the upper limit of *parodii* tube length, while in the present study 70 mm was the maximum, apart from Choreti. The very small leaves on the Peruvian sheets mentioned are different, but they represent the top of a perennial shrub of 0.5 m height. The many specimens with a woody base or fully lignified of various but sometimes considerable size as collected in north-east Argentina show that *P. axillaris* ssp. *parodii* might well have this potential. Co-evolution of the pollinating insect is a necessary assumption.

As to other characters than flower tube length separating the ssp. *axillaris* and ssp. *parodii*, in the original description of the latter no other significant (non-overlapping) difference can be found. There is no reason to believe that statistical clustering of such overlapping characters plays a role, while cultivation of wild species as well as *P. hybrida* made clear that most of the characters referred to are very plastic. During the present herbarium study no additional characters differentiating the two taxa have been found.

### 3.2 The purple-flowered species: *P. integrifolia*

FRIES (1911), in trying to establish characters for the genus *Petunia*, was struck by the fact that in most species the pedicels assume a deflexed position after flowering and pollination. (Indeed, on some sheets of, e.g., *P. integrifolia* loaded with capsules, the short pedicels are pointing down like fish-bones.) According to Fries, only four species, viz., *P. axillaris, P. ericaefolia, P. inflata,* and *P. occidentalis,* lack this character, which was in fact the main basis for separating the latter two from *P. integrifolia. P. occidentalis* was furthermore credited with a smaller overall length of the flower (18–20 mm instead of 25–40) and larger capsules (length 9–11 mm instead of 6–7; "durchgehends" = in most cases). *P. inflata,* as well, was characterized by smaller flowers (length about 25 instead of 25–40 mm; diameter 20–55 instead of 25–30 mm). It can be deduced that *P. inflata* had slightly larger flowers and larger fruit capsules than *P. occidentalis.* Moreover, *P. integrifolia* was suspected to be perennial, the basis of the stem often having a woody nature. Other differentiating characters of *P. occidentalis* as given by FRIES (1911) are that it is an annual species, that it has broader leaves (1–4 instead of 1–2 cm), and that the flowers are not only smaller, but have a narrower tube and the stamina higher implanted. Both apparent qualitative differences, annuality and inflexed position of the pedicels, are investigated below. As to the size of the leaves, the range of variation among different inbred lines of *P. hybrida,* the Garden Petunia, is so wide that the present author cannot believe, in view of the small number of sheets inspected by Fries, that the difference found was significant.

Separation of *P. inflata* and *P. integrifolia* is very difficult. Fries stated that the annual species *P. inflata* is doubtless closely related and perhaps best regarded as a "geographische Art" (= geographic species).

*P. occidentalis* from South Bolivia and North-west Argentina, seems to be isolated by the dry chaco region from the eastern populations (*P. inflata* and *P. integrifolia*). To the south it does not extend as far as *P. axillaris* ssp. *parodii,* so no contact that way round with the La Plata region has been made.

The present investigation, in part based on the same field numbers as studied by Fries, started when living material collected by T. M. Pedersen as well as K. Hagelund was identified as *P. integrifolia* sensu Fries, that is, with deflexed pedicels of the mature fruit capsules (see illustration in WIJSMAN, in prep.) This as well as the other characters hardly seemed sufficient for separating species. The three species rather seemed to represent geographic varieties of one biological species.

In my opinion annuality versus perennial state is not a character separating species in this genus. This is based on fact that in herbarium material in many specimens the stem base is woody while other specimens of the same taxon are herbs. This has been found for *P. axillaris, P. parodii, P. integrifolia,* but also for *P. inflata* (e.g., Balansa s.n., 1874, K, Villa Rica (Paraguay); Hassler 12331, L, Ypacarai (Paraguay)). Moreover, when at the end of the season plants of *P. hybrida* grown in the open attain a considerable size, lignification of the lower stem is normally in full swing, in general concomitantly with the decay set in by the first frosts.

As to the inflexus versus deflexus position of the pedicels, in the *integrifolia/inflata* complex many eastern sheets have deflexed pedicels all-over, and many

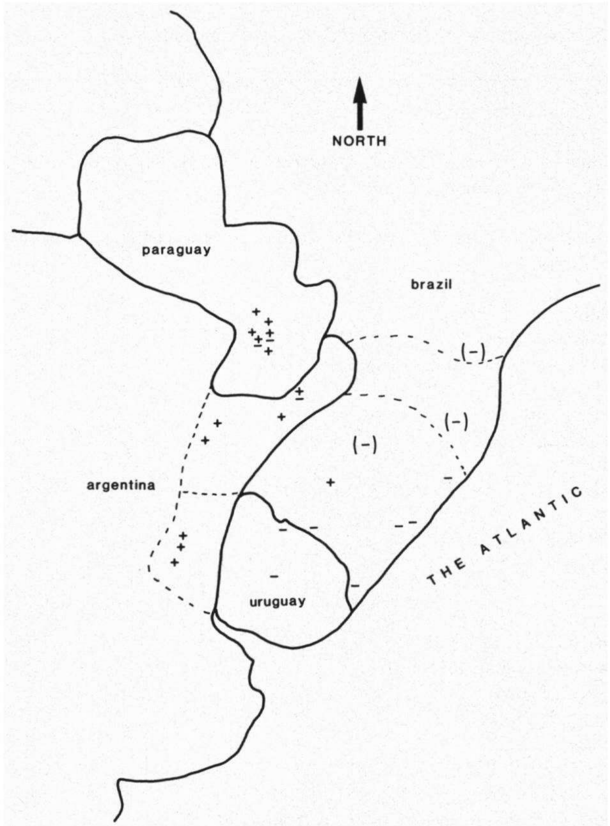

Fig. 2. Geographic distribution of the pedicel condition in *P. integrifolia* s.l. (cf. *table 2*).
– = deflexus; (–) = idem, but some pedicels horizontal or even upright; ± = inflexus, but some pedicels slightly bending down; + = inflexus.

western sheets inflexed all-over; but often in *P. integrifolia* not all pedicels point down, some may rather stand off at an angle of about 90°. In certain cases all pedicels take the intermediate position. For the localities of the different cases see *table 2* and *fig. 2.*

*P. inflata* has distinctly smaller flowers than *P. integrifolia*; the same holds for *P. occidentalis*. The range in total length of the flower in *P. integrifolia* was from 29 to 38 mm (7 sheets). The var. *depauperata* has much smaller flowers. It is, however, a variant of poor soils that can be recognized by its minute leaves. *P. inflata* ranges from 20 to 30 mm (14 sheets). *P. occidentalis* ranges from 20 to 26 mm (5 sheets). In certain specimens of the latter the larger capsules as mentioned by Fries are apparent, but in some other these are of the general *integrifolia/inflata* size. In *P. occidentalis* deflexed pedicels have never been found.

From the geographical distribution of the characters, I conclude that a cline is involved. In going west from, say, Porto Alegre, the deflexus character changes

Table 2. Localities of specimens of *P. integrifolia* s.l. with an indication of the condition of the capsule pedicel.

deflexed pedicels:
- Rio Grande do Sul (Brazil):
  - Torres (Lindeman & de Haas 3755, U); Dom Pedrito (S13); Arroio dos Ratos (S12); Vieira (Archer 4302, K); Porto Allegre (Fox s.n., BM)
- Uruguay:
  - "Bords du Rio Negro" (Anon. 232, anno 1867, K); Rivera (Wright s.n., anno 1928, BM)

deflexed but some aberrant:
- Parana (Brazil):
  - Curitiba (Lindeman & de Haas $2649^{a}$, U)
- Rio Grande do Sul (Brazil):
  - Palmeira das Missẽs (Lindeman & de Haas 3621, U)
- Santa Catharina (Brazil):
  - São Joaquim (Reitz s.n., L)

inflexed but some aberrant:
- Misiones (Argentina):
  - dep. Coinguas (Ac. Nac. Ciec. Exact. s.n., anno 1948, K)
- Paraguay:
  - Cord. Centr. (Hassler 6146, BM)
  - San Bernardino (Hassler 3922, K)

inflexed pedicels:
- Paraguay:
  - Ypacarai (Hassler 12331, K, L, BM)
  - Cerros de Tobaty (Hassler 6146, K)
  - Sapucoli (Teague 334, BM)
  - Asuncion (Balansa 2169, K)
- Misiones (Argentina):
  - Apostoles (Ibarrola 1019, BM)
- Rio Grande do Sul (Brazil):
  - Neu Würtemberg = Panambi (Bornmüller s.n., anno 1904, U)
- Uruguay:
  - Isla Quequay en Rio Uruguay (Rosengurtt B3785, U)
- Corrientes:
  - Nueva Valencia (Pedersen 4650, K)
  - Gral Paz (anon. 397 pro Herb. Mig. Lillo, anno 1944, BM)

into inflexus and the flowers become smaller. The apparent primary intergradation points to *P. inflata* and *P. integrifolia* forming one biological species. The extremes can be given the following names:

*P. integrifolia* (Hook.) Schinz & Thellung ssp. *integrifolia.*

(For a full synonymy see Schinz & Thellung, *Vierteljahrschr. Nat. Ges. Zürich* **60:** 315 (1915) and, especially, R. E. Fries, *Kungl. Svenska Vetensk. Akad. Handl.* **46**(5): 31(1911), sub nomine *P. violacea* Lindley).

*P. integrifolia* (Hook.) Schinz & Thellung ssp. inflata (R. E. Fries) *comb. nov.* Basionym: *P. inflata* R. E. Fries, l.c., 35

From extrapolation the following change in status is proposed:

*P. integrifolia.* (Hook.) Schinz & Thellung ssp. occidentalis (R. E. Fries) *comb. nov.* Basyonym: *P. occidentalis* R. E. Fries l.c., 37.

Obviously there is (clinal) overlap in the characters of the various taxa. Their status as subspecies can be questioned. However, a name available for population groups serves a practical purpose, since as reservoirs of genes especially populations sparsely sampled up to now may yield interesting mutations.

## 4. DISCUSSION

The material as present in four herbaria (Kew, British Museum, Leiden, Utrecht) has been shown to allow division over two biological species. Few particulars are known that may give an idea on the relationship of the different nominal species presently referred to the genus *Petunia*. (FRIES 1911, SMITH & DOWNS 1966). The scarce data on chromosome numbers (cf. SINK 1975) tell that the species dealt with in the present study all have chromosome number $2n = 14$, in contrast to some other species. Moreover, their intercrossability is a classical case and the success story of *P. hybrida* has been told by others (BAILEY 1896, SKAN 1918, STOUT 1952). In contrast to the claims of SKAN (1918) I did not find any evidence pointing to hybridization taking place in nature; my main criterion for mixed descent would have been colour, since F1 hybrids between lines representing *P. hybrida's* progenitor species have a distinct habit.

### 4.1. *P. axillaris* s.l.

As to *P. axillaris* s.l., the geographical taxa had already been recognized (CABRERA, 1977), while CABRERA (1980) indicates that ssp. *parodii* reaches Buenos Aires from the West, while ssp. *axillaris* spans the mouth of La Plata Bay. In the region of genetic contact the same broad variation as found by STOUT (1952) and WIJSMAN (in prep.) in F2 analysis can be expected. Whether this original variation pattern can still be reconstructed under the present man-influenced conditions where *P. hybrida* probably abounds, is an open question. Among the material in both London herbaria there are many sheets from the area dating from the middle of the last century, but labelling is very general and exact localities cannot be found back. Altogether, however, the material from the La Plata area makes an impression of intergradation of the crucial character, viz., tube length.

However, it cannot be excluded that in the La Plata region two full species overlap. That they cross in nature has not been demonstrated; the ratio tube length/limb diameter (around 1.0 in hybrids) could not be measured in herbarium material. However, STOUT (1952) mentions in one case segregation of long- and short-tubed types from seeds collected in the wild.

In Steere's original description of *P. parodii*, the presence of 4 longer stamina of equal length, in contrast to the didynamous condition in *P. axillaris* s.s. (2 long, 2 intermediary, one short), is considered to be an important feature. According to STOUT (1952) the 4 + 1 condition is not found in any other species of *Petunia*. However, on the basis of occasional didynamous "*P. parodii*" plants he concludes that introgression of *P. axillaris* and *P. parodii* is 'possible and probable" and "that there has been natural hybridization in Argentina". In our living material of *P. axillaris* ssp. *parodii*, inbred line S7 as originally obtained from Dr K. C. Sink, Michigan, stamina are of three lengths. Moreover, the 4+1 condition can be found in certain inbred *P. hybrida* lines of the collection of the Institute of Genetics, Amsterdam. Stout indicates recessivity of the 4+1 type, as becomes an "atavistic" mutation (cf. GOTTSCHALK 1971).

Up to now, most white Petunias have been identified as *P. axillaris*. Interestingly, STOUT (1952) has already deduced from the long tube that FERGUSON & OTTLEY's classical material (1932), and, therefore, also MATHER & EDWARDS's (1943), is, in fact, *P. axillaris* ssp. *parodii*. In their turn, FERGUSON & OTTLEY speak of SIMS's *P. nyctaginiflora* (1825) as of a "a short-tubed variety".

If the Peru locality can indeed be included into the range of *P. axillaris* s.l., its area of distribution is very extended and its range of variation impressing. Even if the species only goes north to Cochabamba District, Bolivia, the length of the flower tube, and, therefore, the reach of the pollinating insects, varies by a factor of more than two.

### 4.2 *P. integrifolia* s.l.

As to *P. integrifolia*, SMITH & DOWNS (1966) had already synonymized *P. inflata* and *P. integrifolia*, but no reasons for doing so had been given. Equally, SKAN (1918) says no differences between *P. inflata* and *P. integrifolia* could be found; this is interesting as far as his new living material, the Rowland clone, on STOUT's figures (1952) as well as on SKAN's own illustration has the distinct capsule pedicel folded back, which means, in fact, folded down. That the deflexus character has disappeared from memory as well as from cultivation in any form of *P. hybrida* may well be because capsules pointing down are loosing seeds and are a nuisance to the gardener. That the correct interpretation of Fries's deflexus character has been lost is shown by LAMPRECHT (1966) in his fig. 33, alluding to a slight bend in the end of the pedicel instead of flapping down by a knee-like articule within a few days after pollination.

One can ask what nature the type of *P. integrifolia* had. It has been grown in Glasgow in 1831 from seeds sent by John Tweedie, "of Buenos Aires"; but Hooker mentions that he had specimens sent by James Baird from the River Uruguay near the Rio Negro. In a type envelope in the Kew Herbarium is a sheet dating from 1837; but older cultivated plants are preserved in the Netherlands, e.g., Utrecht Botanic Garden, 1836 (U) with the capsule pedicels pointing down.

*Petunia hybrida* has from time to time been back-crossed to the ancestral species, that is, to populations of different geographic origin. In a horticultural context, for the typical Paraguayan Petunia with small flowers and upright capsule pedicels *P. inflata* may still be a convenient name, as is *P. integrifolia* for the large-flowered plant in Rio Grande do Sul with the deflexed condition. In living material the latter has a flower colour of a warmer, more intense hue, making altogether a strikingly beautiful impression.

Fig. 3. Map of the geographic distribution of the specimens investigated with an indication of the total area of the species. 3a. *Petunia axillaris* ssp. *axillaris* (●) and *Petunia axillaris* ssp. *parodii*(o) The asterisk in Peru relates to *Petunia* spec. as mentioned in the text.

The time has come for utterly rejecting the name *P. violacea* Lindley (1833) as still used particularly in horticultural publications. By common consent it is an illegitimate synonym of *P. integrifolia*. In the past the name has been misapplied to various purple cultivars of *P. hybrida* (FERGUSON & OTTLEY 1932, LOTSY 1913).

The genetic nature of the two characters differentiating *P. integrifolia* ssp. *inflata* from *P. integrifolia* s.s. can be investigated in crosses of extreme examples.

Fig. 3b. ***Petunia integrifolia sensu*** lato.

## 4.3 Final conclusion

The areas of distribution of *P. axillaris* s.l. and *P. integrifolia* s.l. (*fig. 3*) have much in common. The taxa *occidentalis* and *parodii* are sympatric, as are *integrifolia* s.l. and *axillaris* s.s. *Integrifolia* has spread inland becoming *inflata: parodii* spreads south until bridging the disjunction and meeting *axillaris* s.s. near Buenos Aires. The age of the West/East disjunction cannot be too old because it involves both species, while the genetic similarity of the species (WIJSMAN, in prep.) tells us that their separation into two species may not have occurred too long ago. However, in a small isolate like ssp. *occidentalis* fixation of aberrant mutations can be predicted.

The whole present study was aimed at investigating the concept of the possible occurrence of polymorphism for regulatory alleles (differing quantitatively) in the same way as for electrophoretic alleles (with qualitative differences). Establishing the range of variation in both ancestral species of *Petunia hybrida*, and demonstrating the feasibility of introducing new alleles interesting for the study of gene expression, was the impetus for the present publication and its sequel.

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