



A REVISION of the  
GENUS GLYCINE  
and ITS  
IMMEDIATE ALLIES

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## A REVISION OF THE GENUS *GLYCINE* AND ITS IMMEDIATE ALLIES

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### INTRODUCTION

The claim of the Old World leguminous genus *Glycine* to economic importance rests very largely upon its inclusion of the soybean, *Glycine max* (L.) Merr. A few others among the more common and widely ranging species, such as the principally African *G. javanica* L. and the Australian *G. Canescens* F.J.Herm. (*G. sericea* Benth., not Willd.), are of value as fodder, but their use does not compare in importance with that of *G. max*, which is used so extensively for human food and oil.

Agronomists attempting to improve strains in the world's soybean crop have been interested in the wild species of *Glycine* as potential material for interspecific crosses, but the literature on the subject has been not only extremely vague for the most part but frequently decidedly misleading. A tabulation of the species described as *Glycine* from Index Kewensis, for example, results in a total of 286 and the addition of published subspecies and varieties brings the number to 323. So loosely has the genus been defined, even in recent years, that the estimate of valid species within the group by current authors has varied from "some 60" by Hauman<sup>2</sup> to "perhaps 40 or more" by Bailey,<sup>3</sup> and to 16 by Willis.<sup>4</sup> It was in the hope of clarifying the almost chaotic condition of taxonomic information relating to the

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<sup>2</sup> HAUMAN, LUCIEN. SPERMATOPHYTES. *In* Flora du Congo Belge 6: 92-101. Bruxelles. 1954.

<sup>3</sup> BAILEY, L. H. MANUAL OF CULTIVATED PLANTS. 1,116 pp. Macmillan Co. 1949.

<sup>4</sup> WILLIS, J. C. DICTIONARY OF THE FLOWERING PLANTS AND FERNS. Ed. 6, 752 pp. Cambridge. 1948.

genus that the present study was undertaken, and the resulting realignment indicates that the actual number of species throughout its complete range in Africa and Asia (almost entirely tropical with the exception of *G. ussuriensis* Regel & Maack.) is evidently 10, in addition to which 9 infraspecific taxa of varying degrees of distinctness and stability are recognized.

The problem of speciation in *Glycine* was not found to be a major one in the present review of the group; the difficulties were largely generic. The major tasks were two: Adequately to delimit the genus among an extensive series of allies bearing close resemblance to *Glycine* and often strong affinity with it, and to identify the host of names that had been mistakenly associated with *Glycine*. It is hoped that the definition of the genus as here restricted and the accompanying key to related genera will contribute toward the first of these two objectives and that the list of species now excluded from the genus with their attempted reidentification will be found useful.

It was found that genera already described would accommodate the majority of the species that had to be excluded from *Glycine*, but for 11 of the excluded species 2 new genera had to be set up and are characterized in this paper. Because so large a proportion of the species ascribed to *Glycine* were proposed by early authors at a period when descriptions were habitually of such brevity that the characters delineated would apply to several or many different plants under our modern concepts, and because the practice of designating type specimens, to establish beyond question the identity of the plant described, was not yet in vogue, it was necessary to search the principal European herbaria in an attempt to find the specimen upon which each description was based. In the majority of cases this search was successful and the name was satisfactorily disposed of. In a few instances the types are evidently lost and where the description is too fragmentary to offer a decisive clue to the identity of the plant involved, the name must still remain in doubt, although in no case does it seem likely from the evidence available that it can be applicable to a true *Glycine*.

The chief reason for the heterogeneous composition of the genus *Glycine* as earlier defined is well brought out in the following observation by Bentham,<sup>5</sup> made nearly a century ago:

Up to the time of De Candolle's "Prodromus" [1825] the genera *Glycine* and *Dolichos* had become the receptacle for all the Phaseoleae which had no very striking character to distinguish them. He still retained, however, two distinct types, afterwards well separated by Arnott (in Wight and Arnott, "Prodromus Florae Peninsulae Indiae Orientalis")—one with alternate stamens abortive and remarkably hooked pod, the other with the stamens all perfect and the pod straight or slightly incurved at the end—one represented by *G. labialis*

<sup>5</sup> BENTHAM, GEORGE. Linn. Soc. London, Jour. Bot. 8: 63-64. 1865.

L.f., the other by *G. javanica* L. Not being aware that either group had been previously published as a genus, Arnott retained the name *Glycine* for the former as containing the commonest and most widely spread species, and gave to the latter the new name *Notonia*, which he afterwards changed to *Johnia* on perceiving that De Candolle had already published *Notonia* in Compositae. This nomenclature was unfortunate; for present investigations have shown that *Glycine* so limited not only excluded all the species of the elder Linnaeus, but was identical with *Teramnus* Swartz, adopted in the 'Prodromus', and that *Johnia*, on the other hand, comprising *G. javanica* L., which had never yet been generically separated, had much more legitimate ground for retaining the Linnean name.

Recent authors have been less prone to assign nondescript new species of the Phaseoleae to *Glycine*, particularly since the appearance of Bentham and Hooker's *Genera Plantarum*.<sup>6</sup> If any one factor more than another has led contemporary taxonomists to confuse with *Glycine* plants properly belonging to related genera, it is the failure to take into account fundamental differences in seed morphology. The majority of generic keys have been quite misleading in characterizing the seed of such genera as *Glycine* and *Galactia* as estrophiolate, whereas they can be so considered only if a distinction is made between the terms "strophiole" and "caruncle", which is very rarely done. Such a distinction is basic and in order not to cause confusion with reference to traditional keys to the tribe, the term "strophiole" in this publication is restricted to mean an arilloid, cushionlike, cartilaginous outgrowth around the hilum, well illustrated in the seeds of such genera as *Kennedyia*, *Cantharospermum*, and *Paraglycine*, whereas the term "caruncle" is applied to the squamiform, papyraceous appendage to the hilum characterizing true *Glycine*, *Teyleria*, and *Galactia*.

The importance of seed characteristics as taxonomic criteria, not only in *Glycine* but in most of its allies, became so evident in the course of the present study that it seems likely that its significance has been generally underestimated in at least the rest of the Lotoideae (Papilionatae).

## TAXONOMIC HISTORY OF THE GENUS GLYCINE

Linnaeus<sup>7</sup> proposed eight species under the name *Glycine* in 1753 in *Species Plantarum* (pp. 753-754). The cultivated soybean, *Glycine max*, appeared in the same work as *Phaseolus max* (p. 725) and also under the name *Dolichos soja* (p. 727). Of the eight Linnaean species under *Glycine*, the first, *G. apios*, is what we now know as *Apios*

<sup>6</sup> BENTHAM, GEORGE, and HOOKER, J. D. *GENERA PLANTARUM*. 1,040 pp. London. 1862-67.

<sup>7</sup> LINNAEUS, CARL. *SPECIES PLANTARUM*. vol. II, 1,200 pp. Stockholm. 1753. (Paged continuously.)

*americana* Medic.; his *G. frutescens* is *Wisteria frutescens* (L.) Poir.; *G. abrus* was later removed from *Glycine* by Linnaeus himself as *Abrus precatorius* L.; *G. tomentosa* is *Rhynchosia tomentosa* (L.) H. & A.; *G. comosa* and *G. bracteata* are *Amphicarpa bracteata* (L.) Fern.; *G. javanica* L. remains in *Glycine* as the type of the genus; and *G. bituminosa* is *Fagelia bituminosa* (L.) DC.

None of several species ascribed to the genus by Thunberg<sup>8</sup> in 1800 were actually congeneric with *G. javanica* L., nor were those proposed by Willdenow<sup>9</sup> 2 years later in the third edition of the *Species Plantarum*.

In 1825 De Candolle<sup>10</sup> summed up the genus as embracing 21 species, of which only 2 (*Glycine clandestina* Wendl. and *G. javanica* L.) can be admitted to the genus as here defined. De Candolle's generic concept still included such discordant elements as *G. striata* Jacq. (a *Galactia* from the Western Hemisphere); *G. secunda* Thunb. (a *Rhynchosia*); and the Asiatic *Teramnus labialis* (L.f.) Spreng., under 2 names (*G. debilis* Ait. and *G. senegalensis* DC.), although he had accepted Swartz's segregation of the American *Teramnus uncinatus* and *T. volubilis* from *Glycine*.

It was not until 1864 that the first major addition to the genus was made. This was by Bentham,<sup>11</sup> who treated the genus in Australia as comprising six species, all of them still valid although two of his names (*Glycine sericea* and *G. tomentosa*) must be dropped as being later homonyms. Three of his six species were transfers to *Glycine* of species earlier described by other authors under different genera (*Leptocyamus sericeus* F. Müll., *Kennedyia tabacina* Labill., and *Zichya latrobeana* Meissn.); one was Wendland's *G. clandestina* described in 1798 (p. 54);<sup>12</sup> and the remaining two were Bentham's own, although he had described one of them (*G. tomentosa*) a quarter of a century earlier under the untenable generic names *Leptolobium* and *Leptocyamus* and it (along with *G. clandestina* and *G. tabacina*) had been subsequently shifted by Steudel (p. 845),<sup>13</sup> to his superfluous genus *Kennedynella*.

By the time of Bentham and Hooker's *Genera Plantarum* (1867),<sup>14</sup> the genus was recognized as being confined to the Eastern Hemi-

<sup>8</sup> THUNBERG, C. P. PRODRUMUS PLANTARUM CAPENSIIUM. 191 pp. Uppsala. 1800.

<sup>9</sup> WILLDENOW, K. L. IN SPECIES PLANTARUM. 3(2): 1053-1068. Ed. 3. Berlin. 1802.

<sup>10</sup> CANDOLLE, AUGUSTIN, DE and CANDOLLE, ALPHONSE, DE. PRODRUMUS SYSTEMATUS NATURALIS 2: 241-243. Paris. 1825.

<sup>11</sup> BENTHAM, GEORGE. FLORA AUSTRALIENSIS. 2: 242-245. London. 1864.

<sup>12</sup> WENDLAND, J. C. GLYCINE CLANDESTINA. Bot. Beobacht. 58 pp. 1798.

<sup>13</sup> STEUDEL, E. G. NOMENCLATOR BOTANICUS. Ed. 2, v. 1, 852 pp. Stuttgart. 1840.

<sup>14</sup> See footnote 6, p. 3.

sphere and the number of species estimated to be about 12. Species attributed to *Glycine* continued to be proposed for the most part sporadically after this publication as they had earlier, but Bentham's *Glycine falcata* of 1864 was the last of the true *Glycine* species to be described. Since that date all species proposed have proved to be either not congeneric, or synonymous with already named species, or not of specific rank, although a few new names have had to be subsequently adopted because of the rule invalidating later homonyms which went into effect since Bentham's time.

No monographic study of the genus as a whole was undertaken, but three regional treatments are of significance (Taubert's<sup>15</sup> brief summary (pp. 360-362) in Engler and Prantl in 1894 added nothing not already known). In the first of these, that of J. G. Baker,<sup>16</sup> descriptions are given for seven species from that region of which only *Glycine javanica* and *G. petitiana* can be retained in the genus as now circumscribed.

In 1929 E. G. Baker<sup>17</sup> recognized 17 species, of which again all but *Glycine javanica* and *G. petitiana* are now either transferred to other genera or reduced to infraspecific rank.

The most recent, and most detailed, regional treatment is that by Hauman<sup>18</sup> in 1954, where the rich Congo representation of the genus is considered as referable to *Glycine javanica*, with one subspecies and five varieties, and of four additional species which, chiefly because of their strophiolate seeds and pubescent petals among other differences, are here argued to be generically distinct.

## TAXONOMY

### Key to Genera Related to Glycine

- 1a. Leaflets punctate; flowers yellow (the standard often brown- or purple-streaked in *Rhynchosia*); bracteoles none; membranaceous bracts usually fugacious.
  - 2a. Pod many-seeded; seed conspicuously strophiolate.
    - 3a. Legume turgid; glutinous, heavy-scented herb. (South Africa).....*Fagelia*
    - 3b. Legume compressed, strongly depressed between the seeds. (Tropical Asia and Australia).....*Cantharospermum* (*Atylosia*)
  - 2b. Pod 2-seeded; seed estrophiolate or the strophiole ± obsolete; legume compressed.....*Rhynchosia*

<sup>15</sup> TAUBERT, P. LEGUMINOSAE. In Engler, A., and Prantl, K. Die Natürlichen Pflanzenfamilien, t. III. Abt. 3, pp. 70-384, illus. Leipzig. 1894.

<sup>16</sup> BAKER, J. G. In Oliver's [Daniel] FLORA OF TROPICAL AFRICA. 2: 178-180. London. 1871.

<sup>17</sup> BAKER, E. G. THE LEGUMINOSAE OF TROPICAL AFRICA. Pt. II, 953 pp. 1929.

<sup>18</sup> See footnote 2, p. 1.

# Systematic List of Glycine and Its Immediate Allies

## Glycine

### Subgenus LEPTOCYAMUS

- |  |   |
|--|---|
| 1. <i>Glycine clandestina</i> Wendl.     | Australia; Formosa;<br>Micronesia                 |
| 1a. var. <i>sericea</i> Benth.           | Australia   |
| 2. <i>G. falcata</i> Benth.              | Australia   |
| 3. <i>G. latrobeana</i> (Meissn.) Benth. | Australia   |
| 4. <i>G. canescens</i> F.J.Herm.         | Australia   |
| 5. <i>G. tabacina</i> (Labill.) Benth.   | Australia; S. China;<br>S. Pacific Islands        |
| 6. <i>G. tomentella</i> Hayata           | Australia; S. China;<br>Philippines; For-<br>mosa |

### Subgenus GLYCINE

- |  |                              |
|--|------------------------------|
| 7. <i>G. petitiana</i> (A.Rich.) Schweinf.           | Ethiopia                     |
| 8. <i>G. javanica</i> L.                             | India; Malaya                |
| 8a. subsp. <i>micrantha</i> (Hochst.) F.J.Herm.      | Trop. Africa                 |
| 8b. var. <i>claessensii</i> (De Wild.) Hauman        | Uganda to Nyasaland          |
| 8c. var. <i>paniculata</i> Hauman                    | Belgian Congo                |
| 8d. var. <i>longicauda</i> (Schweinf.) Bak.          | Ethiopia to Angola           |
| 8e. var. <i>moniliformis</i> (Hochst.) F.J.Herm.     | Ethiopia and Eritrea         |
| 8f. subsp. <i>pseudojavanica</i> (Taub.) Hau-<br>man | Belgian Congo to An-<br>gola |
| 8g. var. <i>laurentii</i> (De Wild.) Hauman          | Belgian Congo                |

### Subgenus SOJA

- |   |          |
|---|----------|
| 9. <i>G. ussuriensis</i> Regel & Maack. | Asia     |
| 10. <i>G. max</i> (L.) Merr.            | Cultigen |

## Paraglycine

### Section DIGITATAE

- |   |   |
|---|---|
| 1. <i>Paraglycine unifoliolata</i> (Bak.f.) F.J.Herm. | Angola and N.<br>Rhodesia                 |
| 2. <i>P. unicostata</i> F.J.Herm.                     | N. Rhodesia                               |
| 3. <i>P. upembae</i> (Hauman) F.J.Herm.               | Belgian Congo                             |
| 4. <i>P. digitata</i> (Harms) F.J.Herm.               | Tanganyika                                |
| 5. <i>P. radicata</i> (A.Rich.) F.J.Herm.             | N. Rhodesia, Nyasa-<br>land, and Ethiopia |
| 5a. var. <i>rufescens</i> (Hauman) F.J.Herm.          | N. Rhodesia to Kenya                      |
| 5b. var. <i>enneaneura</i> (Hauman) F.J.Herm.         | Belgian Congo and<br>N. Rhodesia          |

## Section HEDYSAROIDES

- |  |                  |
|--|------------------|
| 6. <i>P. hedysaroides</i> (Willd.) F.J.Herm. | Guinea to Angola |
| 7. <i>P. laotica</i> (Gagnep.) F.J.Herm.     | Laos             |
| 8. <i>P. pinnata</i> (Merr.) F.J.Herm.       | China            |
| 9. <i>P. pentaphylla</i> (Dalz.) F.J.Herm.   | India            |
| 10. <i>P. madagascarensis</i> F.J.Herm.      | Madagascar       |

## Pseudoglycine

- |   |            |
|---|------------|
| <i>Pseudoglycine lyallii</i> (Benth.) F.J.Herm. | Madagascar |
|---|------------|

## Teyleria

- |  |                |
|--|----------------|
| <i>Teyleria koordersii</i> (Backer) Backer | China and Java |
|--|----------------|

## Glycine L.

*Glycine* L., Sp. Pl. 753. 1753.

Perennial herbs except for *G. max* (L.) Merr. which is annual; more or less hirsute or strigose to glabrate (never setose). Stems twining, climbing, or procumbent or rarely (in *G. max*) erect, occasionally somewhat woody at the base. Leaves trifoliolate, usually pinnate (digitate in three Australian species), nonpunctate, the stipules small, often deciduous. Flowers small, in axillary, solitary (not geminate) racemes (rarely in a terminal panicle or occurring also singly or in a sessile fascicle in the lower axils) inserted singly along the rachis of the raceme (subgenus *Leptocyamus*) or fascicled along the rachis; the peduncle bracteate, a bractlet also inserted at the base of the pedicel and a pair of bracteoles at the base of the calyx (in the subgenus *Glycine* the fascicles also bracteate), neither the bractlets nor bracteoles accrescent. Pedicels not nodose and articulate at the base or obscurely so. Calyx five-toothed, subbilabiate, the upper pair of teeth more or less connate, the lower three lanceolate to setaceous. Corolla papilionaceous, from scarcely exceeding the calyx to twice its length, white to blue or purplish, glabrous, the petals long-clawed. Standard suborbicular to obovate or rhomboid (not panduriform), subauriculate at the base. Wings narrow, more or less adherent to the keel. Keel shorter than the wings, obtuse, not twisted. Stamens all fertile and isomorphic, included, monadelphous, or diadelphous by the freeing of the vexillar stamen with age. Ovary subsessile, several-to many-ovuled. Style short, slender, slightly incurved. Stigma terminal, capitate. Pod linear or oblong, straight or falcate, more or less cellulose-septate between the seeds, compressed to subcylindrical, unilocular, 2-valved, the valves dehiscing spirally, apiculate but not clearly uncinatate; seeds ovoid or oblong to subspherical, estrophiolate, with a short, lateral hilum and a small, scalelike, papyraceous caruncle.

Type species: *Glycine javanica* L., Sp. Pl. 753. 1753.

Ten species native to tropical and warm-temperate Africa and Asia, except for *G. max* which is known only in cultivation. None of the species are native to the New World.

Characteristics distinguishing *Glycine* from its nearest allies are: Leaves invariably trifoliolate; vesture not bristly spreading; inflorescence not geminate; pedicels not nodose and articulate at the base or only obscurely so; bractlets and bracteoles not accrescent; corolla always glabrous; petals long-clawed; standard suborbicular to rhomboid, not panduriform; seeds estrophiolate, carunculate; caruncle a membranaceous, scalelike flap.

#### Key to Subgenera

- 1a. Flowers not clustered, inserted singly along the elongated rachis of the raceme (single flowers, generally cleistogamous, also often in the lower leaf-axils)-----1. Subgenus *Leptocyamus* (p. 10)
- 1b. Flowers clustered along the rachis of the raceme, or inserted irregularly on the rachis of a greatly shortened raceme or in the axils of the leaves.
  - 2a. Pod at maturity obliquely constricted (almost septate) between the seeds, narrow, usually straight, 3- to 8-seeded; flowers fasciculate along the elongated rachis of the raceme, with a bract at the base of the fascicle-----2. Subgenus *Glycine* (p. 24)
  - 2b. Pod not constricted between the seeds, rather broad, straight or curved, 2- to 4-seeded; flowers in axillary clusters or short racemes, without a fascicle-bract-----3. Subgenus *Soja* (p. 36)

#### 1. Subgenus **Leptocyamus** (Benth.) F.J.Herm.

*Leptocyamus* Benth. (as genus), Linn. Soc. London, Trans., Bot. 18: 209. 1839.

*Leptocyamus* Benth. (as section), Fl. Austral. 2: 243. 1864.

*Leptolobium* Benth. (as genus), Ann. Wien Mus. 2: 113. 1838, not Vog. 1837.

Species of this subgenus are confined to Australia, the South Pacific islands, Philippine Islands, and southern China. They differ from those of the other subgenera in having the flowers inserted singly, rather than in clusters, on the rachis of an elongated raceme, and (except in *G. falcata*), in regularly having additional, generally cleisto-

gamous, flowers solitary or clustered in the lower axils. Three of the species also have digitately trifoliolate leaves, a condition not found in the other subgenera. The seeds are usually of two types within each species, very different in appearance, one smooth and often glossy, the other variously muriculate or papillose and foveolate. The latter condition is due to the true seed coat being covered by the dried, persistent remains of the perisperm, which otherwise remains attached to the inner wall of the pod. As it partially disintegrates upon the seed-surface it shrivels in definite patterns usually forming tubercles or, in the case of *G. tomentella*, becoming foveolate as well as papillose.

#### Key to Subgenus *Leptocyamus*

- 1a. Leaves digitately trifoliolate, the three leaflets equally petiolulate.
  - 2a. Stems, elongate, twining----- 1. *G. clandestina*
  - 2b. Stems short, erect, decumbent or ascending, not twining.
    - 3a. Leaflets oblong-lanceolate or oblong, 1-6 cm. long, coriaceous, gray-green, coarsely net-veined beneath; no single or clustered flowers in the lower leaf-axils; upper calyx-teeth free above the middle; pods falcate, reflexed.  
2. *G. falcata*
    - 3b. Leaflets obovate or suborbicular, 0.7-2 cm. long, membranaceous; flowers in the lower leaf-axils solitary or fasciculate; upper calyx-teeth united nearly to the tip; pods straight, ascending----- 3. *G. latrobeana*
- 1b. Leaves pinnately trifoliolate, the terminal leaflet inserted at some distance from the lateral ones.
  - 4a. Plant hoary; leaflets canescent, silky-strigose, linear to narrowly oblong-lanceolate, 2-6 cm. long, acute... 4. *G. canescens*
  - 4b. Plant not hoary; leaflets strigose, velvety-tomentose or glabrous, at least some of the leaflets usually obovate or oval, obtuse.
    - 5a. Stems strigose to glabrous, slender; leaflets of the lowest leaves usually broadly obovate to oval, obtuse, those of the upper ones elliptic-lanceolate to linear, acute; calyx-teeth lanceolate, strigose to glabrous, equaling or shorter than the tube----- 5. *G. tabacina*
    - 5b. Stems tomentose-villous, generally coarse; leaflets all ovate to oblong-elliptic, obtuse; calyx-teeth lanceolate-attenuate to setaceous, hirsute, longer than the tube... 6. *G. tomentella*