A REVISION OF THE GENUS INCARVILLEA

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The Subgeneric Divisions of Incarvillea

In the early stages of its history the limits of *Incarvillea* were not clearly understood. Sprengel, Poiret and others described plants belonging to other Bignoniaceous and Gesneriaceous genera as Incarvilleas. In this way the name *I. grandiflora* came to be applied both to *Tecoma grandiflora* and to *Aeschynanthus grandiflorus*.

The natural order to which *Incarvillea* and *Amphicome* were to be referred was also uncertain. For example, Don (Gen. Syst. iv, 655: 1837) rightly placed *Incarvillea* in the Bignoniaceae but placed *Amphicome* at the end of the Gesneriaceae with the words "A genus hardly known whether it belongs to the order Bignoniaceae or to the present". A. P. de Candolle (Ann. Sci. Nat. Sér. II, i, 279: 1839) considered that *Incarvillea* belonged to the Cyrtandraceae. In this Meisner (Pl. Vasc. Gen. i, 302: 1843) followed his example. The genus was, however, restored to the Bignoniaceae as a subtribe by Alphonse de Candolle (Prod. ix, 237: 1845). Bureau (1864) in his monograph of the Bignoniaceae divided the family into three groups in the second of which, the *Tecomeae*, he included *Incarvillea* and *Amphicome*.

An account of the classification of *Incarvillea* must inevitably include a consideration of the status of *Amphicome*. A paper on its history and nomenclature by B. L. Burtt and the present author has already appeared (Notes Roy. Bot. Gard. Edin. xxi, 155: 1953). In preparation for his Illustrations of the Botany of the Himalayan Mountains (1835), Royle first named the plants before him as *I. diffusa* and inscribed the plates for this work accordingly. He then became aware of the extent of the differences between his specimens and the species of *Incarvillea* already described, renamed them as *Amphicome arguta* and, accordingly, had the captions of the plates erased and reinscribed. At the same time, he submitted the material to Robert Brown for his opinion. This was that *Amphicome* merited only subgeneric status and Brown supplied the description which was incorporated in the text of Royle's work in 1836.

In 1837, without explanation, Don revived *Amphicome* as a genus, and in the following year, Lindley (Bot. Reg. xxiv t. 19) pointed out that "the characters assigned to the latter [i.e. *Amphicome*], as a subgenus are quite sufficient for a higher purpose, in an order the distinctive characters of which are such as those of the dicarpous Monopetalae". In this he was followed by de Candolle, Hooker and Engler.

In systematic works at this time *Amphicome* was differentiated from *Incarvillea* by reason of the latter's pinnatisect leaves, ten-toothed calyces and seeds with entire hyaline wings. It must be remembered here that only the species of what are now recognized as the subgenera *Incarvillea* and *Amphicome* were known; none of the species that constitute the subgenus *Pteroscleris* had been described. Thus Chatterjee (Kew Bull. 1948: 185) found that, with the exception of the seed distinction, the above characters

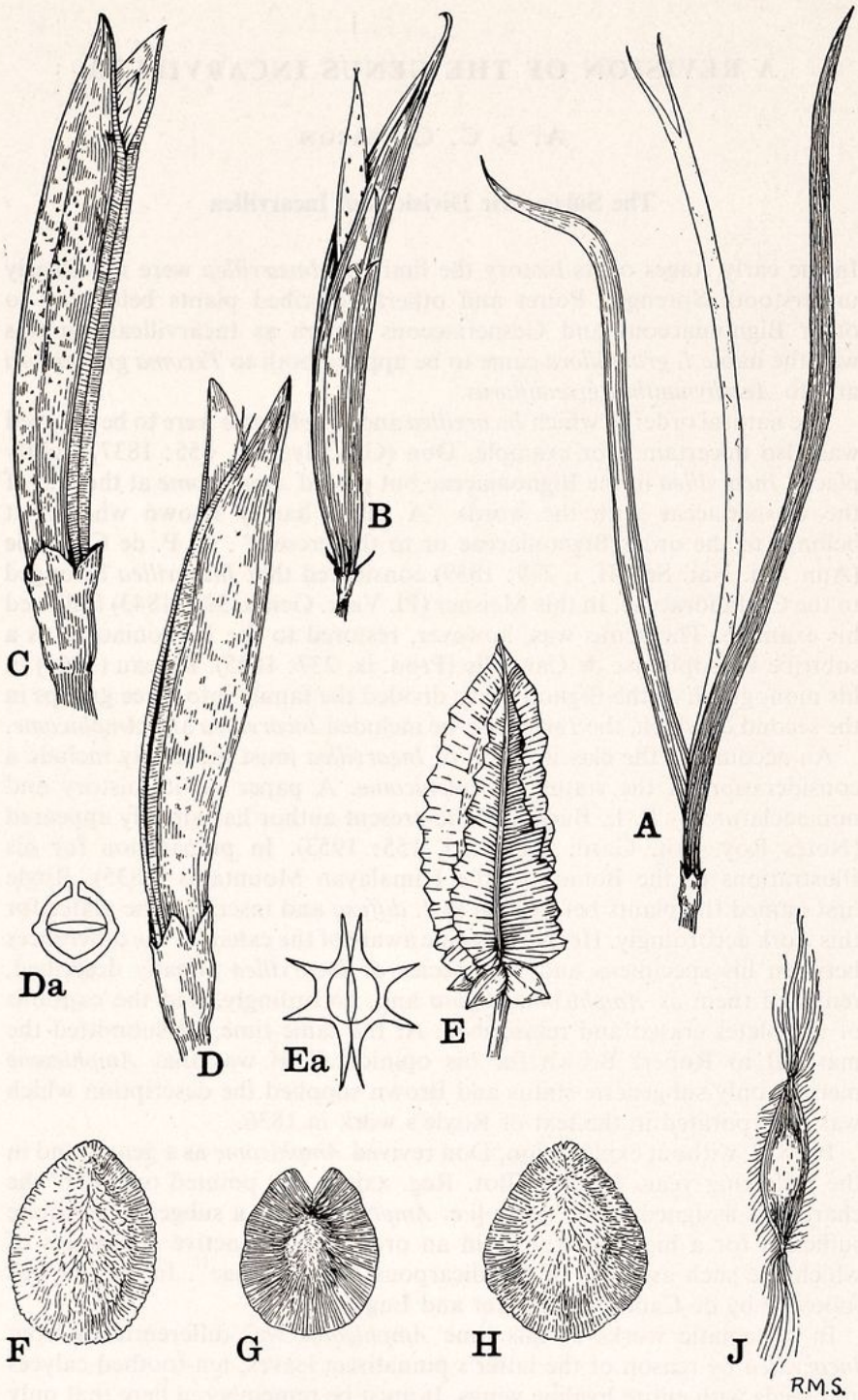

FIG. 1. Capsules and seed in *Incarvillea*.

A–E, capsules (× 1): A, *I. arguta;* B, *I. sinensis;* C, *I. compacta;* D, *I. compacta*, posterior view; Da, *I. lutea* in T.S.; E, *I. semiretschenskia;* Ea, *I. semiretschenskia* in T.S. F–I, seeds (× 4): F, *I. semiretschenskia;* G, *I. sinensis;* H, *I. lutea;* J, *I. arguta.*

were useless and that, with amendment of the description so far as the seed character is concerned, the species of *Amphicome* could be accommodated within the genus *Incarvillea*.

There is some justification for the separation of *Amphicome*. Its capsules dehisce, at first perhaps, by a split on the posterior surface but eventually the anterior surface ruptures as well. Although few herbarium specimens show this, it is the case with *I. arguta* in cultivation and is in line with the bivalvular dehiscence which is common in the Bignoniaceae in general. The capsules in the subgenus *Incarvillea*, however, never dehisce on the anterior surface and those of *Pteroscleris*, only in the upper third of the capsule on that surface. The valves of *Amphicome* are frequently twisted but those of the other subgenera may be curved but never twisted. The texture too differs: subligneous in *Pteroscleris*, coriaceous in *Incarvillea* and fibrous in *Amphicome*.

Yet these differences do not warrant generic separation when the characters which they have in common are taken into account. Besides those mentioned by Chatterjee (l.c.), they include: the similarity in habit between *I. sinensis* and *I. arguta*, the close agreement in their floral anatomy and the *Amphicome* seeds which, while having two finely lacerated comas, still show at their margins a membranous portion similar in structure to the seed-wing of *I. sinensis*. Also, both agree in having pendulous seeds, an unusual feature in the Bignoniaceae in which they are normally horizontal (the Mexican *Tourettia* is the only other aberrant genus in this respect). According to Bureau (l.c.), the ovules are at first horizontal but become pendulous on the formation of their integuments.

Baillon (1888), with only *I. sinensis* and the specimens which Bureau later described as *I. delavayi* before him, proposed the division of *Incarvillea*, as then recognized, into the subgenera *Incarvillea* and *Pteroscleris* on the basis of capsule and seed wing textures. Even with the addition of later species, this arrangement appears to be a sound one and is adopted in this revision. *Amphicome*, however, must be understood as constituting a third subgenus for, if it were left as a separate genus, *Incarvillea* and *Pteroscleris* would have to be similarly treated. This treatment of *Amphicome* is identical with that which Brown proposed.

To this arrangement a fourth subgenus, *Niedzwedzkia*, must be added. It was proposed as a monotypic genus by Fedtschenko in 1915 based on material collected by Niedzwedzki in Semiretschensk, the eastern province of Turkestan. On account of its fruit structure (see fig. 1, E) he placed it in the Pedaliaceae but, at the same time, drew attention to the similarity in habit between it and *I. olgae*.

The systematic position of *Niedzwedzkia* was reviewed by Vassilczenko (Not. Syst. U.R.S.S. xviii, 219: 1957) when the characters of both Bignoniaceae and Pedaliaceae were examined with reference to this plant and, in the Flora U.S.S.R. xxiii: 5 (1958), he transferred it to the former. In doing so the importance of two characters, the stamens and the seeds, was overlooked.

As is pointed out in a later section of this paper the stamens of *Incarvillea* are unique. The stamens of *Niedzwedzkia* are identical in structure and adhere to the style in the same way.

The seeds in *Incarvillea*, as already stated, are pendulous from their point of attachment on the septum which divides the capsule. The same is

true in *Niedzwedzkia*. In the Pedaliaceae the seeds are horizontal or ascending, never pendulous.

There are other corroborating characters which indicate that *Niedzwedzkia* was wrongly placed by Fedtschenko. The pollen of the Pedaliaceae which, as Erdtmann (Pollen Morphology 316: 1952) points out, is similar to that of *Incarvillea*, seems nevertheless to be sufficiently distinct from the latter to avoid confusion. In the Pedaliaceae the exine is slightly rough and the colpae are relatively broad and wedge shaped. *Incarvillea* pollen has a smooth exine with narrower colpae. The pollen of *Niedzwedzkia* is definitely the *Incarvillea* type and matches most closely the grains of the species belonging to the subgenus *Incarvillea*. Of the specimens examined, only one capsule at Edinburgh shows the mode of dehiscence and also that it differs from that of the other subgenera. Here, it takes place in a line parallel to the septum (septifragal) instead of at right angles to it, and passes through the lateral wings (see fig. 1, Ea). There is no doubt that this is a natural dehiscence line and not an artificially created one. This type of dehiscence is characteristic of the tribe *Bignonieae* but there are no signs here of the ligneous threads which often occur between the valves in the latter tribe.

The mucilage glands which are universal in the Pedaliaceae (Metcalfe & Chalk, Anatomy of the Dicotyledons 2: 1950) are absent in *Niedzwedzkia* as they are in *Incarvillea*. Instead, the microscopic stipitate glands found on the vegetative parts of *Incarvillea* are present especially on the bracts and calyx of *Niedzwedzkia*.

The above characters indicate that *Niedzwedzkia* must not only be accommodated in the Bignoniaceae but be included in the genus *Incarvillea* and its introduction there seems to provide the key to the relationship between the other subgenera.

There are two obvious differences between *Niedzwedzkia* and the other species: the calyx is almost polysepalous and the capsule has six broad longitudinal wings recalling an extreme condition of some ridged *Pteroscleris* capsules, e.g. those of *I. lutea* and *I. forrestii*. But neither of these is so important as the manner in which the capsule dehisces: this is definitely septifragal whereas, in all the other species of *Incarvillea* hitherto described, it is loculicidal.

It might well be argued that, as the capsule dehiscence in Bignoniaceae is regarded as a fundamental character dividing the family into tribes, it must be treated with similar importance here. Thus, it would be impossible for *Niedzwedzkia* and the other subgenera of *Incarvillea* to be encompassed within the limits of the one genus; they would, on the contrary, appear to constitute a herbaceous tribe or sub-family of the Bignoniaceae, such as Endlicher (Gen. Pl. 710: 1839) proposed, containing both types of capsular dehiscence as well as the characters which *Incarvillea*, *Amphicome*, *Pteroscleris* and *Niedzwedzkia* have in common: the bristled anther lobes, the incarvilleoid pollination mechanism and the pendulous seeds. Within such a tribe it would be permissible to recognize the above as four separate small genera.

Such a course would upset the established nomenclature of several well known species, e.g. *I. delavayi*, *compacta*, *younghusbandii* would have to be renamed as species of *Pteroscleris*; *I. arguta* and *emodi* would have to

revert to being called *Amphicome*. Only *I. sinensis*, *olgae* and *potaninii* could then be truly called Incarvilleas.

Much better, therefore, that since this is a small group of little more than a dozen species, it should be permitted to remain as a genus while at the same time recognizing its possible tribal status. Nomenclaturally, this course results in creating a new combination for *Niedzwedzkia* only.

Pollination Mechanism

The pollination mechanism and structure of the stamens in *Incarvillea* are unique among the flowering plants. This claim has been made and fully substantiated by Knapp (Öst. Bot. Zeit. ci, 208–219: 1954) and, as there are also two earlier (and somewhat inaccurate) papers by Maillefer (Bull. Herb. Boiss. Ser. II, 92–97: 1908) and Cutting (Ann. Bot. xxxv, 63–71: 1921) on the pollination mechanism of this genus, it is only necessary here to give an outline of its functioning.

The stamens, style and stigma lie against the posterior wall of the tubular corolla. The style is longer than the stamens so that the stigma stands nearest the mouth of the corolla (see fig. 2, A). The lobes of the stigma,

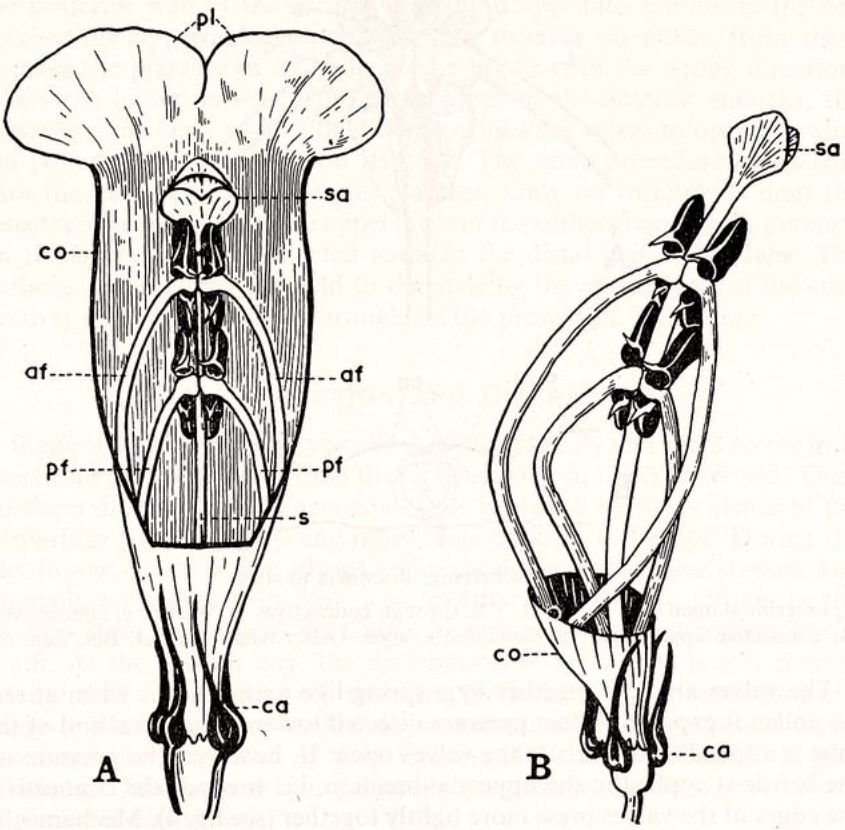

Fig. 2. *Incarvillea sinensis*, organization of flower parts.

A, anterior view (× 2½); B, oblique view with corolla partly cut away (× 3). af, anterior filament; ca, calyx; pf, posterior filament; pl, posterior lobes; s, style; sa, stigma. (After Knapp in Öst. Bot. Zeit. ci.)

which are weakly strigose on their inner surfaces, are sensitive and close together on stimulation.

As in other genera of the Personales the anthers are arranged in pairs on either side of the style, the anterior above the posterior (see fig. 2, B). In *Incarvillea* the anther lobes are set at right angles to their filaments and each is provided with a bristle which stands at right angles to its surface and projects downwards into the tube of the corolla. From the bristle to the distal end of each lobe run the dehiscence valves. Between the bristle and the connective the surface of the lobe is hollowed and the bristle itself is hinged on thin-walled cells at the base of this indentation (see fig. 3, A.) The connective, which is relatively massive, bears at its apex two appendages which, with those of the opposite connective, surround the style and hold the anther firmly to it (see fig. 3, B).

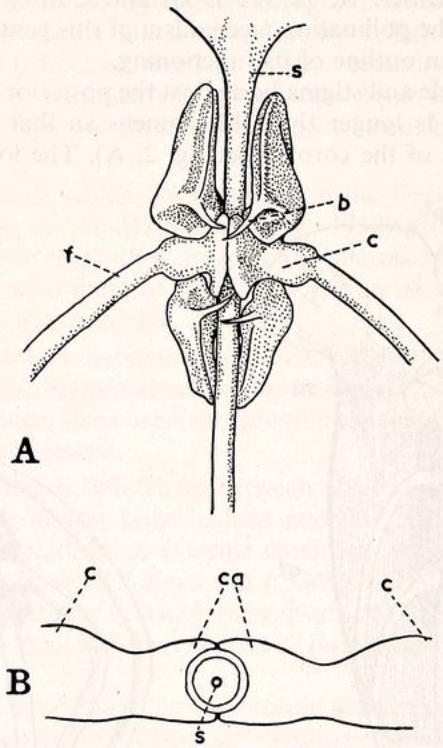

FIG. 3. Adherence of anthers to style.

A, anterior stamen pair (× 8); B, T.S. through connectives. b, bristle; c, connectives; ca, connective appendages; f, filaments; s, style. (After Knapp in Öst. Bot. Zeit. ci.)

The valves are held together by a spring-like tension, thus when at rest no pollen is exposed. When pressure directed towards the distal end of the lobe is applied to the bristle the valves open. If, however, the pressure on the bristle is applied in the opposite direction, i.e. towards the connective, the edges of the valves press more tightly together (see fig. 4). Mechanically these movements depend on the distribution of thickened and unthickened cells in the anther wall. (Knapp l.c.)

When an insect (e.g. a bee) visits the flower the following sequence of events is put in train. The back of the insect touches first against the bilobed

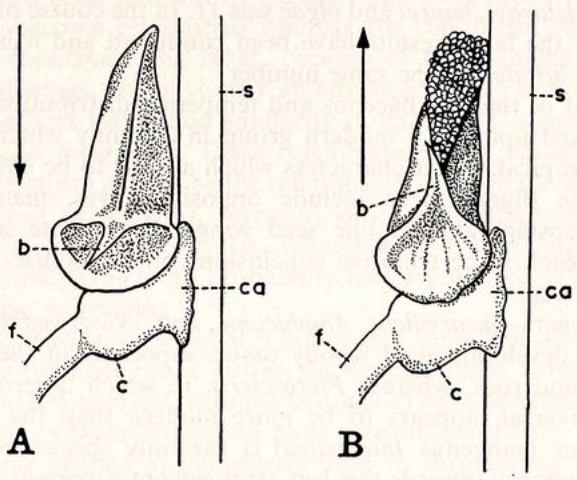

FIG. 4. Pollen release: single anther lobe (× 16).
A, valves closed; B, valves opening with distally directed pressure on bristle. b. bristle; ca, connective appendage; f, filament; s, style. (After Knapp in Öst. Bot. Zeit. ci.)

stigma depositing pollen on it, whereupon the lobes fold together against the posterior wall of the corolla. Moving deeper into the flower the bee reaches the uppermost anther lobes but receives no pollen from them because the pressure of its body on the bristle is in the wrong direction. When the insect moves to the lower lobes of the anterior stamens, the pressure of its body against the bristles causes the valves to open allowing the pollen to fall passively on its back. The same procedure holds true with the anthers of the posterior stamens. Only on withdrawal does the insect receive pollen from the upper lobes of the anthers because the pressure on the bristles is then directed towards the distal end of the lobe. The anthers, because they are held to the style by the appendages of the connective, remain in position throughout the process of pollination.

EVOLUTION AND DISTRIBUTION

Bignoniaceae is today a typically American family and there seems little reason for believing other than that it originated in the New World. Their northern distribution in Caenozoic times is proved by the evidence of the Bembridge (Isle of Wight) and other fossil deposits in Europe. During the Pleistocene, however, the advancing ice sheets destroyed these stations and Bignoniaceous genera in Asia were restricted to suitable refugia in the Pamirs, Himalayas and S.W. China, as well as to tropical regions in the south. At the present day, the distribution of *Incarvillea* is still centred around such refuge areas or, extending from them, has spread along the fringe of the monsoon area. The disjunct distribution of *I. arguta* in N.W. India and the gorge area of S.W. China and its absence from E. Nepal, Sikkim and Bhutan may be explained by the greater effects of the monsoon in the latter territories.

Chromosome number gives no guide to the development of the group. An early study by Sugiura (Cytologia vii, 544: 1936) gave a haploid number of 9 for *I. compacta* and *delavayi* but Bowden (Amer. Journ. Bot. xxvii, 357: 1940) on reinvestigating, found that the haploid chromosome number of

I. compacta, *delavayi*, *mairei* and *olgae* was 11. In the course of preparation of this paper the latter results have been confirmed and it has also been found that *I. arguta* has the same number.

On account of their herbaceous and temperate distribution, *Incarvillea* must be looked upon as a modern group in a family which is typically woody and tropical. Other characters which appear to be basic and widespread in the Bignoniaceae include opposite leaves, membranous or coriaceous capsules and hyaline seed wings. With these in mind it is possible to reach some tentative conclusions on the course of evolution within this group.

The subgenera *Incarvillea*, *Amphicome* and *Niedzwedzkia* all show considerable development of woody tissue, especially in the lower parts of the stem and root, whereas *Pteroscleris*, in which tuberous roots are probably universal, appears to be more modern than the other three. While *I. olgae* (subgenus *Incarvillea*) is the only species with opposite leaves, the tendency towards this leaf arrangement is present in *Incarvillea* and *Amphicome*. In *Pteroscleris* (except the acaulous species) and *Niedzwedzkia* the leaves are decidedly alternate.

The membranous capsules of *Amphicome* and the thinly coriaceous ones of *Incarvillea* are more primitive than those of *Pteroscleris* and *Niedzwedzkia*.

In the matter of seed wings, the thick opaque and often reduced wings of *Pteroscleris* and *Niedzwedzkia* must be considered advanced when compared with the hyaline structures of *Incarvillea* and *Amphicome*.

Thus, in a phylogenetic arrangement of these subgenera, there are grounds for placing *Amphicome* and *Incarvillea* as being more or less equally primitive, although the latter is regarded here as being more advanced in view of the presence in it of an annual species. *Pteroscleris* is obviously nearly related to *Incarvillea*, but the relationship of *Niedzwedzkia* to the other subgenera is more difficult to assess. The fact that it has a different capsular dehiscence shows that it must be set aside from the other subgenera. It indicates, perhaps, that the *Incarvillea* stock is very old and that, when it diverged from the main bignoniaceous stock, it contained elements with both capsular types (see fig. 5). In the main stream

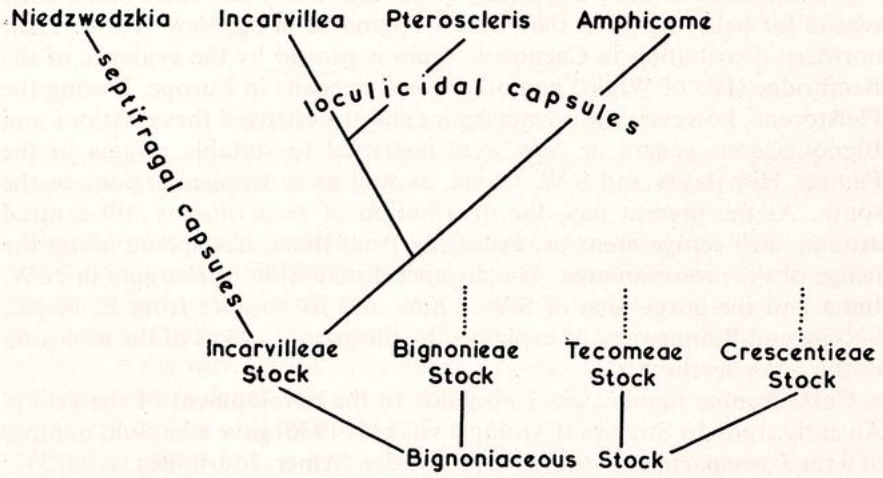

FIG. 5 Diagram of the hypothetical derivations of the subgenera of *Incarvillea*.

of Incarvilleas, or at least in the majority surviving today, the loculicidal capsule has become established whereas the septifragal capsule persists only in *Niedzwedzkia*. The latter, because of their winged capsules and reduced seed wings, are obviously an advanced group but, on account of their bipinnatisect leaves and similarity in habit to *I. olgae*, may also be compared with *Incarvillea*. These resemblances may equally well be the result of parallelism as may be the relationship between the winged capsule and the ridged valves of *I. forrestii*; other bignoniaceous genera, e.g. *Cuspidaria*, have winged capsules. Whatever the true estimation, the subgenus *Niedzwedzkia* is in all probability best considered as being isolated from the other subgenera.

A range of crosses, by which it is hoped that some indication of relationship may be obtained, have so far shown that those between *I. mairei*, *compacta* and *delavayi* (i.e. within *Pteroscleris*) have produced viable seeds but that those between subgenera have been unsuccessful.

The criteria applied at subgeneric level in formulating a satisfactory arrangement have been similarly employed in consideration of the species.

In *Amphicome* the wide ranging and often basally woody *I. arguta* with its disjunct distribution appears to be older and more primitive than *I. emodi* which is a specialized crevice plant.

In the subgenus *Incarvillea*, the annual *I. sinensis* ssp. *sinensis* is advanced and the perennial ssp. *variabilis* derived from it perhaps as a polyploid although the evidence for this is not incontestable. *I. olgae* and *potaninii*, however, both appear to be old relic species.

The subgenus *Pteroscleris* may be divided into two groups; the stemless and the stemmed. In the first group, *I. delavayi*, *mairei* and *younghusbandii*, the last named is regarded as being the most advanced and adapted to high alpine conditions although *I. mairei* is also plastic and adaptable as evidenced by its subspecies and forms.

In the stemmed group *I. lutea* may be regarded as the ancestral type with the others viz. *I. altissima*, *forrestii* and *beresowskii* as derivatives; *I. altissima* and *forrestii* because of their reduced calyces and simplified leaves being the most advanced.

In this speculative arrangement the acaulescent *I. compacta* appears to fall between the two groups but seems to be more closely allied to the acaulous group.

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INCARVILLEA Juss. Gen. 138 (1789)

Syn.: *Amphicome* Royle, Ill. Bot. Him. Pl. t. 72, fig. 1 (1835).
Niedzwedzkia B. Fedtsch. in Bull. Jard. Bot. Pierre Grand xv, 399 (1915).

Acaulous or stemmed, annual or perennial herbs up to 2 m. high. *Root* simple or branched, woody or tuberous. *Leaves* all radical or all cauline (at flowering time) or both present, alternate rarely opposite, exstipulate, pinnate or pinnatisect, rarely undivided or bipinnatisect, usually puberulous at least on the veins; rachises ± cylindrical, grooved on upper surface; lateral leaflets 0–11 pairs ovate, elliptic or linear, upper leaflets often decurrent on the rachis, margins usually serrate; terminal leaflet suborbicular or similar to lateral leaflets. *Inflorescence* terminal, one flowered or racemose several—many flowered, occasionally paniculate; pedicels subtended by a short bract and bearing two smaller bracteoles (often very close above the bract which then appears as if tripartite). *Flowers* zygomorphic, aestivation imbricate. *Calyx* hypogynous, tube campanulate, gamosepalous rarely almost polysepalous; teeth 5, lanceolate, subulate or reduced to minute points. *Corolla* gamopetalous, infundibuliform; tube cylindrical at base as far as insertion of stamens, campanulate above; lobes 5, subequal, rounded or emarginate. *Stamens* 4, epipetalous, didynamous, included; anther lobes 2, divaricate, each beset with a single stout bristle; dehiscence introrse, connective broad, style-clasping; staminode absent or variable [Rohrhofer in Öst. Bot. Zeit. lxxx: 1–25 (1931)]. *Pollen* grains subspherical, exine somewhat granular, 6–10 colpate (in subgenus *Pteroscleris* 8–10 colpate, 60–84 μ diam. at equator; 6–9 colpate 44–60 μ diam. in other subgenera). *Disc* collar-like, seldom more than 1 mm. high. *Ovary* 0·5–1 cm. long, bicarpellate, superior, cylindrical, bilocular; septum transverse, becoming freed from the capsule wall at maturity; ovules anatropous in 1 or 2 series along the margins on both sides of the septum. *Style* filiform, glabrous. *Stigma* horizontally bilobed. *Capsules* subligneous, coriaceous or membranous, cylindrical, quadrangular ridged or 6-winged; dehiscence follicular or bivalvular. *Seeds* pendulous, elliptical or ovate, plano-convex in section, surrounded by a wing or bearing a coma of fine hairs at each end. *Cotyledons* uncrumpled, radicle superior.

Type species: *Incarvillea sinensis* Lam.

Key to Subgenera

1. Calyx almost polysepalous, reflexed in fruit. Capsules ligno-coriaceous, 6 winged. Seed-wing rim-like . . . *Niedzwedzkia* (p. 350)
   Calyx gamosepalous, not reflexed in fruit 2

2. Calyx teeth subulate with thickened bases or reduced to minute points, plicae bifid or simple. Capsules coriaceous cylindrical; dehiscence follicular. Seed wing hyaline . . . *Incarvillea* (p. 320)
   Calyx teeth lanceolate or rounded, often broad, bases not thickened 3

3. Anther lobes pilose. Capsules cylindrical membranous; dehiscence bivalvular. Seeds with a coma of hairs at either end *Amphicome* (p. 313)
   Anther lobes glabrous. Capsules subligneous, ± quadrangular or ridged. Seed wing thick, non-hyaline *Pteroscleris* (p. 328)

Incarvillea subgen. **Amphicome** (Royle) R.Br. apud Royle, Ill. Bot. Him. 296 (1836).

Syn.: *Amphicome* Royle, Ill. Bot. Him. Pl. t. 72 fig. 1 (1835); G. Don, Gen. Syst. iv: 655 (1837); Lindley, Bot. Reg. xxiv: t. 19 (1838); Endl., Gen. Pl. 710 (1839); Paxton, Mag. Bot. vi: 79 (1839); De Candolle, Prodr. ix: 237 (1845); Hooker, Bot. Mag. t. 4890 (1855); Bureau, Monogr. des Bignoniac. (1864); Benth. & Hook. f., Gen. Pl. ii: 1048 (1876); C. B. Clarke in Hook. f. Fl. Brit. Ind. iv: 385 (1885); Baillon, Hist. des Pl. x: 51 (1888); Schumann in Engl. & Prantl, Nat. Pflanzenfam. iv: Abt. 3b, 232 (1894); Collett, Fl. Simlensis 369 (1902); L. H. Bailey, Stand. Cycl. Hort. i: 278 (1917); R.H.S. Dict. Gard. i: 102 (1951).

Erect or ascendent perennial herbs somewhat woody at the base. *Leaves* subopposite at base of stems and branches, alternate above, pinnate. *Corolla* tube pubescent with long stalked glands at the base within (see fig. 6, D); lobes eglandular. *Anther* lobes pilose. *Capsule* elongate, linear, cylindrical; dehiscence bivalvular, valves thin fibrous. *Septum* bifid at the apex. *Seeds* elliptical or narrowly ovate with tuft of hair 5 mm. long at both ends.

Of the two species in this subgenus one, *I. emodi*, is confined to Western Himalaya and the other represented there but spreading discontinuously to S.W. China.

The subgenus is probably most easily recognized by its long narrow thin walled capsules and the hair-tufted seeds which they contain (see fig. 1, A & J). In texture, the leaves appear to be thicker than those in the other subgenera and punctate due to the presence of glands sunk into pockets of the epidermis (see fig. 6, A). In their arrangement they recall the subgenus *Incarvillea*: those of *I. emodi* basally arranged as in *I. potaninii*, those of *I. arguta* subopposite at the base of the stem or branch and alternate above as in *I. sinensis*. The absence of subsessile glands from the corolla lobes and the hairy anthers are both unique features.

Key to species of subgenus Amphicome

Plants up to 50 cm. high. Stems unbranched, leaves aggregated at the base. Calyx lobes rounded, apiculate . . . . 2.*I. emodi*
Plants up to 1·5 m. high. Stems branched, leaves not aggregated at the base. Calyx lobes subulate . . . . . 1. *I. arguta*

1. **Incarvillea arguta** (Royle) Royle, Ill. Bot. Him. 296 (1836); Burtt & Grierson in Notes Roy. Bot. Gard. Edin. xxi: 155 (1953).

Syn.: *Incarvillea emodi* Wall. Cat. 487 (first example). (1829) nom. nud. *Amphicome arguta* Royle, Ill. Bot. Him. t. 72 fig. 1 (1835); G. Don, Gen.

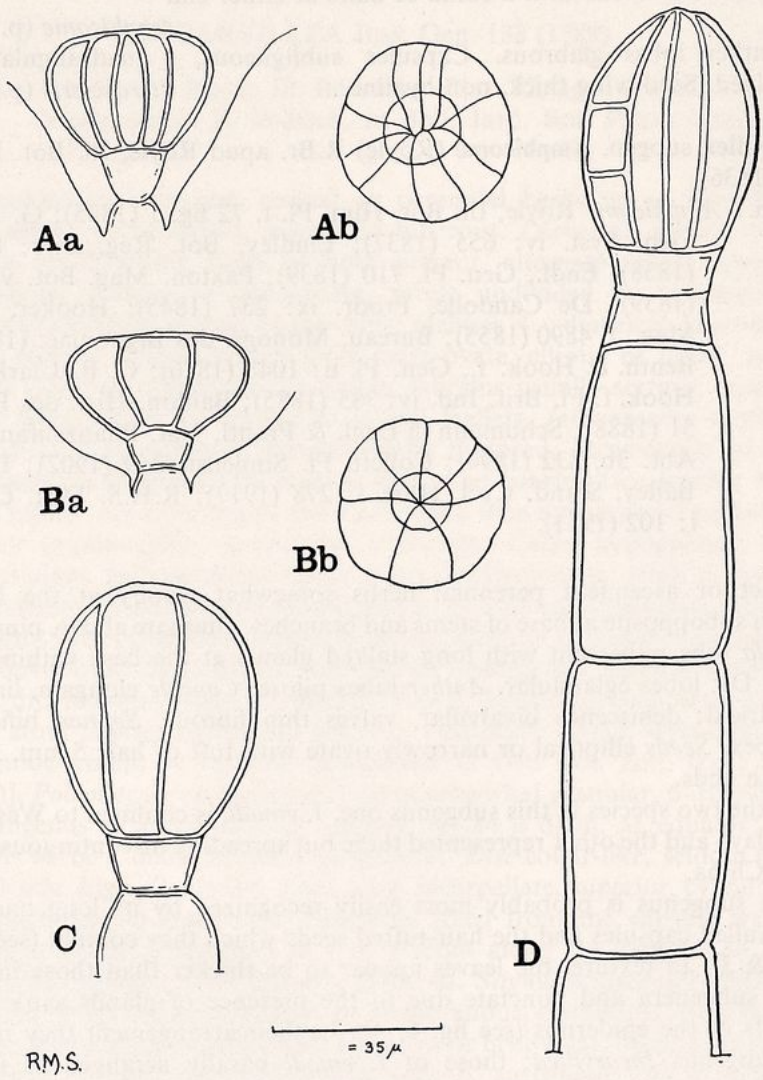

FIG. 6. Glands in *Incarvillea*.

A, *I. emodi*, leaf glands: Aa, in T.S., Ab, surface view. B, *I. semiretschenskia*, leaf glands: Ba, in T.S.; Bb, surface view. C. *I. mairei*, gland from corolla lobe; D, *I. arguta*, long stalked gland from lower corolla tube.

Syst. iv: 665 (1837); Lindley, Bot. Reg. xxiv: t. 19 (1838); DC., Prod. ix: 237 (1845); Stewart, Punjab Pl. 148 (1869); C. B. Clarke in Hook. f. Fl. Brit. Ind. iv: 385 (1884); Franchet in Nouv. Arch. Mus. Paris, Sér. II, x: 63 (1887); Baill., Hist. Pl. x: 52 (1888); Diels in Bot. Jahrb. xxix: 577 (1901); Collett, Fl. Simlensis 369 (1902); Strachey, Pl. Kumaon 132 (1906); Léveillé, Cat. Pl. Yunnan 19 (1915); Bamber, Pl. Punjab 403 (1916); Osmaston, Forest Fl. Kumaon 383 (1927); L. H. & E. Z. Bailey, Hort. Sec. 49 (1941); R.H.S. Dict. Gard. i: 102 (1951).

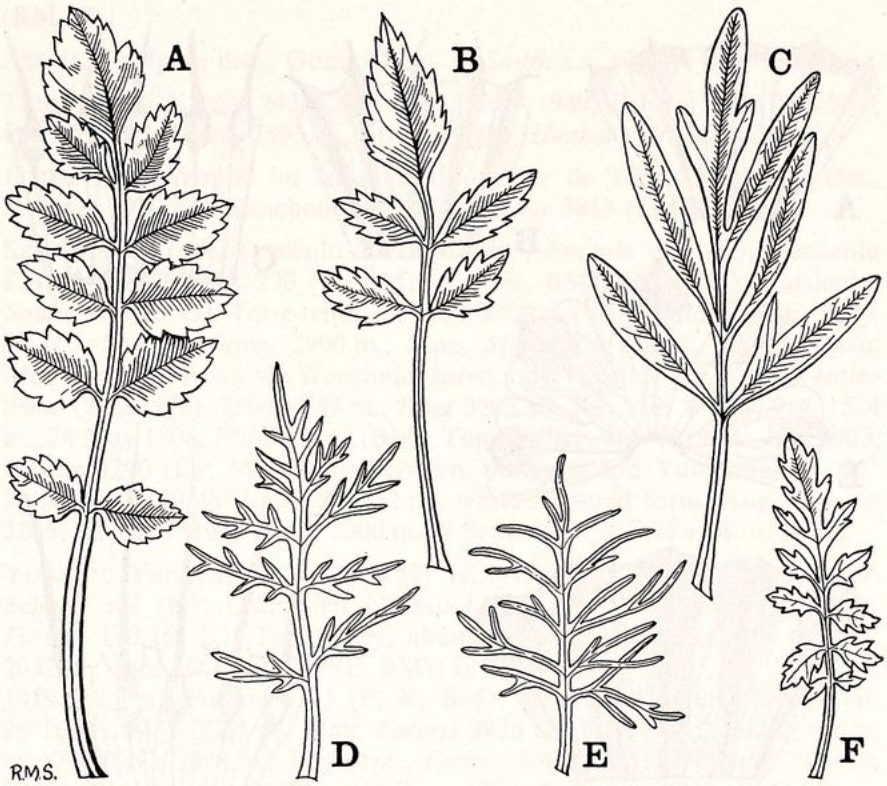

FIG. 7. Leaf types in *Incarvillea* (excluding subgenus *Pteroscleris*).

A, *I. emodi* (× 2/3); B, *I. arguta* (× 2/3); C, *I. olgae* (× 2/3); D, *I. sinensis* (× 1); E, *I. semiretschenskia* (× 1); F, *I. potaninii* (× 1).

Incarvillea diffusa Royle, Ill. Bot. Him. t. 72 fig. 1 (1835)—seen only in one copy; Chatterjee in Kew Bull. 1948: 185 and in Bull. Bot. Soc. Bengal ii, 63 (1948).

Amphicome diffusa (Royle) Sprague in Kew Bull. 1933: 386.

Herb erect 0·2–1·5 m. high, glabrous or puberulent somewhat woody at the base. *Leaves* alternate, pinnate 5–20 cm. long; lateral leaflets 2–6 pairs, opposite or subopposite, 1–5 cm. long 0·5–2 cm. broad, lanceolate or elliptic, obliquely rounded at the base, acute or acuminate at the apex, margins acutely serrate, punctate beneath; terminal leaflet 2–5 cm. long 0·5–2·5 cm. broad, similar in shape (see fig. 7, B). *Inflorescence* terminal, raceme 5–20 flowered; pedicel 8–20 mm. long subtended by a short subulate bract 3 mm. long and bearing two minute bracteoles less than

1 mm. long. *Calyx* campanulate, tube 5–8 mm. long; teeth subulate 1–4 mm. long, ciliate (see fig. 8, B). *Corolla* pink or white, tube 2·5–3·8 cm. long, glandular pubescent at the base within (see fig. 6 D); lobes 0·5–1 cm. long 0·9–1·4 cm. broad, rounded, subsessile glands absent. *Anther* lobes ovate 2 mm. long 1 mm. broad, pilose. *Staminode* 1·2 cm. long, filiform tapering to flattened apex. *Capsule* linear, cylindrical, curved, membranous 8–20 cm. long 0·2–0·3 cm. broad. *Seeds* very narrowly elliptic, 2 mm. long 1 mm. broad, pale brown; coma of whitish hairs at both ends c. 5 mm. long (see fig. 1, J).

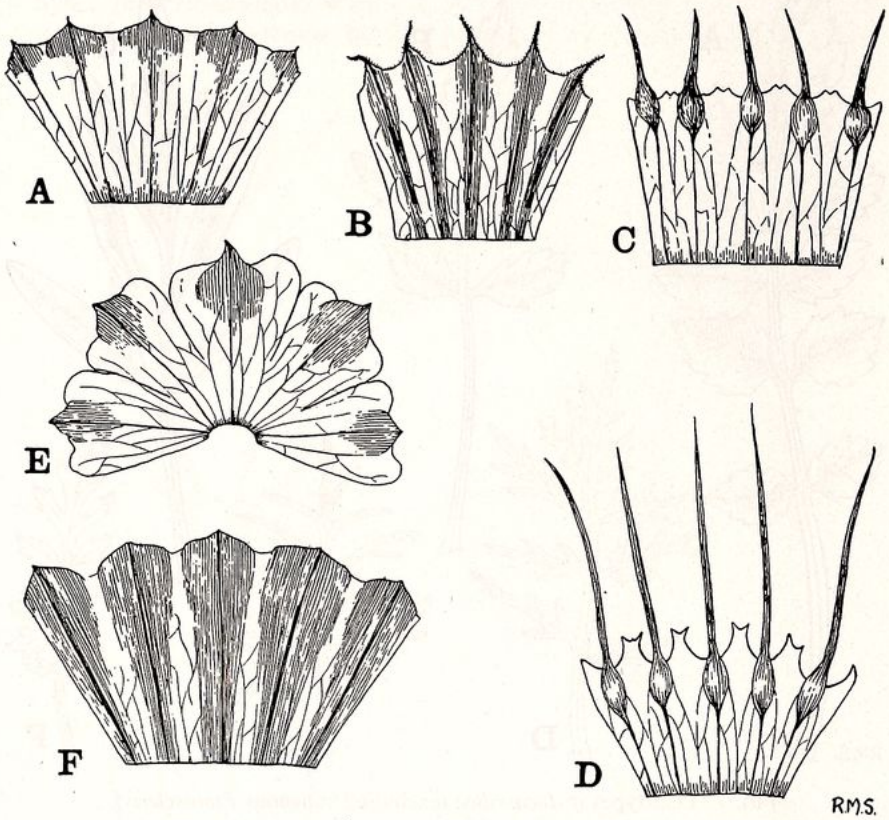

FIG. 8. Calyces in *Incarvillea* (excluding subgenus *Pteroscleris*) (× 4).
A, *I. olgae;* B, *I. arguta;* C, *I. potaninii;* D, *I. sinensis;* E, *I. semiretschenskia;* F, *I. emodi.*

HABITAT. Dry stony situations and on limestone ledges.

PUNJAB. Turanda in lower Kunawar, *Royle* s.n. (BM. holotype); Valley of Buspa, *Jacquemont* s.n. (P. syntype, non vidi); without locality, *Blinkworth* Herb. *Wallich* 487 pp. (BM); Theog rocks towards Mahan, Simla, 2440 m., July 1885, *Collett* 208 (K); Simla hills, *Drummond* 22130 (K, G), 22131 (K); Kunawar, *Drummond* 22129 (K), 22341 (E, K); Kulu to Lahaul, *Drummond* 23095 (E, K); Ganges Valley near Suki, *Duthie* 83 (BM, G); Kumaon, Danli River, 2133 m., *Strachey & Winterbottom* 2 (K, BM); Tehri Garhwal, Gangoltari, 2440 m., *Gamble* 13 (K); Theog rocks, Simla, 2133 m., *Gamble* 6495A (K); Bashahr, Ralli to Barary, 1980 m., *Lace* 210 (E); Bashahr, Wangtu to Chagaon, 1675 m., *Lace* 701 (E); Wangtu, 1585 m., May 1889, *Lace* s.n. (E).

NEPAL. En route to Tanjet, 2133 m., July 1949, *Polunin* 1446 (BM); Tibrikot, 2285 m., 31 May 1952, *Polunin, Sykes & Williams* 2132 (BM); Kumlik near Timikot, 2438 m., 5 June 1952, *P.S.W.* 4276 (BM, E); near Jumla 2285 m., 5 Oct. 1952, *P.S.W.* 5507 (BM, E); Ghasa, N. of Dhana, 2133 m., 25 May 1954, *Stainton, Sykes & Williams* 663 (BM, E); Thinigaon, Muktinath Himal, 3048 m., 24 June 1954, *S.S.W.* 1382 (BM, E); near Gurjakhana, 2285 m., 26 July 1954, *S.S.W.* 3640 (BM); Kabra, Kuli Gardahi Valley, 1980 m., 31 May 1954, *S.S.W.* 5489 (BM, E); Thinigaon (N. of Tukucha) Kali Gandaki, 3505 m., 26 Sept. 1954, *S.S.W.* 8020 (BM, E).

ASSAM. Goalpara dist., Goma Duar, *E. Smith* s.n. (G).

TIBET. Lendi Khola, 2438–2743 m., 11 July 1949, *Polunin* 853 (BM) Wa, Pasho Dist., Kham, 2895 m., 21 July 1936, *Hanbury Tracy* 54 (BM).

KWEICHOW. Abonde sur les murs de la ville de Tchen liu tchou, Oct., *Bodinier* 1980 (E); Sanchouen, July, *Cavalerie* 3813 (E, K).

SZECHUAN. Prope Tatsienlu, 14 July 1893, *Potanin* s.n. (K); Tatsienlu 2743–3962 m., *Pratt* 270 (K, BM); 725 (K, BM); 804 (BM); Tatsienlu, *Soulié* 416 (K, G); Tong-tchouen, 2500–2900 m., June, *Maire* 41 (E, BM), 98 (E), Siaou-ou-long, 2900 m., June, *Maire* 356 (E, K, BM); Motsu, *Maire* 784 (E); Roadside Wenchnan-hsien, July, *Fang* 1501 (E, K); Kwantin-hsien (Tatsienlu), 2560–2743 m., *Fang* 3503 (E, K); Min Valley, 914–1524 m., 24 May 1908, *Wilson* 2042 (BM); Tung Valley, 914–1219 m., July 1903, *Wilson* 4290 (K); Mountains between Yungpeh and Yungning, lat. 27° 20′N. long 100°48′E., 3048–3352 m., white flowered form, Aug., *Forrest* 22057 (E, K); Muli, Gutu, 2300 m., 8 Sept. 1937, *T.T. Yu* 14210 (BM).

YUNNAN. Yunnan-sen, *Maire* 1531 (E); Chang Yi Chou, 2000 m., *O. Schoch* 364 (K); Chungtien plateau to Yangtze, 2743–3048 m., Sept., *Forrest* 110 (E, K); Tali Valley, abundant on the walls of city of Tali; 2032 m., June, *Forrest* 4730 (E, BM); E. flank of Tali range, lat. 25°40′N., 1980–2285 m., *Forrest* 6795 (E, K, BM); Lankong-Hoching divide, lat. 26°16′N., 2438–2743 m., May, *Forrest* 9958 (E, K, BM); Lichiang range, lat. 27°30′N., 3048 m., July-Sept., *Forrest* 10872 (E, K, BM), 12793 (E), 27930 (E); Atuntze, 2650 m., 14 Sept. 1937, *T .T. Yü* 10210 (BM).

KANSU. Prope pagum Yu-ling-kuan, 5 Sept. 1885, *Potanin* s.n. (K).

In distribution, ranging from Punjab to Western China with one outlying station in Assam, *I. arguta* is a relatively widespread species but is absent from eastern Nepal and Bhutan presumably because of the more humid climate of these areas (from field notes it appears to prefer arid habitats). In an examination of the staminodes in Bignoniaceae Rohrhofer (Öst. Bot. Zeit. lxxx: 1931) found that these structures varied within quite wide limits in this species. In the largest examples they are soft structures, two-thirds as long as the shortest stamens and their vascular bundles reach only into their lower parts. When the staminodes are smaller (2–3 mm. long) the vascular strands end in the corolla below the point of insertion. This species can, however, display considerable irregularity in its whole staminal development as cultivated individuals show. Flowers with five fertile stamens are not uncommon and varying degrees of development of the posterior stamen may also be observed in the same raceme.

Fasciated flowers, always amongst the lowest in the raceme, have occurred on several occasions on the plant at Edinburgh. Yet, this apart, the species is remarkably stable and distinct from other species, for, whilst the leaves have the same arrangement and calyx teeth and corolla tube similar to those in *I. sinensis*, it is nevertheless easily distinguished by the leaf division and fruit characters. It is also readily distinguishable from *I. emodi* as is shown in the key, and from the species of the subgenus *Pteroscleris*, not only by the fruit characters, but also by the thickish punctate leaves, the subulate calyx teeth and the shorter corolla tubes.

Royle's material of this species is missing from his collection at Liverpool Botanic Garden. The specimen at the British Museum is inscribed "*Incarvillea diffusa* Rle. MSS. Turanda in Lower Kunawar, Valley of Buspa, Jacquemont". The handwriting has been identified as Royle's and it appears that here he has annotated his own specimen which is regarded as the holotype.

Seed of this plant was given to the Royal Horticultural Society by Royle, but only one seedling from this source flowered and provided material to illustrate Lindley's account of the species (Bot. Reg. xxiv, t. 19: 1838). It is not completely hardy but flowers well in a cool greenhouse.

2. **Incarvillea emodi** (Lindl.) Chatterjee in Kew Bull. (1948) 2.

Syn.: *Incarvillea emodi* Wall. Cat. 487 (1829) nom. nud. (second example).

Amphicome emodi Lindl. Bot. Reg. xxiv: t. 19 (1838) in nota; DC. Prod. ix, 237 (1845); Hook., Bot. Mag. t. 4890 (1855); Fl. des Serres Ser. II, i, t. 1109 (1856); Floricult. Cab. 129 (1856); Boiss., Fl. Orientalis iv, 80 (1879); C.B.Cl. in Hook. f. Fl. Brit. Ind. iv, 385 (1884); Gartenflora xxxiv, 370 (1885): Collett, Fl. Simlensis 369 (1902); Bamber, Pl. Punjab 403 (1916); L. H. Bailey, Stand. Cycl. Hort. i, 278 (1917); Basu. Ind. Med. Pl. t. 710 (1918); L. H. & E. Z. Bailey, Hort. Sec. 49 (1941).

Ascendent herb 15–50 cm. high, glabrous or pubescent. Stem 1–5 cm. long, bearing prominent leaf scars. Leaves somewhat fleshy, pinnate, 15–25 cm. long, usually crowded basally; lateral leaflets 4–5 pairs, opposite, 1–4 cm. long, 0·6–1·8 cm. broad, ovate, obliquely rounded at the base, acute at the apex, margins dentate or rarely pinnately divided into 3–5 segments, punctate, glabrous or slightly to densely pubescent; terminal leaflet similar or somewhat smaller, distinct or confluent with the uppermost pair of lateral leaflets (see fig. 7, A). *Inflorescence* terminal, raceme 6–18 flowered, secund; pedicels 1–3 cm. long subtended by narrow bracts 5–8 mm. long and bearing two bracteoles 3–6 mm. long close above it. *Calyx* tube 4–7 mm. long, campanulate, glabrous or pubescent; teeth rounded, apiculate, 1–2 mm. long, 2–3 mm. broad (see fig. 8, F). *Corolla* cyclamen purple (R.H.S. Col. Code 30/2) with maize yellow throat, tube 3·5–5·8 cm. long, glandular pubescent near base within; lobes 1–1·5 cm. long, 1·5–2·5 cm. broad, rounded, eglandular. *Anther* lobes 0·25 mm. long, 0·15 mm. broad, ovate, pilose. *Staminode* short, crooked terminally. *Capsule* 6–15 cm. long, 2–3 mm. broad, membranous, elongate, subulate, curved. *Seeds* very narrowly elliptic, 4–5 mm. long 1 mm. broad, testa minutely rugose; coma of hairs c. 5 mm. long at both ends.

HABITAT. On rocky ground and in rock crevices.

AFGHANISTAN, without locality, *Griffith* 4073 (K); Kamarzan, *Watt* 4739 (E).

W. PAKISTAN. Peshawar, *Stocks* s.n. (K); Hazara, *Duthie* 22075a (K); Kohat Pass, Mar. 1907, *Dean* s.n. (K); Mt. Tilla, *Aitchison* 15 (K), 1095 (K); Rawalpindi Dist., Danobi, Kahuta Tehsil, 1380 m., 27 Mar. 1938, *R. N. Parker* 3418 (K); Khyber Pass, 1126 m., *Lester Garland* s.n. (K); Swat, 914 m., *R. R. Stewart* 27507a (BM); Hazara Dist., Abbotabad, 1400 m., 24 Mar. 1958, *Burtt* B481 (E).

KASHMIR. Jhelum valley, Domel, 762 m., 27 Mar. 1939, *Sherriff* s.n. (BM).

INDIA. Punjab, Banks of Sutlej, near Belaspoor, 609 m., *Madden* s.n. (K); Dakochara near Pundon, 609 m., 18 Jan. 1889, *Watt* 2829 (E); Kalka below Simla, 1609 m., Feb. 1889, *Watt* s.n. (E); Deoprayag, 457 m., *Strachey & Winterbottom* s.n. (K.); Suen Range, *Wallich* 487 pp. (CGE Holotype, BM); Jaunsar Dist., below Deoban, 2440–2740 m., 11 Apr. 1897, *Duthie* 19861 (BM); Konain, 2135–2440 m., *Duthie* 21004 (E, K, BM, G.); Mat. Kangra, *Gamble* 22837 (K); Bodyar, *Gamble* 23123 (K); Konain, 7295 m., *Gamble* 26526; Jaunsar Dist., Chakrata, *Saklani* 104 (G).

NEPAL. Bheri River, below Gajarkot, 760 m., 1 Apr. 1952, *Polunin, Sykes & Williams* 1829 (BM, E); Kuehani, 915 m., *P.S.W.* 3797 (BM).

The short true stem of this species, giving it the appearance of an acaulescent herb, at once distinguishes it from *I. arguta*, the other species belonging to this subgenus. Each year 1–2 cm. are added to the length of the stem which may persist over several years and attain 5–6 cm. in length. In this respect it may be compared with *I. potaninii* but differs in its punctate leaves, calyx teeth, hairy anther lobes as well as fruit and seed characters. The species is also remarkable for its early flowering period, January to April, in the field; most other species flower in midsummer.

It was not introduced into cultivation until 1852 when seeds were sent to Kew by Major Vicary, and these flowered for the first time in October three years later. It has proved to be a tender plant, requiring greenhouse treatment.

In two respects the indumentum of this species is unique. While several other species have subsessile glands on their leaves, in none are they so deeply set into pits as to give the surface such a distinctly punctate appearance. Also, whereas a stumpy puberulence is a commonplace on vegetative parts in this genus, it is occasionally replaced here by a truly tomentose pubescence. Clarke (Fl. Brit. Ind. iv, 386) notes that "the Afghanistan examples referred to *A. emodi* are all hairy". While this statement appears to be correct, it must be pointed out that hairy forms are not confined to this region. Pubescence in varying degree has been observed on specimens from Srinagar, Garhwal, Jaunsar and Swat. These represent no more than sporadic forms; genetically, perhaps, no more than the manifestations of a single gene pair. *Duthie* 21004, from Jaunsar, is particularly interesting in showing this variability, for some specimens of this gathering are densely pubescent while others are quite glabrous.

Under his catalogue No. 487 Wallich published, in 1829, without description *Incarvillea emodi* which included material not only of this species but also of *I. arguta*. Wallich's specimen of the latter is therefore older than the

type which was collected by Jacquemont in his expedition of 1828–31. Lindley writing about this species (Bot. Reg. xxiv, t. 19: 1838) made no reference to Wallich or his collection, but remarked that *A. emodi* was "a still finer species found (on the Emodi Mountains) near Sirinuggur (Srinagar) and on the Suen range of hills with much larger and more numerous flowers, a more robust foliage and more considerable stature". That much of this does not apply to *I. emodi* as at present understood, may be explained if one bears in mind the mixture of Blinkworth's specimens under Wallich's 487. Thus, although incorrect and fragmentary, Lindley's description is nevertheless the first accredited one and the specimen in his herbarium at Cambridge is here regarded as the holotype. (The author is indebted to Dr. P. D. Sell for examining this specimen.)

Incarvillea Subgenus **Incarvillea**

Syn.: *Incarvillea* Subgen. *Euincarvillea* Baillon, Hist. des Pl. x, 52 (1888); K. Schumann in Engler & Prantl, Nat. Pflanzenfam. IV: 3b.; 232 (1897); Regel in Gartenflora 49: 450 (1900).

Incarvillea (pro genus) Juss. Gen. 138 (1789); Don, Gen. Syst. iv, 665 (1837): Fenzl in Denkschr. Regensb. Ges. iii, 225 (1837); Endl. Gen. Pl. 710 (1837); Meissner, Gen. Pl. Vasc. Comm. 302 (1843); De Candolle, Prod. ix, 237 (1845); Orb. Dict. Univ. d'hist. Nat. vii, 28 (1849); Bureau, Monogr. des Bignoniac. 1864); Benth. & Hook. f. Gen. Pl. ii, 1049 (1876).

Annual or perennial herbs, often becoming woody at the base. *Leaves* opposite or alternate, pinnate, pinnatisect or bipinnatisect. *Inflorescence* terminal, panicle or simple raceme. *Calyx* tube campanulate, teeth swollen at the base, subulate or reduced to minute points, sinuses membranous drawn up into bifid teeth, thus calyces appear to be ten toothed (see fig. 8, D). *Capsules* coriacious, cylindrical, acuminate at the apex, dehiscing longitudinally on the posterior side only. *Septum* entire at the apex. *Seed* wing hyaline, entire.

In literature from Jussieu's time up till 1888 when Baillon described the subgenus *Pteroscleris*, *Incarvillea* referred to this, the type subgenus, only; such descriptions do not apply to the genus as understood today, the ten-toothed calyx, the siliquaeform capsule and membranous seed-wings are characters only of this subgenus.

Two of the species belonging to this subgenus are confined to what appear to be relic stations while the third is widely distributed and ranges further than any other species of *Incarvillea.*

Key to the species of subgenus Incarvillea

1. Inflorescence a racemose panicle. Calyx cup-shaped almost without teeth. Leaves opposite throughout . . . 3. *I. olgae*
   Inflorescence a simple raceme. Calyx distinctly toothed, sinuses elongated into bifid teeth. Leaves not opposite throughout . . 2

2. Leaves aggregated at the base of stems, simply pinnatisect 4. *I. potaninii*
   Leaves not aggregated at the base of stems, bipinnatisect 5. *I. sinensis*

3. **Incarvillea olgae** Regel in Gartenflora xxix, 3, t. 1001 (1880) et xxx, 377 (1881); Pl. Nov. Fedtsch. 62 (1882); Nicholson, Illust. Gard. Dict. ii, 181 (1886); Lubbock, Seedlings ii, 342 (1892); Regel, in Gartenflora xlix, 450 (1900); Fedtsch., Veg. Turkestan 700 (1915); L. H. Bailey, Stand. Cycl. Hort. iii, 1645 (1917); L. H. & E. Z. Bailey, Hort. Sec. 382 (1941); L. H. Bailey, Man. Cult. Pl. 905 (1949); Vassilczenko, Flora U.S.S.R. xxiii, 3 (1958).

Syn.: *I. koopmanni* W. Lauche in Deutsch. Gart. 39 et tab. (1880); Gard. Chron. 725 (1880); Hook. f., in Bot. Mag. t. 6593 (1881); Bull. Soc. Tosc. Ortic. vi, 279 (1881).

Erect, perennial herb 75–100 cm. high, glabrous, somewhat woody at the base up to 8 mm. thick. *Leaves* cauline, opposite, pinnate 5–15 cm. long; lateral leaflets 3–4 pairs 3–6 cm. long, 0·4–1·3 cm. broad, narrowly elliptic, apiculate at the apex, cuneate at the base (the upper ones decurrent on the rachis), margins entire or with 1–2 pairs of teeth, lower leaflets with a vein arising independently from the rachis and running parallel to the midrib, terminal leaflet similar in shape to the lateral ones 3–5 cm. long, 5–8 mm. broad, distinct or confluent with the uppermost pair of lateral leaflets (see fig. 7, C). *Inflorescence* racemose-paniculate, 3–10 flowers per branch; pedicels 0·5–1 cm. long subtended by an elliptic bract 5 mm. long with two linear bracteoles close above it. *Calyx* tube campanulate 4–5 mm. long; teeth minute; plicae membranous simple (see fig. 8, A). *Corolla* rose (rarely white), tube 2·7–3·5 cm. long, glandular hairs present at the base within; lobes rounded 0·5–0·9 cm. long, 1–1·3 cm. broad. *Staminode* 2–3 mm. long, crozierform. *Capsule* terete 4·5–7·5(–9) cm. long 0·5–0·6 cm. broad, acuminate at the apex. *Seeds* ovate, 3·5 mm. long 1·5 mm. broad; wing whitish, hyaline, 1·5 mm. broad at the sides, 3 mm. broad at base and apex.

HABITAT. Clayey or stony ground in river valleys and on adjacent slopes.

TURKESTAN. Inter Soch et Ochna, 30 June 1871, *O. Fedtschenko* s.n. (Holo. LE, iso. P.); Sudseite des Pahschif Passes, oberhalb Torifin, Karategin, 2740 m., 11 Aug. 1881, *Regel* s.n. (LE, K, US); Shignan prov., on the river Pyandzh between the mouth of the river Gunt and the valley of the Sochar, *Korshinsky* 3367 (US); Vallis fl. Chingou apud Tavildara, in glareosis, *Gonczarov*, *Grigorjev* et *Nikitin* 3490 (K, GH, US); valley of the Kafironigan river, *Rusanov* 24 (K, GH); fl. Pjandsh supra pagum Siz et fl. Ob-i-mazar pagum Songvar, *Rajkova* 445 (E, P).

BOKHARA. Hissar, 2050 m., *Lipsky* 1117 (LE, BM).

AFGHANISTAN. Faizabad, 17 June 1878, *Newssky* s.n. (LE); Sarn-Kotal, Hindu Kush, 2 Oct. 1924 (Vavilov Expedn.) *Bukinich* s.n. (LE); Kabul prov.: Salanga River, 30 Sept. 1924, *Bukinich* s.n. (LE).

This species has three unique characters each of which keeps it distinct from all other members of the genus. The leaves, which in other species are alternate or, as in *I. sinensis*, opposite at the base of the stem or branches and alternate above, are here oppositely arranged throughout. Its inflorescence while still preserving the racemose arrangement of flowers which is characteristic of the genus, is paniculate, not simple. The calyx, normally campanulate with prominent teeth, is here reduced to a short cup with only minute points projecting from the lip (see fig. 8, A).

The first records of this species in cultivation came in 1880, the year in which it was described, when it appears that seedlings from two different sources were being grown. Regel saw only immature plants consequently this description was based on dried and imperfect material for, according to him, the species was biennial and was characterised by its punctiform stigma. The young plants which he saw were raised from seed sent by General-Major Korolkow and were grown by Lauche at Potsdam and Leichtlin at Baden-Baden. Lauche, however, also received seed from his son-in-law, Koopmann, at Margilan near Taschkend. Plants from this seed flowered in 1880 and, without reference to Regel, he described them himself as *I. koopmanni* differentiating this species from *I. olgae* by its larger flowers, curved corolla tubes and two-lipped stigmas; observations which might be expected to arise from a comparison of good cultivated with indifferent wild material.

In November of the following year the Botanical Magazine (t. 6593) figured *I. koopmanni* and Hooker wrote of it 'I retain it as a species distinct from *I. olgae* with great hesitation suspecting it to be a luxuriant state of that plant'. In the same month Regel published a statement in Gartenflora pointing out that the two were synonymous and that although Leichtlin had found the species to be monocarpic it appeared to be a hardy perennial at Leningrad but remained unflowered there. A letter from Regel to this effect, and prompted perhaps by Hooker's article, is preserved in the Kew Herbarium.

4. **Incarvillea potaninii** Batalin in Acta Hort. Petrop. xi, 492 (1892) et xiv, 179 (1895).

Erect perennial herb up to 25 cm. high, fibrously woody at the base, up to 8 mm. thick, branched. *Stem* branched glabrous, striate, somewhat flexuose. *Leaves* often clustered at the base of stems, alternate, glabrous 6–10·5 cm. long, segments 3–7, pinnate below, pinnatifid above, decreasing in size upwards, subopposite or alternate, up to 2 cm. long 0·5–1 cm. broad, ovate or elliptic, margins narrowly revolute, irregularly toothed or lobed or sometimes pinnatifid, cuneate or decurrent at the base, apiculate at the apex, terminal segment similar to the lateral ones (see fig. 7, F). *Inflorescence* terminal, racemose, 3–6 flowered; pedicels 0·5–2 cm. long subtended by an obovate bract 8 mm. long, apiculate at the apex, with two smaller bracteoles in its axil (thus appearing as if a tripartite bract). *Calyx* campanulate glabrous; tube 5–6 mm. long; teeth subulate 4–5 mm. long, swollen at the base; plicae membranous simple or 1 mm. long and bifid at the apex (see fig. 8, C). *Corolla* rose, tube 3·5–4·5 cm. long, with scattered subsessile glandular hairs at the base within; lobes rounded, 1·2 cm. long 1·7 cm. broad, margins ciliate. *Staminode* c. 1 cm. long swollen at the apex. *Capsule* straw-coloured, cylindrical, acuminate at the apex, 5–6 cm. long 0·6 cm. broad. *Seeds* ovate to suborbicular, 4·5 mm. long 2·5 mm. broad; wing hyaline 1·5–2 mm. broad.

HABITAT. Stony mountain slopes.

MONGOLIA. Gobi, Kobden-usu inter lacum Gaschium-nor et Montes Tostu, 13 Aug. 1886, *Potanin* s.n. (Holo. LE); fons Udshiim in rupibus, 16 Aug. 1886, *Potanin* s.n. (K, P, GH); vallis inter montes Nemegetu et Zomzo, 20 Aug. 1886, *Potanin* s.n. (US); between Noyan and Bogdo-ula,

Unatov 13880 (LE); Khobdo, *Grubov* 6086 (LE); Khushu-ulu (?), *Grubov* 7037 (LE).

The leaves of this plant often appear to be clustered around the base of the stem, but the stem proper is short here, 2–5(–8) cm., and passes gradually into the peduncle. In this respect, the species is similar to *I. emodi* in the subgenus *Amphicome*. Its closest affinities, however, are with *I. sinensis* the calyx of which is almost identical although the teeth of the latter are frequently longer and finer. Its leaves, like those of *I. olgae*, are more coarsely divided than they are in *I. sinensis*, but both these species have well developed leafy stems. The seed wings are somewhat narrower than those of *I. olgae*, but the seeds themselves are correspondingly larger.

From its present known localities, it appears to be endemic to this barren, little explored region of the Mongolian Altai where it is isolated from the rest of the genus. Spatially, *I. compacta* is closest in the Richthofen Range in Kansu, 400 miles distant, and *I. sinensis*, at its nearest, approaches to within 500 miles in the Mongolian Ordos. There is little doubt that the species has occupied its present site at least since the Pleistocene period and, with the subsequent amelioration of climate, has been unable to spread from it due to the lack of suitable habitats.

Unfortunately, there is no record of this species in cultivation.

5. **Incarvillea sinensis** Lam. Encycl. iii: 243 (1789); Ill. Gen. ii, t. 527 (1794).

An erect annual or perennial herb often woody at the base, puberulent especially above. *Stem* terete striate 15–50(–85) cm. high. *Leaves* bipinnatisect or occasionally tripinnatisect 4–12(–16·5) cm. long, opposite at the base of stem or branch alternate above, glabrous or puberulent beneath, primary segments 4–7 pairs, 5–8(–8·5) cm. long, the lower ones divided again into 2–3 pairs of linear or linear-lanceolate, acute segments 0·2–1·5 cm. long 1·5–3(–4·5) mm. broad (see fig. 7, D). *Inflorescence* racemose, 4–18 flowered; pedicels up to 1 cm. long subtended by a narrowly elliptical subulate bract 0·5–1 cm. long with two oppositely arranged bracteoles of similar size and shape inserted immediately above it. *Calyx* tube campanulate, 2·5–4 mm. long; teeth subulate puberulent, 4–10 mm. long swollen at their bases; plicae membranous 0·5–1 mm. long bifid at the apex (see fig. 8, D). *Corolla* tube 1·9–3·9 cm. long, glandular pubescent at the base within; lobes rounded or emarginate 4–10 mm. long 0·8–1·3 cm. broad. *Staminode* short or absent. *Capsule* terete, 3·8–11 cm. long 3·5–7 mm. broad, acuminate and curved at the apex. *Seeds* ovate, plano-convex 2·5 mm. long 1·5 mm. broad surrounded by a white or yellowish hyaline wing 1–2 mm. broad, entire or irregularly split.

I. sinensis is unique in the genus on account of its bipinnatisect leaves. It is divided into two subspecies.

Annual herbs with simple ± unbranched roots. Calyx teeth 5·5–10 mm. long. Corolla red or reddish-purple. Capsules 6–11 cm. long. Seed wings 1·5–2 mm. broad . . . . . 5a. subsp. *sinensis*

Perennial herbs with woody branched roots often bearing remains of previous years stems; calyx teeth 3·5–5(–7) mm. long. Corolla pale rose or rose-pink. Capsules 4–5·5 cm. long. Seed wings 1–1·5 mm. broad . . . . . 5b. subsp. *variabilis*

5a. subsp. **sinensis**

Syn.: *I. sinensis* Lam. Encycl. iii, 243, (1789); Ill. Gen. ii, t. 527 (1794); Bunge, Enum. Chin. Pl. 45 (1834) et Mem. Acad. Imp. Sci. St. Petersb. 11: 120 (1835); G. Don, Gen. Syst. iv, 665 (1837); De Candolle, Prod. ix, 237 (1845); Bureau, Monogr. Bignoniac. t. 23 (1864) and Bull. Herb. Boiss. Sér. II, vii, 96 (1908); Franch., Pl. David. 229 (1884); Forbes & Hemsley in Jour. Linn. Soc. xxvi, 236 (1890); Batalin in Acta Hort. Petrop. xiv, 178 (1895); Regel in Gartenflora xlix, 449 (1900); Palibin (Fl. Kwantung Penins.) in Acta Hort. Petrop. xxi, 227 (1903); Komarov (Fl. Manchuriae) in Acta Hort. Petrop. xxv, 46 (1907); Vilmorin, Fl. de pleine terre 524 (1909); Sato, Wild Fls. Manch. & Mongol. 58 (1927); Hand.-Mazz., Symb. Sinicae vii, 888 (1936); R.H.S. Dict. Gard. ii, 1049 (1951); Vassilczenko in Komarov, Fl. U.S.S.R. xxiii, 4 (1958).

I. chinensis Poir. Dict. Sci. Nat. xxiii, 52 (1823), non *I. chinensis* Spr. Syst. ii, 836 (1825) (= *Campsis adrepens*).

HABITAT. Growing in hills and plains in sandy soils of fields and waste places and on top of the Tartar Wall around Peking.

CHIHLI. Peking and environs: *d'Incarville* s.n. (holo. P., non vidi); *Bodinier* s.n., Aug. 1888, (E, P) Sept. 1888 (E); *Bretschneider* 1881 s.n. (GH); *Dorsett & Morse* 5575 (GH, US); *A. David*, July 1865, s.n. (P), 462 (P); *S. W. Williams*, Aug. 1876, s.n. (GH); *Meyer* 1014 (GH); Tang-ho, *Clemens* 4102 (E), 4102a (E); Ting Tcheon, *Chanet* 587 (E); Sulu hsien, *Beach* 29 (US); Patachou, *Sheehan* 42 (US); vallis fluv. Sha-le, *Potanin* s.n., June 1884 (P, K).

SHANTUNG. Meng Shan, Fei-hsien, *T. Y. Cheo & L. Yen* 117 (P, GH, BM).

MONGOLIA. Chahar Prov. near Kalgan, *Kozlov* 33 (US); Si-tai-pin Shan Mts., *Kozlov* 207 (US); Suiyuan, Wusutu, Ta Ching Shan, *Martin & Soderbom*, 18 Aug. 1938, s.n. (GH); environs de Gehol, 42° lat. N., *David* 2089 (P); planities circa Kuku-hoto prope oppid. Tu-tseum, 2 Aug. 1884, *Potanin* s.n. (P, K, LE).

MANCHURIA. Harbin, 4 Aug. 1937, *Skvortzov* s.n. (GH).

SHANSI. Tsiliyu ad montem Ho-Schan, 1600–2100 m., *Licent* 12343 (P, GH); Makia pou, *Licent* 224 (P, K, BM), 393 (P, K); Plaine de Toumet, Chen-hoai-ze, *Licent* 5615 (P); W. of Lungchuan Tsun, Wenshui, *Kang* 21 (GH); Tung Tsa, *Lee* 6100 (US).

SHENSI. Litsiuen, *Pelliot-Vaillant* 1122 (P).

KANSU. Vicinity of Lichen, Ping-Fan, 1750–2050 m. *R. C. Ching* 288 (US).

5b. subsp. **variabilis** (Batalin) Grierson, **comb. nov.**

Syn.: *I. variabilis* Batalin in Acta Hort. Petrop. xii, 177 (1892), and xiv, 180 (1895); Haage & Schmidt in Gartenflora xlvii, 222 (1898); Hook. f. in Bot. Mag. t. 7651 (1899); Regel in Gartenflora xlix, 450 (1900); Vilmorin, Fl. de Pleine Terre 525 (1909); L. M. Bailey, Stand. Cycl. Hort. iii, 1645 (1917); Gard. Chron. Ser. III, lxiv, 184 (1918); Wehrhahn, Die Gartenstauden ii, 946 (1931); L. H. & E. Z. Bailey, Hort. Sec. 382 (1941);

L. H. Bailey, Man. Cult. Pl. 905 (1949); R.H.S. Dict. Gard. ii, 1049 (1951) and Suppl. 246 (1956).

I. variabilis Batalin var. *latifolia* Batalin l.c.

I. variabilis Batalin var. *fumariaefolia* Batalin l.c.

HABITAT. Roadsides and dry stony pastures in open situations.

SHANSI. Si Loan ts'oun, *Licent* 3027 (P, K, BM).

KANSU. Tien Tang Ssu, 9000 ft., *Farrer* 595 (E); prope oppid. Sigu, 23 June 1885. *Potanin* s.n. (iso. var. *fumariaefolia*, P, K); ad fl. Gtel-gol, June-Aug. 1885, *Potanin* s.n. (LE); prope pagum Shun-dan-sien, 7 Sept. 1885, *Potanin* s.n. (iso. var. *latifolia*, P); vers Ta la tch'e, *Licent* 4041 (P); Lan tcheon, *Licent* 4446 (P, K, BM); San chen li p'on, *Licent* 6199 (P, K); 288 (W).

SZECHUAN. Li fan fu, 17 Aug. 1893, *Potanin* s.n. (P, K, LE); ad fluv. Poi-ho, 11 July 1885, *Potanin* s.n. (holo. LE non vidi, iso. K, P); Tatsien-lu, 2440–4080 m. *W. P Fang* 3712 (GH, US, E, K); Sungpan-hsien, *W. P. Fang* 4455 (GH, US, P, E); descending to Mao kung, 3400–3000 m., *F. T. Wang* 21275 (GH).

YUNNAN. Doker-la, 27°11′N., 2050 m., *Handel-Mazzetti* 7980 (E); Chungtien Plateau, lat. 27°30′N., 3048–3350 m., *Forrest* 12800 (E); Bei ma shan, lat. 28°12′N., 3350 m., *Forrest* 14552 (E, K), *Rock* 9935 (GH, W).

S.E. TIBET. Tsarong, Salwin Kui-chiang divide, lat. 28°40′N., long. 98°15′E. *Forrest* 19038 (E, K, BM).

Batalin (l.c.) had only a limited quantity of material before him which he was able to arrange into four varieties. On examining a larger suite of specimens, however, it becomes apparent that the characters which he used to differentiate them (indumentum, shape of leaf segment and proportions of the calyx) are uncorrelated and occur at random. These varieties are therefore considered to be untenable. Hooker was not able to identify precisely the plant figured in Bot. Mag. t. 7651 with any one of them.

Only the variety *przewalskii* requires further comment. It was differentiated as having yellow flowers with densely puberulent and narrow leaf segments. But *Rock* 13245, which in other respects clearly belongs to this group, has broadish, almost glabrous leaf segments and yellow flowers. In the same way, *Farrer* 97 has narrow subglabrous segments but cultivated specimens from seed of this number have broader leaf segments than the parent plant. Because of these differences, according to Gard. Chron. (9 Nov. 1918), and "for the sake of distinction in gardens," Mr. W.W. Smith gave the name *Incarvillea variabilis* var. *farreri* to Mr. Farrer's plant. This variety appears in horticultural literature (e.g. L. H. & E. Z. Bailey, Hortus Second 382 : 1956) and is confused there as a yellow flowered form of *I. delavayi* (of which there is none).

It must be acknowledged, therefore, that *I. variabilis* is polymorphic and that the varieties which Batalin created must be regarded as forms only two of which need be recognized:

forma **variabilis** the polymorphic pink-flowered plant which is widespread in Western China to which the foregoing specimens belong.

forma **przewalskii** (Batalin) **nov. comb.** (Syn. *I. variabilis* var. *przewalskii* Batalin l.c.; *I. variabilis* var. *farreri* W.W.Sm. in Gard. Chron. Ser. III, lxiv, 184. 9 Nov. 1918) the yellow-flowered plant variable in leaf shape and

indumentum which is confined to Kansu and Shensi. To this the following specimens belong:

SHENSI. Da Loung Chan, 2200 m., *Pelliot-Vaillant* 1080 (P), 1082 (P).

KANSU. Tetung australe, 7500 ft., 27 July 1880, *Przewalsky* s.n. (K, syntype of var. *przewalskii* Batal.); Hsining River beyond Hsiang tang, 8000 ft., *Rock* 13245 (E, K); Siku, *Farrer* 97 (E): Hsia Mo K'ou near Lichen, 2000–2300 m., *R. C. Ching* 324 (US).

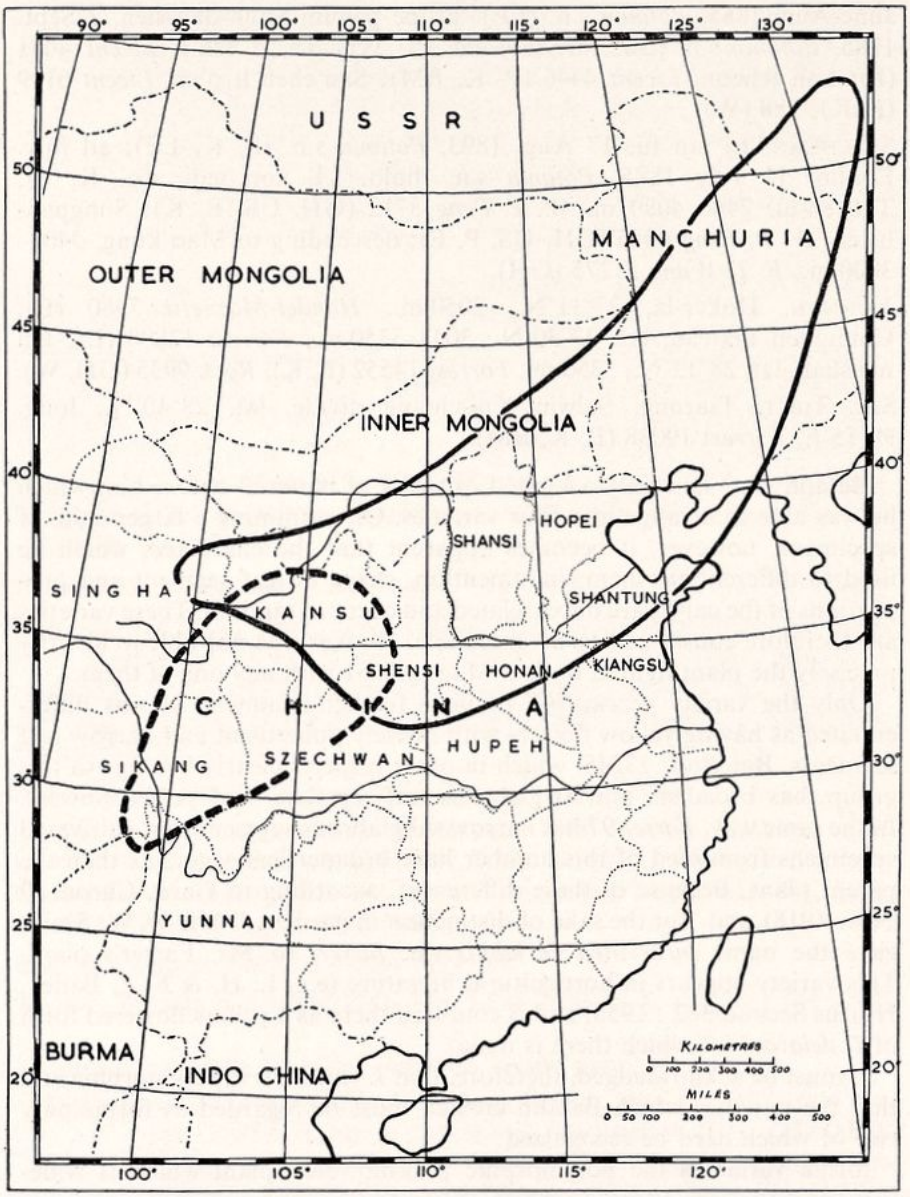

FIG. 9. Distribution of *Incarvillea sinensis*.
subsp. *sinensis* ————
subsp. *variabilis* – – – – – –

Batalin cites three other syntypes in the Leningrad herbarium which have not been examined:

SHENSI: prope oppidum Mien, 22 May 1875, *Piasezky* s.n.

KANSU: prope oppidum Tsin, 3 June 1875, *Piasezky* s.n.; jugum Tetung boreali, 1 Aug. 1880, *Przewalsky* s.n.

Hooker (l.c.) pointed out that the corolla tube is longer in subsp. *variabilis* but this is not strictly correct. In subsp. *sinensis* it normally measures 2·5 cm. long and in specimens of subsp. *variabilis* from Kansu and Szechuan it averages 3·5 cm. long but in Yunnan 2·5 cm. is the commonest length. In other respects, however, the Yunnanese specimens are typical of this subspecies.

As is shown in the map (fig. 9) subsp. *sinensis* has its main distribution in eastern China and Manchuria and extends westwards as far as Kansu and Shensi where it overlaps the range of subsp. *variabilis*. The few recorded altitudes in respect of subsp. *sinensis* show it to be a native of the plains and hills up to 2100 m. In subsp. *variabilis*, however, none come from stations below 2000 m. and 3350 m. appears to be its maximum altitude. Whereas the former subspecies appears to belong to the plains and hills, the latter belongs to the mountain (although not truly alpine) floras.

Urban (Ber. Deutsch. Gart. Gesell. xxxiv: 754. 1916) noted that the pollen grains of subsp. *sinensis* had 6–7 colpae whereas those of subsp. *variabilis* had 8. On examining several samples of pollen, however, this difference was not found to be constant. In both subspecies grains with 7–8 colpae were found although rare grains with 6 and 9 colpae were seen.

Rohrhofer (Öst. Bot. Zeit. lxxx: 5, 1931) found that the staminode in *I. sinensis* was either a small hook-like structure or represented by a minute swelling in the throat of the corolla (l.c. t. 5 fig. 6–8). The illustration in Bureau's Monograph (1868) where the staminode is figured as a straight filiform structure half as long as the shortest stamens is inaccurate. The statement by Hooker that the staminode is always completely absent in subsp. *variabilis* is certainly untrue. Hook-like staminodes are present in the flowers of *Potanin* s.n. (7 Sept. 1885), the type of Batalin's *I. variabilis* var. *latifolia*. A survey of the species in respect of these vestiges might prove rewarding but good corollas are all too scarce in herbarium material and mostly glued to the sheets.

I. sinensis has, of course, the longest history in cultivation of any of the species of this genus through the efforts of Pierre Nicholas Le Cheron or d'Incarville as he called himself to distinguish him from his two brothers (see Fournier, Voyage des Missionaires français 79–83. 1932 also Franchet in Bull. Soc. Bot. Fr. xxix, 2–13, 1882 and F. B. Forbes in Jour. Bot. xxi, 9–15, 1883). He and others of the French missionary fraternity sent seed to Paris. It is unlikely that seeds of subsp. *variabilis* were included in their packages and the introduction of this subspecies is ascribed to Potanin.

Today it is not a widely cultivated species. *I. sinensis* (i.e. subsp. *sinensis*) does not appear in any of the recent catalogues but subsp. *variabilis* is advertised by a few. If the samples tried at Edinburgh are characteristic, their flowers are not clear pink as shown in Bot. Mag. 7651 but an uninteresting creamy pink. It is grown as an annual but will overwinter if brought indoors.

According to Bretschneider (Jour. Roy. As. Soc. xvi, 51, 1881) *I. sinensis*

is listed by Chou Ting Wang in his Kui Huang Pen ts'ao written at the beginning of the fifteenth century A.D. This is a treatise on plants fit for supporting life in times of scarcity; the leaves may be included in the starvation diet. This species is said to have been mentioned in the *materia medica* of the semi-mythical emperor Shen-nung of the twenty-eighth century B.C. but no original copy of the latter's work is extant, nor was one seen by any of the authorities who came after him. Laufer (Sino-Iranica, Field Mus. Nat. Hist. xv, 548, 1919) states that the text in which we have it at present is "a reconstruction based on quotations and teems with interpolations and anachronisms".

Incarvillea subgenus **Pteroscleris** Baillon, Hist. des Pl. x, 52 (1888); K. Schumann in Engler & Prantl, Nat. Pflanzenfam. iv; Abt. 3b: 232 (1897); Regel in Gartenflora xlix, 450 (1900).

Perennial herbs, acaulous or with erect stems up to 2 m. high. *Rootstock* often fleshy, branched, the upper parts covered with foliar remains. *Stems* absent of cylindrical, striate, usually puberulent at least above. *Leaves* alternate, undivided, pinnate or pinnatisect; rachis ± cylindrical, grooved on upper surface, usually puberulent; lateral leaflets 0–11 pairs confined to upper part of rachis, ovate or elliptic, rounded, cuneate or cordate at the base, acute or obtuse at the apex, margins entire or crenate-serrate, puberulent especially on the veins; terminal leaflet (or lamina in entire leaved plants) ovate to orbicular. *Inflorescence* terminal (sometimes also axillary) one flowered or few—many flowered raceme; pedicels short subtended by a bract and bearing two smaller bracteoles. *Calyx* tube campanulate usually strongly ribbed; teeth lanceolate or triangular often folded, acute or obtuse at the apex. *Corolla* tube 4–6 cm. long; lobes 1·5–2 cm. long 1·5–3·5 cm. broad, covered with shortly stalked glands. *Capsules* ligno-coriaceous, elongate, straight or curved, ± quadrangular, acute or acuminate at the apex, dehiscing longitudinally on both surfaces but only in the upper third on the anterior surface. *Septum* entire at the apex. *Seeds* ovate, plano-convex; wing opaque, narrow, entire or notched or reduced to a rim.

Type species: *Incarvillea delavayi* Bur. et Franch.

The eight species belonging to this subgenus are distributed in the mountainous region of Western China with two species, *I. mairei* and *I. lutea*, extending from there along the Himalayan range into Southern Tibet and a third, *I. younghusbandii*, confined to the Tibetan Plateau.

The subgenus is based primarily on the fruit characters and the species are most easily recognized by the somewhat woody capsules, the valves of which separate along their entire length on the posterior surface, but only at the apex on the anterior (see fig. 1, A & D). The seeds while being covered by an opaque testa, as are those of *Niedzwedzkia*, have a clearly developed wing, similarly opaque. Vegetatively, their leaves are membranous in texture and entire or pinnately, never bipinnately, divided. The calyx tube is usually distinctly ribbed and its teeth broad but lightly folded along their length. The corolla is normally larger than in other subgenera.

As may be seen in most herbarium specimens the roots of *I. mairei compacta*, *younghusbandii* and *delavayi* are tuberous, but in *I. lutea* and other tall growing species with well developed underground parts which penetrate deeply into the soil, the roots are seldom well collected except

in the rare, more complete specimens where the looseness of the outer tissues indicates a fleshy nature. Thus probably all the species belonging to the subgenus *Pteroscleris* are tuberous-rooted although old roots often show considerable development of brittle, woody tissue. In the other subgenera there is no evidence of tuber formation and their underground parts may be strongly woody. This is especially the case in *I. sinensis* ssp. *variabilis* and in *I. olgae*.

The roots of seedlings of *I. delavayi* were investigated by Rimbach (Deutsch. Bot. Gesell. xxxix, 288–290: 1921) who found that there was a seasonal fluctuation in the size of the cortex. This, from the thick turgid condition of the autumnal root, diminished, with the burgeoning of spring

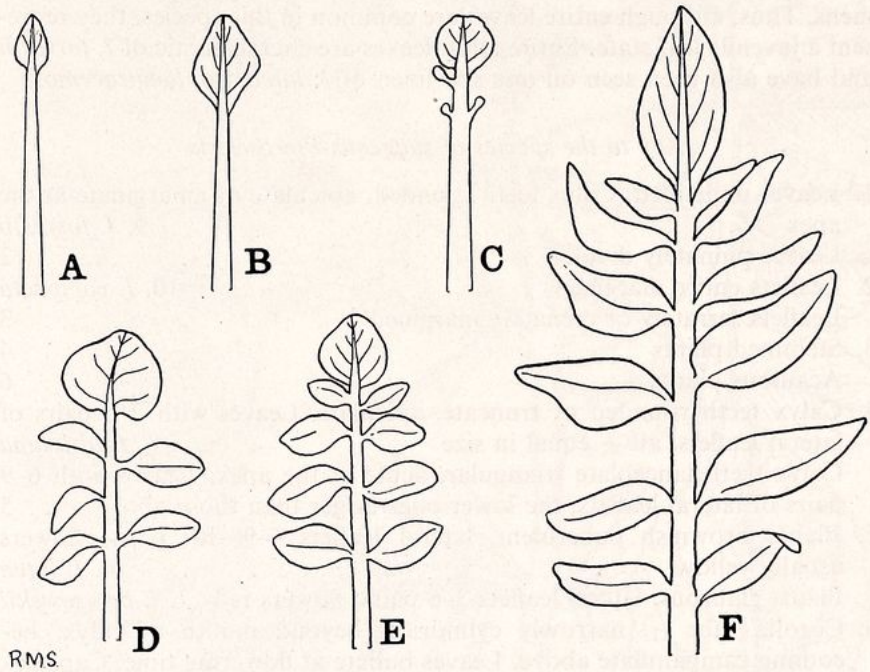

FIG. 10. Succession of leaf form in *I. compacta* (× 1).
A & B single juvenile leaves. C, D, & E, intermediate leaves. F, adult leaf.

and consequent depletion of the food materials, to a skin of flaccid cells around the stele. This factor may explain the absence of fleshiness in roots of some flowered herbarium specimens. Two months after this collapse a new cortex was laid down in preparation for the following season. Rimbach was unable to state which food materials were expended except to point out that it was not starch. Microchemical tests now reveal that inulin is the principal carbohydrate stored.

The lateral leaflets number from 1 to 12 pairs and, although compound leaves are often notoriously variable, the number of leaflets is, within certain limits, constant in each particular species. In *I. compacta* and *I. mairei*, however, juvenile leaves and cataphylls are usually present. The latter occur in several species belonging to the subgenus *Pteroscleris*, but more particularly in the acaulous species, where they are developed around the root stock or at the base of the stem. Normally they are ligulate in

outline, elaminate and about 2 cm. long, but others may develop a cap of photosynthetic tissue and resemble the cotyledons. From this condition they merge gradually with the juvenile leaves and the succession from juvenile to adult leaf form is often apparent in flowering specimens. The first and second leaves to appear in spring are entire, without lateral leaflets, the third may have 2–3 pairs of leaflets, the fourth and fifth add another pair and finally, in the sixth and seventh, the adult number is attained (see fig. 10). *I mairei* may reach flowering condition without developing lateral leaflets or only with rudimentary ones. This phenomenon must to some extent be governed by the age and size of the plant but genetical and environmental factors may also be operative. The leaves of other species may behave similarly but it has not been observed from herbarium specimens. Thus, although entire leaves are common in this species, they represent a juvenile leaf state. Entire adult leaves are characteristic of *I. forrestii* and have also been seen on one specimen of *I. lutea* ssp. *longiracemosa*.

Key to the species of subgenus Pteroscleris

1. Leaves undivided. Calyx teeth rounded, apiculate or emarginate at the apex . . . . . 9. *I. forrestii*
   Leaves pinnately divided 2
2. Leaflets entire margined . . . . . 10. *I. compacta*
   Leaflets serrately or crenately margined 3
3. Stemmed plants 4
   Acaulous plants 6
4. Calyx teeth rounded or truncate, apiculate. Leaves with 2–3 pairs of lateral leaflets, all ± equal in size . . . 8. *I. altissima*
   Calyx teeth lanceolate triangular, acute at the apex. Leaves with 6–9 pairs of lateral leaflets, the lower ones larger than those above . 5
5. Plants brownish puberulent, lateral leaflets 6–9(–10) pairs, flowers usually yellow . . . . . 6. *I. lutea*
   Plants glabrous, lateral leaflets 3–6 pairs, flowers red 7. *I. beresowskii*
6. Corolla tube ± narrowly cylindrical beyond mouth of calyx, becoming campanulate above. Leaves bullate at flowering time. Capsules crescentic. Dwarf Tibetan plants . . 12. *I. younghusbandii*
   Corolla tube campanulate from mouth of calyx. Leaves ± smooth at flowering time. Capsules curved or straight 7
7. Lateral leaflets 4(–7) pairs. Terminal leaflet (1·2–)2·5–5(–8·5) cm. broad, usually distinct from uppermost lateral leaflets which are without a second main vein parallel to the midrib. Calyx teeth longer than broad at the base . . . . . 11. *I. mairei*

   Lateral leaflets 4–11 pairs. Terminal leaflet 0·9–2·5 cm. broad, usually confluent with uppermost pair of lateral leaflets which have a second main vein parallel to the midrib. Calyx teeth broader at the base than long . . . . . 13. *I. delavayi*

6. **Incarvillea lutea** Bur. et Franch. in Journ. de Bot. v, 137 (1891).

Erect perennial herb (8–)25–100(–130) cm. high, generally greyish-brown puberulent. Rootstock fleshy, little branched, 1–2 cm. broad, in the upper part scaly with foliar remains. *Leaves* cauline (radical leaves only

FIG. 11. Leaves in *Incarvillea* subgenus *Pteroscleris* (× 2/3).
A, *I. lutea;* B, *I. lutea* subsp. *longiracemosa;* C, *I. altissima;* D, *I. delavayi;* E, *I. younghusbandii;* F, *I. mairei.*

rarely present), alternate, pinnate below, pinnatifid above, 10–30(–40) cm. long; lateral leaflets (0–)6–9(–10) pairs, (1·5–)2–8 cm. long 0·6–2·3(–3·6) cm. broad, narrowly ovate or elliptic, cuneate at the base, obtuse or acute at the apex, margins entire, crenate or serrate, puberulent on the veins especially beneath, upper leaflets frequently incompletely divided from the rachis and with a second main vein parallel to the midrib; terminal leaflet 2·3–5(–9·5) cm. long 0·6–2(–5·5) cm. broad, elliptic, cuneate at the base or confluent with the uppermost pair of lateral leaflets (see fig. 11, A). *Inflorescence* terminal, 6–12 flowered raceme and often with smaller axillary inflorescences; pedicels 5–10 mm. long subtended by a linear-lanceolate bract 1–2 cm. long and bearing two bracteoles 4–6 mm. long. *Calyx* campanulate, tube (1·2–)1·4–1·7(–1·9) cm. long often with scattered black spots; teeth ovate (4–)6–7(–9) mm. long (5–)7–8(–10) mm. broad. *Corolla* pale yellow sometimes of a greenish hue with brown or crimson spots and streaks in the throat, but yellowish-red (*Wang* 70733) and red specimens (*Wang* 70897) have been found; tube (4–)4·5–5(–5·5) cm. long; lobes 1·5–2 cm. long 2–3 cm. broad, rounded or emarginate at the apex, covered with shortly stalked glands. *Staminode* a short point c. 1 mm. long. *Capsule* 6–9·5 cm. long 0·7–1·3 cm. broad, roughly quadrangular 4- or 6-ribbed, acuminate at the apex, curved towards the anterior surface. *Seeds* ovate or orbicular, plano-convex, 4–4·5 mm. long 3–4·5 mm. broad, yellowish brown, often glossy above, greyish puberulent beneath; wing 1 mm. broad.

I. lutea was, as its name suggests, described as having yellow flowers and the view that this colour is invariable appears to have become rooted. An analysis of collectors notes, however, reveals that this belief is fallacious; specimens with yellow tinged with green, reddish yellow, pale yellow more or less blotched, spotted and streaked inside and out with brownish crimson (*Ward* 4197) and even red flowers have been collected. These specimens match the type material except in flower colour, and red and yellowish red specimens have been collected from the "*locus classicus*" itself. Thus, the flower colour is variable and, although usually yellow, may contain differing amounts of red pigment. Unfortunately, there has been no attempt at an accurate definition of the latter but it appears to be a brownish-crimson, blood red rather than the magenta pink of *I. delavayi*, *altissima*, etc.

Bureau and Franchet point to the greyish-brown puberulence as being characteristic and, in typical examples, it marks out the course of the veins on the leaf and is generally present on the rachises, stems, etc. providing a ready means of identifying fruiting material of this species. When a wide range of specimens is studied, however, the expression of this character is seen to be variable, but, although it may become sparse, e.g. in subsp. *longiracemosa*, it is always present.

I. lutea, therefore, is now defined as a stemmed species up to 2 m. in height, with leaves bearing in most cases 6–9 pairs of leaflets which are usually distinctly greyish brown puberulent, and having flowers normally yellow in colour, but sometimes containing varying amounts of red pigment. The above characters as well as the capsule shape distinguish it from *I. beresowskii*. From *I. altissima* and *I. forrestii*, the other two stemmed species of the subgenus *Pteroscleris*, it is distinguished by its more divided leaves and longer ovate-triangular calyx teeth. Confusion with extreme

forms of the caulescent *I. compacta* is also impossible because the leaves of *I. lutea* are always crenate serrate.

The species is divided here into two subspecies:

Leaves not markedly aggregated at the base, lateral leaflets 6–9 pairs, densely puberulent especially on the veins: S.W. China
6a. subsp. *lutea*

Leaves often basally aggregated, lateral leaflets 3–5 pairs, sparsely puberulent . . . . . 6b. subsp. *longiracemosa*

6a. subsp. **lutea**

Syn.: *I. lutea* Bur. et Franch. in Journ. de Bot. v, 137 (1891); Batalin in Acta Hort. Petrop. xiv, 178 (1895); Gard. Chron. iii. 50: Suppl. 130 (1911) et fig.; L. H. Bailey, Stand. Cycl. Hort. iii, 1645 (1917); Wehrhahn, Garten-Stauden ii: 946 (1931); Hand.-Mazz. Symb. Sin. vii, 888 (1936); L. H. & E. Z. Bailey, Hort. Sec. 382 (1941); R.H.S. Dict. Gard. ii, 1049 (1951) et Suppl: 246 (1956); Cowan, Journeys & Pl. Introd. of George Forrest 167 et tab. (1952).

I. principis Bur. et Franch. in Journ. de Bot. v, 136 (1891); Batalin in Acta Hort. Petrop. xiv, 179 (1895); Limpricht in Fedde Repert. Beih. xii, 486 (1922); E. H. Wilson, Plant Hunting ii, 163 (1913).

Plants often without radical or basal leaves at flowering time. *Lateral leaflets* 6–9(–10) pairs, densely puberulent on the veins. Terminal leaflet usually 1–2 cm. broad, confluent with the uppermost lateral leaflets. *Calyx* tube broadly campanulate, teeth sub-hemispheric folded along their midrib (see fig. 12 E and F).

HABITAT. Dry sandy soil of mountain slopes and amongst scrub on ledges of cliffs. Flowering: May and June.

YUNNAN. Coteaux rochailleux au-dessus des sources du Lankien-ho, près du col de Hee-chan-men, 31 Mai 1889, *Delavay* 4349 (holo. P); E. flank of Lichiang range, lat. 27°25′N., 3050–3350 m., *Forrest* 2338 (E, BM); 5774 (E, BM, P); Chungtien area, *Forrest* 30842 (E); E. slopes of Likiang range, 2895–3050 m., *Rock* 3482 (US, BM, E); Peshmee Po, E. slopes of Likiang Range, *Rock* 3560 (US, E, P); Sa Ba, E. slopes of Likiang Range, 3350 m., *Rock* 5687 (US, E); Sa Ba road, *Rock* 11412 (US); Mt. Satseto, E. slopes of Likiang range, 3350 m., *Rock* 24961 (E); Lao-chun shan, S.W. of Shi-ku, 3200 m., *Rock* 25109 (E); supra vic. Nguluko prope urbem Likiang, 2900 m., *Handel-Mazzetti* 6637 (W); Likiang range, 2600–3000 m., *T. T. Yü* 15175 (E, BM, GH); 15328 (E, GH, BM); Likiang range, *R. C. Ching* 30199 (GH); 30693 (GH); Likiang hsien, 2300 m., *C. W. Wang* 70733 (GH); 70897 (GH).

SZECHUAN. Avant Batang (without date), après Batang, ravin boisé, 15 June 1890, *Prince Henri d'Orléans* s.n. (P, syntypes of *I. principis*); inter Tatsienlu et Batang in ditione litangense, 29 May 1893, *Kachkarow* s.n. (LE); mountains around Muli, lat. 28°12′N. long. 101°E., 3350 m., *Forrest* 28415 (E, BM); 30642 (E, BM); mountains of Kulu, E. of Muli Gomba, 3400–4000 m., *Rock* 16496 (US, E): 17991 (US, E); Mt. Siga, N.E. of Kulu, *Rock* 18122 (US); mountains of Yetsi, 3960 m., *Rock* 24443 (E, K); infra vic. Yiwanschui, inter Yenyuen et Yungning 2800–3400 m.,

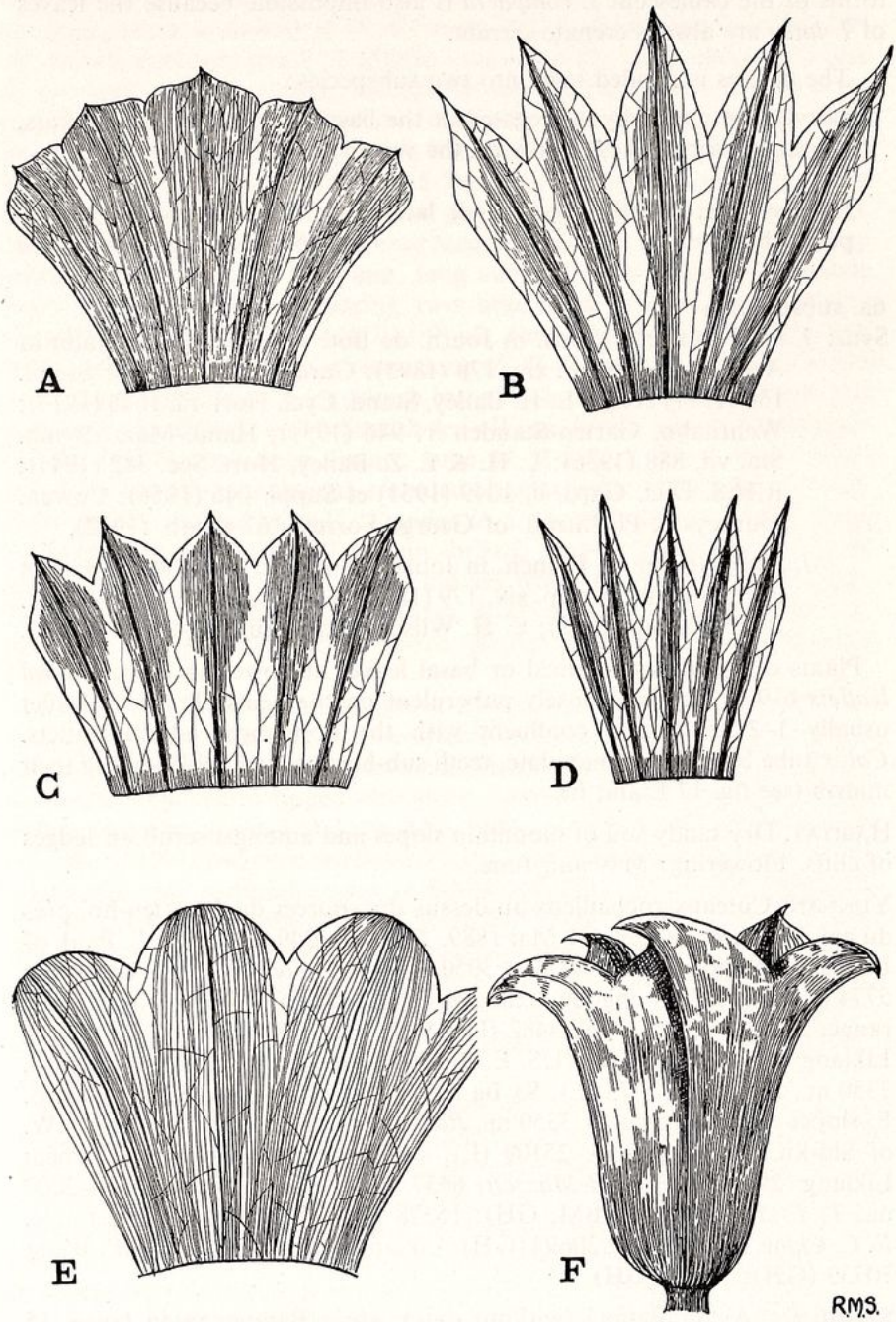

FIG. 12. Calyces in *Incarvillea* subgenus *Pteroscleris* (× 2).
A, *I. forrestii;* B, *I. mairei;* C, *I. delavayi;* D. *I. younghusbandii;* E, F, *I. lutea* subsp. *lutea.*

Handel-Mazzetti 2940 (W); inter Hunka et Woloho, 3000 m., *Schneider* 1526 (US, E, GH); Muli Kulu, 3300 m., *T. T. Yü* 14271 (GH, E); Litang river divide, 3350 m., *Kingdon Ward* 4197 (E).

The syntypes of *I. principis*, which was described in the same paper as *I. lutea*, were collected by Prince Henri d'Orléans and Bonvalot in the neighbourhood of Batang. Both specimens are incomplete making it impossible to assess the original habit of the plants. The leaflets are somewhat narrower than in mature leaves of typical specimens of *I. lutea* but have their puberulence. The flower colour, described by Bureau and Franchet as "rouge" and "rouge grenat", is not recorded on the field notes of the specimens but is consistent with the above variation. The only other specimen seen from this region (*Kachkarow* s.n.) is typical although stunted; it also has narrow leaflets similar to those of the syntypes. Other specimens, identified as *I. principis*, have proved on examination to be *I. compacta* or *I mairei*. The former is the case with J. F. Rock's white-flowered plant (*Rock* 14401) mentioned in his monograph on the Amnye Ma-Chhen Range, p. 96 (1956), and this is probably also true of the plants which Wilson (l.c.) and Limpricht (l.c.) encountered, although specimens of them have not been examined.

6b. subsp. **longiracemosa** (Sprague) Grierson, **stat. nov.**
Syn.: *I. longiracemosa* Sprague in Kew Bull. 1907: 320.

Leaves usually confined to the lower parts of the stem. Lateral leaflets (0–)3–5 pairs, sparsely puberulent. Terminal leaflet 2–5·5 cm. broad, distinct from uppermost pair of lateral leaflets. Calyx tube often narrowly campanulate, teeth triangular acuminate usually somewhat narrower than in subsp. *lutea*.

HABITAT. Stony hillsides and grassy valleys. Flowering: June to August.

TIBET. Between Phari and Shigatze, 1882, *King's Collector* (Lama Ligyen Gyatska) s.n. (holo. *I. longiracemosa*, K); Yam Dok Cho, 4570 m., Aug. 1904, *Walton* s.n. (K); Kyimdong Dzong, Tsangpo valley, 3655–3800 m., *Ludlow & Sherriff* 1827 (E, BM); 2628 (BM); Sanga Choling, 3800 m., *L. & S.* 2252 (BM); Karutra, Chayul Chu, 3960 m., *L. & S.* 2342 (BM); Dechen Dzong, 3960 m., *L. & S.* 9626 (BM, E); Kharta, 3655 m., *Kingdon Ward* 11729 (BM); vicinity of Lhasa, 3960 m., *Richardson* 209 (BM, E).

In its leaves this subspecies is similar to *I. altissima* (or, as in the one entire leaved example, to *I. forrestii*) but the disposition of leaves, length of calyx teeth and flower colour at once differentiate it.

Sprague described *I. longiracemosa* from two inadequate specimens, one of which consists of the inflorescence only, and related it to *I. principis*. The flower colour remained for some years in doubt until the collections of Ludlow & Sherriff showed, as had been suspected, that it is usually yellow although considerable red pigmentation may also occur (e.g. *L. & S.* 2252 "more mature flowers blood red inside"), and manifested the true affinities of these plants.

Horticulturally, *I. lutea* appeared at first sight to be a very valuable acquisition, and George Forrest looked upon it as one of the most beautiful alpines from the mountains of N.W. Yunnan. But, although seed, introduced by him and later by Ludlow & Sherriff, germinated freely and

produced healthy plants, it is reported only to have been flowered by a few growers, they include Sir Herbert Maxwell in 1935 (from Forrest seed) Mr. Hartley of Devonhall in the early 1930s (this is certainly from Chinese and, possibly, Forrest seed as a photograph, still extant, shows) and by Sir Frederick Stern at Highdown in 1938 (from seed of Ward 5623 from Tsangpo).

The note by A. J. Smith in Gard. Chron. 15 Aug. 1931, p. 131 is treated as being a case of faulty identification. Although none of the plants that he flowered profusely have been examined he records that they flowered in the same season in which they were sown as seed. It is impossible that *I. lutea* should behave in this way but yellow flowered forms of *I. sinensis* ssp. *variabilis* can easily do so.

At the present time yet another record has been established in the garden of Mr. Masterton of Aberfeldy. The plant has been examined and found to belong to subsp. *longiracemosa*. It was grown from L. & S. seed (9626?) and has remained unflowered for more than 10 years. This long vegetative condition appears to be true of most of these records: the first note on the cultivation of this species (Gard. Chron. 19 Aug. 1911) relates to plants which were sown in 1907 and were still flowerless at the time of writing. Stern's plant was grown from seed of Ward 5623 collected in 1924 and flowered in 1938.

It is uncertain what factor or factors determine the "ripeness to flower" condition, perhaps long spells of strong summer sun such as in 1959, perhaps also feeding has a bearing on it, Masterton's plant received a heavy dressing of poultry manure in 1959. This plant was allowed to grow unprotected and probably the others were also. The addition of a sheltering pane of glass or open ended barn cloche may be found to be rewarding.

7. **Incarvillea beresowskii** Batalin in Acta Hort. Petrop. xiv, 181 (1895).
Syn.: *I. wilsoni* Sprague in Kew Bull. 1912: 43.

Herb erect up to 2 m. high, branched below, glabrous. Rootstock scaly with foliar remains in the upper part. *Leaves* radical and cauline, alternate, pinnate 10–40 cm. long; lateral leaflets 3–6 pairs, 1·3–8·5 cm. long 0·5–3 cm. broad, ovate or elliptic, usually somewhat obliquely cuneate at the base, obtuse or acute at the apex, margins crenate-serrulate, upper leaflets sometimes incompletely divided from the rachis and with a second main vein parallel to the mid rib; terminal leaflet 2–7 cm. long 1–3·2 cm. broad, obovate or elliptic. *Inflorescence* terminal and axillary, few to twelve or more flowered raceme; pedicels 0·5–1 cm. long subtended by a lanceolate bract 0·5–1·5 cm. long and bearing two smaller bracteoles. *Calyx* tube campanulate 1–1·4 cm. long; teeth broadly triangular 4–6 mm. long 4–7 mm. broad at the base. *Corolla* rose or carmine, tube 3·5–5 cm. long; lobes rounded or emarginate 1·3–2 cm. long 1·5–2·3 cm. broad, covered with shortly stalked glands. *Capsule* 8–10 cm. long 1·2–1·3 cm. broad, quadrangular or somewhat six-ribbed at the base, acute at the apex. *Seed* greyish-brown, sometimes with blackish streaks, greyish puberulent beneath, ovate 4·5 mm. long 3 mm. broad; wing 1 mm. broad crenulate.

Flowering: May to June.

SZECHUAN. Sung pan ting, prope Kui hua, 5 May 1894, *Beresowsky* s.n. (holo. LE, iso. K.); Hsao Chin Ho Valley near Monkong-ting (now Mowkung) 2100–2400 m., June 1908, *Wilson* 3058 (holo. *I. wilsoni*, K., iso. GH); Min Valley near Mao chon, 2438 m., *Wilson* 4292 (K); descending to Mao kung Hsien, 3400–3000 m., *F. T. Wang* 21264 (GH).

The type specimens of this species were both gathered as the plants were just beginning to flower and it would appear that, as in other species, the vegetative parts do not grow to their full stature till flowering is well advanced. They are not representative of the species and unfortunately both Wilson's and Wang's specimens, which are more mature, are dismembered. Thus, when Sprague differentiated *I. wilsoni* from *I. beresowskii* on account of pedicel, bract and corolla sizes, he was comparing mature with immature plants. Pedicels and bracts are both to some extent accrescent and the extremes of corolla size in *I. lutea* are as great as they are here.

The species may be distinguished from *I. lutea* by its lack of brownish puberulence which is so distinctive in the latter and by the leaves, which have fewer lateral and usually larger terminal leaflets. In most cases, for red-flowered specimens of *I. lutea* are not unknown, the flower colour is also diagnostic and the capsule less strongly acuminate. It resembles *I. lutea*, however, in the disposition of its leaves and the presence in the uppermost leaflets of a second main vein parallel to the midrib and independent of it.

As a letter from Kiating, dated 30 Sept. 1904 (preserved in the herbarium at Kew), shows, the holotype specimen of *I. wilsoni* was not Wilson's first acquaintance with this plant for he says of it "The flowering stems of this plant are erect 4–6 ft. high, slightly branched below and bear flowers from base to summit. I know nothing of the size or colour of the flowers since the plants met with were in fruit only and to make identification more difficult, die after flowering." This fruiting material, preserved with the letter (seed No. 1418) was provisionally identified as *I. beresowskii* but, on a later gathering (W4292), Wilson wrote "if new, please name *I. veitchii*". As to its suggested monocarpic nature; in the absence of experimental data this must remain a matter of conjecture although it must be remembered that its allied species appear to be true perennials.

8. **Incarvillea altissima** G. Forrest in Notes Roy. Bot. Gard. Edin. xiii, 164 (1921).

Erect herb up to 2 m. high, subglabrous. *Rootstock* 1·5 cm. thick, in the upper part scaly with foliar remains. *Leaves* cauline only at flowering time, alternate, pinnate 15–30cm. long, lateral leaflets 2–3 pairs, subopposite oblong or ovate 5–15 cm. long 2·5–8·5 cm. broad, obliquely rounded or cuneate at the base, obtuse or acute at the apex, margins crenate, sparsely puberulent on the veins especially beneath; terminal segment broadly ovate 7–14 cm. long 3–13 cm. broad, obliquely cordate or cuneate at the base. *Inflorescence* terminal, raceme 25–30 flowered; pedicels 5–10 mm. long subtended by a linear lanceolate bract 1·2–2·5 cm. long and bearing two smaller bracteoles. *Calyx* tube campanulate 1·4–2·1 cm. long; teeth rounded or truncate, very shortly apiculate, 2–2·5 mm. long 5·5–6 mm. broad at the base. *Corolla* rose coloured, tube 5–5·5 cm. long; lobes rounded or emarginate 1·6–1·8 cm. long 2·5–2·8 cm. broad, covered with

shortly stalked glands. *Staminode* linear c. 1 mm. long. *Capsule* quadrangular or ridged 5–7 cm. long 0·7–1·3 cm. broad, acuminate at the apex and curved towards the anterior surface. *Seed* broadly ovate 4·5–5 mm. long 3·5–4 mm. broad, glossy brown above, yellowish beneath; wing 1 mm. broad.

HABITAT. Dry open situations amongst rock and scrub. Flowering: June to August.

YUNNAN. On the Tong Shan, Lat. 27°20′N., 2743 m., Aug. 1914, *Forrest* 13135 (holo. E.); same locality, Sept. 1918, *Forrest* 17062 (E); Yung-peh mountains, lat. 26°42′N., July 1918, *Forrest* 16651 (E, K); region of Tungshan, Yangtze drainage basin, E. of Likiang, Aug. 1923, *Rock* 10455 (US, E); banks of Yangtze at Latu, region of Tungshan, *Rock* 10484 (US).

SZECHUAN. Mountains east of Yung-ning, lat. 27°30′N., long. 100°36′E., 2133 m., July 1921, *Forrest* 20584 (E).

In spite of its name this is not the tallest growing species of the genus; no specimens are recorded taller than 6 ft. and there are several instances of *I. lutea* attaining this height. It is obviously related to this species in its cauline leaves and inflorescences but is differentiated by the division of the leaves, length of calyx teeth, and flower colour. Forrest himself related this species to *I. beresowskii* from which both calyx and capsule, as well as the very long raceme, differentiate it and the latter is a more northern plant. In its short calyx teeth it resembles *I. forrestii* but this species is immediately distinguished by its simple leaves.

There is no record of this species in cultivation.

9. **Incarvillea forrestii** Fletcher in Notes Roy. Bot. Gard. Edin. xviii, 310 (1935).

Erect herb 15–60 cm. high, puberulent. *Rootstock* 0·8–1 cm. broad in the upper part, scaly with foliar remains. *Leaves* radical and cauline, entire, petiole 3–15 cm. long, grooved and puberulent above; lamina ovate 6–20 cm. long 4–14 cm. broad, truncate, cuneate or rounded at the base, obtuse at the apex, margins crenate, venation pinnate 7–10 pairs of veins, puberulent on the veins on both surfaces. *Inflorescence* terminal, raceme 6–12 flowered; pedicels 5–10 mm. long, subtended by a linear-lanceolate bract 5–12 mm. long and bearing two smaller bracteoles. *Calyx* tube campanulate 1·4–2 cm. long; teeth obtuse or rounded apiculate 2–5 mm. long 5–9 mm. broad at the base. *Corolla* pale rose irregularly streaked with purple and yellow inside the tube, rarely white; tube 4·5–5 cm. long; lobes rounded 1·4–1·8 cm. long, 1·8–2·2 cm. broad, covered with shortly stalked glands. *Capsule* 6-ridged, 4–9 cm. long 5–7 mm. broad, apex acuminate, curved towards anterior surface. *Seed* ovate 5·5–6 mm. long 3·3–4 mm. broad; wing 0·75–1 mm. broad.

HABITAT. Dry limestone cliffs facing south and in openings in thickets on alpine meadows. Flowering: May to July.

YUNNAN. Chungtien plateau, lat 27°30′N., 3048 m., July 1914 (flowers white), *Forrest* 12676 (holo. E); Chien-chuan-Mekong divide, lat. 26°40′N. long. 99°40′E. 3350–3655 m., July 1922, *Forrest* 21526 (E, K); without locality, *Forrest* 30633 (E, BM).

SZECHUAN. Muli range, N. flank 3655 m., 13 June 1922, *Kingdon Ward* 5214 (E); Western slopes of Mt. Mitzuga, Muli Territory, 3500 m., May to June 1932, *Rock* 24051 (E).

Without doubt *I. forrestii* is related to *I. lutea* as is shown by the disposition of leaves and inflorescences, but differs from it in the division of its leaves, the calyces and flower colour. *I. forrestii* is, however, the only known species of *Incarvillea* in which the leaves are always undivided. Such leaves do occur in *I. mairei*, where they are always radical and represent a juvenile leaf form, and also, in one instance in *I. lutea* subsp. *longiracemosa* where they are probably abnormal.

The few capsules of this species which have been examined are distinctly six-ridged and recall, to some extent, the winged structure of the subgenus *Niedzwedzkia*. While it is not suggested that there is any close relationship between *Niedzwedzkia* and the present species, the latter nevertheless demonstrates how the 6-winged capsule has been derived by proliferation of the tissues along the middle and margins of each valve first into ridges, as here, then into wings.

There is no record of the species in cultivation.

10. **Incarvillea compacta** Maxim. in Bull. Acad. St. Petersb. xxvii, 521 (1881) et Mélange Biol. ix, 294 (1881); Regel in Gartenflora xxxi: 1 t. 1068 (1882); Lubbock, Seedlings ii, 342 (1892); Batalin in Acta Hort. Petrop. xiv, 181 (1895); Regel in Gartenflora xlix, 449, t. 1479 (1900); L. H. Bailey, Stand. Cycl. Hort. iii, 1645 (1917); Wehrhahn, Gartenstauden ii, 946 (1931); L. H. & E. Z. Bailey, Hort. Sec. 382 (1941); L. H. Bailey, Man. Cult. Pl. 905 (1949); R. H. S. Dict. Gard. ii, 1049 (1951) et Suppl. 246 (1956).

Syn.: *I. bonvaloti* Bur. et Franch. in Journ. de Bot. v, 141 (1891).

An acaulescent perennial herb 10–15 cm. high in flower, up to 30 cm. high in fruit. *Rootstock* 8–10 cm. diam. in the upper part, frequently branched and covered with foliar remains. *Leaves* radical or basal 3–14 (–20) cm. long, pinnate (liguliform cataphylls frequently present up to 1·7 cm. long) lateral leaflets 4–9 pairs (in adult leaves) opposite or subopposite 0·5–4 cm. long 0·3–2 cm. broad, subsessile narrowly ovate, acute at the apex, cordate at the base, margins entire, puberulent on the veins on both surfaces; terminal leaflet elliptic, orbicular or oblate 0·7–4 cm. long 0·4–4 cm. broad, with 1–4 pairs of veins. *Inflorescence* racemose (normally compressed) bearing up to ten flowers; pedicels 1–5 cm. long (10 cm. long in fruit) borne in the axil of a linear bract 2–3(–4) cm. long with two smaller linear bracteoles close above it. *Calyx* tube campanulate 1·2–1·8 cm. long often thickly covered with black spots; teeth deltoid 0·6–1·2 cm. long 0·5–0·7 cm. broad at the base. *Corolla* lobes Cyclamen purple (R.H.S. Col. Code 30) fading to Phlox purple (R.H.S. Col. Code $_{6}$32); tube purple outside, Aureolin yellow (R.H.S. Col. Code 3/1) with a few purple lines ventrally within. White flowered specimens have occasionally been found. Tube 4–6·5 cm. long; lobes orbicular or oblate 1·7–2·8 cm. long 2–3·9 cm. broad, retuse at the apex covered with subsessile gland. *Staminode* minute crozierform. *Capsule* woody distinctly quadrangular 7–11 cm. long 9–13 cm. broad, ± straight usually thickly covered with black spots. *Seeds* dark grey-brown 3·5–5 mm. long 2–3·5 mm. broad; wing 0·5 mm. broad.

HABITAT. On moist stony slopes often in exposed situations and limestone cliff faces.

TIBET. Tibet borealis, 1884, *Przewalsky* s.n. (E, P); Tibet boreali-orientalis, Terra Tangutorum, 1884, *Przewalsky* (P); route de Lhasa à Batang, 22 Mai, *Bonvalot & Prince Henri d'Orléans* s.n. (P. holo. of *I. bonvaloti*); Northern slopes of Yellow River valley, south of Radja, 3650 m., *Rock* 13974 (US, P); Upper Dachso and Wajo la, 3650–3900 m., *Rock* 14087 (E, K); Wajo Valley, 3950 m.—a white-flowered form—*Rock* 14401 (GH).

KANSU. Upper source of Hwang-ho, 1880, *Przewalsky* s.n. (holo. LE, non vidi); On po, Nan Chan 3500 m., *Pelliot-Vaillant* 945 (P); Ni Mar Lan K'ou, en route to Labrang, 3000–4200 m., *R. C. Ching* 766 (US); about the "Wolvesden Pass" and "Chebson Abbey", 3050–3350 m. *Farrer & Purdom* 509 (E); limestone boulders of Kwadjaku Stream, north of Minshan range, 2925 m., *Rock* 12476 (E, K, US); Nashtrrh gorge across eastern end of Richthofen range, 3650 m., *Rock* 13301 (E, GH); Kadjaku valley, T'ao River basin, 2600–3050 m., *Rock* 13653 (GH, E, K).

SZECHUAN. In ditione Batangensi, 7 June 1893, *Kashkarov* s.n. (P, K); Tongolo (Principauté de Kiala) 1893, *Soulié* s.n. (P); S.W. of Muli, 4250–4575 m., *Kingdon Ward* 4072 (E); Liang ho Kou, 3950 m., *T. K. Wang & T. S. Wen* 687 (GH); Mount Mitzuga west of Muli Gomba, 3050–3875 m., *Rock* 16077 (E, US).

YUNNAN. Without precise localities, *T. T. Yü* 8230 (GH), 9065 (GH); Bai-ma-shan, Atuntze, 4100 m. *T. T. Yü* 10777 (E, BM); Bai-ma-shan, 3400–3500 m., *C. W. Wang* 69443 (GH), 69701 (GH); Mekong-Salwin Divide, lat. 28°10′N., 3650–3950 m., *Forrest* 14098 (E, K, BM); 18700 (E, K); Bei-ma-shan, lat. 28°18′N. long. 99°10′E., 4250–4575 m., *Forrest* 20180 (E); Na-Shu-to Shan, Mekong-Yangtze Divide, lat. 28°30′N. long. 99°12′E., 4250 m., *Forrest* 20611 (E); Bei-ma-Shan, 3950–4100 m., *Rock* 10368 (E, US); 27785 (E, K, BM); 23383 (E, K, BM, GH).

I. compacta is differentiated from its nearest ally *I. mairei* by the greater number of lateral leaflets, the margins of which are entire. Although compound leaves are notoriously variable, those of *I. compacta* are remarkably constant and it is only where the juvenile leaf form occurs in otherwise mature specimens that confusion arises. *Ridley* 16 (E) from Sining, Kansu provides such a case. The leaves bear only two pairs of reduced leaflets giving it the appearance of a specimen of *I. mairei*. But reduced though the leaves are, they bear no serrations and the leaflets have the same shape as those of *I. compacta*. It is also significant that the herbarium sheet of *Rock's* 12476 at Edinburgh bears a similar specimen along with two other normal ones.

Mature specimens of *I. compacta* often have a short stem which, at anthesis, is usually hidden among the foliage but in some specimens, e.g. *Rock* 12476 and *Farrer* 509, more strongly developed stems bearing several leaves may be readily seen. Such a structure is not present in *I. mairei*, *I. younghusbandii* nor *I. delavayi* where the flowers are borne on leafless peduncles. Here, however, the inflorescence is racemose although in specimens gathered early in the season the flowers may appear to be borne individually on the crown of the plant.

Three other characters are distinctive in this species: the long bracts, the

long straight markedly quadrangular capsule with thickly lignified walls and the presence of black spots on the flower parts. The latter are not confined to this species but are often so abundant as to give the calyx and capsule a blackish colour.

In cultivation *I. compacta* is not as widely grown as it deserves to be for it makes a good display during June. Here at Edinburgh it succeeds in well-drained conditions in almost full sun.

11. **Incarvillea mairei** (Lévl.) Grierson, **comb. nov.**
Syn.: *Tecoma mairei* Lévl. Cat. Pl. Yunnan 20 (1915).

Acaulous perennial herb. *Rootstock* fleshy, often branched, 4–6 mm. broad in the upper part, surrounded by foliar remains sometimes in whorls. *Cataphylls* up to 2 cm. long usually present, ligulate. *Leaves* radical 4–16(–25) cm. long, pinnate; lateral leaflets borne on petiolules c. 1 mm. long or less (but in East Himalayan examples as much as 1 cm. long) 0–4(–7) pairs, up to 4(–7) cm. long 1·5(–5) cm. broad, ovate or oblong, cordate or rounded at the base, obtuse or acute at the apex, margins serrulate or crenate, puberulent on the veins on both surfaces; terminal leaflet (1·5–)3–6·5(–14) cm. long (1·2–)2·5–5(–13) cm. broad, broadly ovate or oblong, cordate or rounded at the base, obtuse at the apex, margins crenate or serrulate (sometimes only at the base) with 5–8 (–11) pairs of veins. *Flowers* solitary or several, peduncle 3–25 cm. high (up to 50 cm. high in fruit) simple or branched. *Calyx* tube campanulate 1·1–1·9 cm. long, often with a few scattered black dots at the base; teeth triangular 0·5–0·8(–1·0) cm. long 4–8 mm. broad at the base. *Corolla* tube crimson outside, yellow, white or grey within (3·3–)4–6(–6·5) cm. long 0·6–1·3 cm. broad (*in sicco*) at the base, level with the calyx teeth apices; lobes crimson 1·1–2·8 cm. long 1·3–3(–3·5) cm. broad, ± orbicular or oblate, rounded or emarginate at the apex, covered with shortly stalked glands. *Staminode* c. 3 mm. long curved. *Capsule* somewhat woody, the surface usually covered with scattered black dots 5–9 cm. long 0·7–1·2 cm. broad ± straight or crescentic, acuminate at the apex, ± square in section. *Seeds* grey or brown, ovate or very broadly ovate, plano-convex 4–6 mm. long 2–3·75 mm. broad; wing 0·75–1·0 mm. wide, usually entire.

I. mairei stands distinct on account of its leaves which usually bear up to four and sometimes as many as seven pairs of serrulate leaflets and have large veiny terminal leaflets (see fig. 11, F). The flowers are borne on a peduncle and, unlike *I. compacta*, a short stem is never developed. The calyx and capsule, normally with a few scattered black spots, are never so densely covered as in *I. compacta* and the capsule, although similar, is less strongly quadrangular than in the latter species and is somewhat shorter. In proportion, the calyx teeth of *I. mairei* are longer than they are broad at the base whereas, in *I. delavayi*, they are shorter than broad (see fig. 12, B & C).

The species is divided into two varieties:

Peduncles branched above the middle; leaves with 2–4(–7) pairs of leaflets . . . . . 11a. var. *mairei*
Peduncles branched at or below the middle; leaves with 0–2(–4) pairs of leaflets . . . . . 11b. var. *grandiflora*

11a. var. **mairei**

Syn.: *I. grandiflora* Bur. et Franch. var. *brevipes* Sprague in Kew Bull. 1909: 263; Léveillé, Cat. Pl. Yunnan 20 (1915); L. H. Bailey, Stand. Cycl. Hort. iii, 1645 (1917); A. Edwards in Gard. Chron. Ser. III, lxxxv, 379 (1929); L. H. Bailey, Man. Cult. Pl. 905 (1949); R.H.S. Dict. Gard. ii, 1049 (1951) et Suppl. 246 (1946).

Tecoma mairei Lévl. Cat. Pl. Yunnan 20 (1915).

I. compacta Maxim. var. *brevipes* (Sprague) Wehrhahn, Gartenstauden ii, 947 (1931).

Peduncles c. 18·6 cm. high (5–30 cm. in flower, up to 50 cm. in fruit) branched above the middle and bearing 2–3(–5) flowers. *Leaves* c. 12 cm. long (3·5–24 cm.); lateral leaflets (0–)2–4(–7) pairs, 1·2–3·5(–7) cm. long (0·6–)1–1·7(–5) cm. broad; terminal leaflet (1·5–)3–7(–14) cm. long (1·2–)2·5–5(–13) cm. broad. *Calyx* tube (1·1–)1·3–1·6(–1·9) cm. long, usually distinctly blackish ribbed, with or without a few black dots; teeth (4·5–)5–8(–10) mm. long (4–)5–8 mm. broad at the base. *Corolla* tube purplish outside, aureolin (R.H.S. Col. Code 3/1), with purple lines within, (4–)4·5–6(–6·5) cm. long, 0·6–1·3 cm. broad at the base level with the calyx teeth; lobes Fuchsia purple (R.H.S. Col. Code 28/1) fading to Petunia purple (31/1), (1·5–)2·2–2·5(–2·8) cm. long (2–)2·5–3·2(–3·5) cm. broad. *Capsule* 5·5–8 cm. long 0·9–1·2 cm. broad. *Seeds* very broadly ovate, brown with a few blackish streaks, 4–6 mm. long 3–3·75 mm. broad, surrounded by an entire wing 0·75–1 mm. broad.

HABITAT. Open dry mountain pasture. Flowering in May and June.

YUNNAN. Without locality, *Delavay* 2873 (P); col du Lopin chan, 25 May 1886, *Delavay* s.n.; près du col de Yen-tze-hay (Lankong), 3500 m. *Delavay* 2228 (P); au col du Hee-chan-men, 3000 m., 21 May 1887, *Delavay* s.n. (P); Yen-tze-hay, 17 June 1887, *Delavay* s.n. (P, LE); au-dessus du col de Yen-tze-hay, 3500 m., 5 Sept. 1887, *Delavay* s.n. (P); au col du Lopin Chan, 3500 m., 31 Aug. 1888, *Delavay* s.n. (P); N. end of Lichiang Valley, lat. 27°12′N., 2743 m., *Forrest* 2131 (syntype of var. *brevipes*, E, K); E. flank of Lichiang Range lat. 27°20′N., 3350 m., *Forrest* 2464 (syntype of var. *brevipes*, E); W. flank of Lichiang Range, lat. 27°30′N., 3650 m., *Forrest* 5917 (E, K, BM); Lichiang Range, lat. 27°40′N. 3350 m., *Forrest* 10271 (E, K, GH); without locality, *Forrest* 28820 (E); Yung-ning, *McLaren's Collector* N33 (E, K, BM); E. slopes of Lichiang Snow Range, *Rock* 3324 (US, K, E); at 2895 m., 33801 (US, E); at 3500 m., 3798 (US); 4127 (US, BM, E, P); 4128 (US, E); Sa Ba, E. slopes of Lichiang Range, 3350 m. *Rock* 6122 (US, E); between Loyu and Dyipalo, W. slope of Lichiang Range, *Rock* 8549 (US); Sa Ba, E. slopes of Lichiang Range 3350 m. *Rock* 8683 (US, E); Gassuko, E. slopes of Mt. Dyinaloko, N. peak of Lichiang Range, 3655 m., *Rock* 8991 (US, E); Mt. Satseto, E. Slopes of Lichiang Range, 3500 m., *Rock* 24852 (US, K, BM, E); Kan-Lai-tzi, 3048 m., *Kingdon Ward* 239 (E); prope urbem Likiang, 2750–3600 m., *Handel-Mazzetti* 3793 (W); in regione Lichiang, *Schneider* 3872 (GH); without locality, *T. T. Yü* 11481 (GH); Chungtien, 3200 m., *T. T. Yü* 13955 (E, BM); 13974 (E, BM); Lichiang Range, 2400 m., *T. T. Yü* 15165 (E, BM, GH); N. flank of Haba Snow Range, *K. M. Feng* 1223 (GH); Pai-Shu-ho, N.E. Lichiang Snow Range, *R. C. Ching* 30135

(GH); without locality, *C. W. Wang* 70967 (GH); rochers sous brousse mont de Pe-long-tsin, 3200 m., *E. E. Maire* s.n. (holo. *Tecoma mairei*, E, iso BM.; Rehder misidentified this as *I. delavayi*—Journ. Arn. Arb. xvi, 315: 1935); sur rochers de mont sous brousse à Pe-long-tsin, 3200 m. *Maire* 824/1914 (E, BM).

Although this variety is centered in the Lichiang area it does occur further afield and around Chungtien a form with 6–7 pairs of leaflets is found. These are usually smaller plants; peduncles 8–12·5 cm. high, leaves 7–10·7 cm. long with narrower terminal leaflets (1·5–2·7 cm. broad). To this form the following specimens belong:

E. slope of Bei-Ma-Shan, lat. 28°12′N., 3950–4260 m., *Forrest* 13825 (E, K, BM); Mountains W. of Hsiao Chungtien, 3800–3950 m., *Rock* 24642 (US, E, K, BM, GH). 25262 (E, GH); without locality, *T. T. Yü* 11914 (GH).

Two specimens from Szechuan also approach this multifoliolate form: without precise locality, *Soulié* s.n. (P); ascending to Fu-Pien Hsien, 3900 m., *F. T. Wang* 21422 (GH). On the other hand, *Soulié* 310 (P) Terrain secs à Tongolo) belongs to the typical form except that the terminal leaflets are narrow (1·2–2·2 cm. broad) and the corolla tubes measure 4–4·5 cm. long. Both of the above Soulié specimens are labelled "*Incarville longipes* Bur. et Franch", an unpublished name, in Bureau's handwriting.

From Kansu, two *Farrer* specimens belong to this variety. They are *F*34 (E)—limestone crevices on the cliffs of the "Thundercrown range" 2438–2590 ft. and F89 (E)—limestone ledges; mountain behind Siku. In appearance they are somewhat unlike other specimens of this variety on account of their oblong terminal leaflets borne on long (3–10 cm.) rachises with only one (rarely two) pairs of lateral leaflets or without any. These cannot be depauperate specimens of *I. compacta* as was once thought for their leaves are serrulate, they have no vestige of a stem and their calyces are unspotted. On the other hand the inflorescence and flowers are those of var. *mairei*.

This variety remains distinct from var. *grandiflora* on account of its larger size, its better developed lateral leaflets, its short pedicels and its ± straight capsules. Because of the similarity in their inflorescences it was confused by Bureau with *I. delavayi* which, in the original description, he distinguished from *I. mairei* chiefly by the greater number of flowers, the number of leaflets being regarded as variable; "*folia . . . segmentis rite numerosis sed in altioribus montium paucis, paucissimis et imo nullis et tunc limbus indivisus*". Consequently six of the specimens collected by Delavay which he cites with the original description, belong to this variety. The leaf of *I. delavayi* with 6–11 pairs of lateral segments is pinnatisect above and pinnate only towards the base of the leaf. Further, the terminal segment is always smaller than the lateral segments so that the leaf tapers from base to apex. In *I. mairei* the opposite is the case (see fig. 11, D & F).

In cultivation var. *mairei* seems to rank equally in popularity with *I. delavayi*. There seems to be no question of its hardiness and it makes a good display during June. It was introduced by Messrs. Bees from Forrest seed.

11b. var. **grandiflora** (Wehrhahn) Grierson **comb. nov.**

Syn.: *I. grandiflora* Bur. et Franch. in Journ. de Bot. v, 138 (1891); *non* Poir. in Dict. Sci. Nat. xxiii, 52 (1821) *nec* Spreng. Syst. ii, 836 (1827). Batalin (*in synon. sub I. compacta*) in Acta Hort. Petrop. xiv, 182 (1895); Rev. Hort. 1899: 12 cum ic; Garden lvi, 22 (1899); Journ. Hort. Ser. III, xlvi, 357 (1903); Vilmorin, Hort. Vilm. 238 (1906); Silva Tarouca, Freiland Stauden 126 (1910); Lévl. Cat. Pl. Yunnan 19 (1915); L. H. Bailey, Stand. Cycl. Hort. iii, 1645 (1917); Limpricht in Fedde Repert. Beih. xii, 486 (1922); Hand.-Mazz., Symb. Sinicae 7 (1936); L. H. & E. Z. Bailey, Hort. Sec. 382 (1941); L. H. Bailey, Man. Cult. Pl. 905 (1949); R.H.S. Dict. Gard. ii, 1049 (1951) et Suppl. 246 (1956).

I. compacta Maxim. var. *grandiflora* Wehrhahn, Die Garten-Stauden ii, 947 (1931).

Peduncles c. 11 cm. high (5·5–15 cm. in flower, up to 36 cm. in fruit) bearing a solitary flower or branched below the middle and bearing 2–3 flowers. Leaves c. 9 cm. long (3–23 cm.); lateral leaflets 0–2(–4) pairs, (1–)1·5–4(–4·5) cm. long (0·6–)1·3–3 cm. broad; terminal leaflets (2–)3–4·5(–7) cm. long (2–)2·5–4(–7) cm. broad. *Calyx* tube (1·4–)1·7–1·9(–2·1) cm. long, normally with distinct dark ribs and with a few scattered black spots at the base; teeth 5–8 mm. long 6–7 mm. broad. *Corolla* tube crimson outside yellow within (4–)4·5–6 cm. long 0·5–1·1 cm. broad at the base level with the calyx teeth apices; lobes crimson 2–2·75 cm. long 2·3–3·5 cm. broad. *Capsule* 6–7(–9) cm. long 0·7–1·1 cm. broad. *Seeds* very broadly ovate, brown with a few blackish streaks, glabrous above, with scattered whitish puberulence beneath, 4–4·5 mm. long 2–3 mm. broad, surrounded by an entire wing 1 mm. wide.

HABITAT. In open stony alpine meadows; flowering during May and June.

SZECHUAN. Entre Batang et Litang, gazon secs après Batang, *Bonvalot & Prince Henri d'Orléans* 21 (holo. P.); in ditione Litangensi, 10 June 1893, *Kachkarow* s.n. (P, K); inter Litang et Hochuca, 15 June 1893, *Kachkarow* s.n. (P); inter stationes Tungolo et Olunshi, 17 June 1893, *Kachkarow* s.n. (LE); Tatsienlu, 13 June, 15 June & 29 June, 1893, *Potanin* s.n. (LE); Tatsienlu, *Soulié* 315 (P, K), 806 (P, K); without locality, *Forrest* 30655 (E); Mountains S. of Muli, Mt. Gibboh, 3960 m., *Rock* 16022 (US); Mount Mitzuga, W. of Muli Gomba, 3700 m., a white flowered form, *Rock* 16072 (US, K); at 3900 m., *Rock* 16165 (E, US); Djesi-La and Djesi-Longba, S. of Tatsienlu, 4450 m., *Rock* 17728 (P. US); N. of Chiu-Lung-Hsien, in Minya Country, S.W. of Tatsienlu, 4250 m., *Rock* 17757 (US); Mountains of Yetsi, N. of Kulu, Muli Territory, 3650 m., *Rock* 23909 (US, K, BM, E); Mountains of Kulu, Muli Territory, 3650 m., *Rock* 23930 (E, K, BM); Mountains of Yetsi, 3650 m., *Rock* 24424 (GH, K, BM, E); inter Kalapa et Linku, 3700–4000 m., *Schneider* 1245 (E, GH, US); in reg. Yenyuan-Hsien prope Linku, 4000 m., *Schneider* 3571 (E, GH, US); in montis Linku-liangdse, 27°48′, inter oppidum Yenyuan et castellum Kwapi, 3600 m., *Handel-Mazzetti* 2264 (W, P, K, E); 5–10 miles S.W. of Muli, 3350–3650 m.—a white flowered form, *Kingdon-Ward* 4060 (E); Litang River divide, 3350 m., *Kingdon Ward* 4196 (E); Tatsienlu,

McLaren's Collector AC. 145 (E); Muli, 3400 m., *T. T. Yü* 14254 (E, GH, BM); Muli, Wachin, Deongomba, 3500 m., *T. T. Yü* 14762 (E, BM).

YUNNAN. Yen-tze-hsi, 17 June 1887, *Delavay* s.n. (P); without locality *Forrest* 28516 (E, BM); 29158 (E); Haba Shan, N. of Yangtze loop, 3650 m., *Rock* 24766 (E, K, BM, US), 24808 (US, K, BM, E); Yu-lung shan, 3500 m., *Rock* 25338 (E); Lo Shiueh, *McLaren's Collector's* s.n. (E); without locality *T. T. Yü* 11947 (GH); Chungtien, Haba, 3600 m., *T. T. Yü* 13554 (E, BM, GH); Chungtien, Haba, 3500 m. *T. T. Yü* 15312 (GH, BM, E); N. flank of Haba snow range, *K. M. Feng* 1106 (GH); E. Chungtien, Chia-tze on Yangtze near Tung-patze, *K. M. Feng* 2458 (GH); Li Kiang Hsien, 2500 m., *C. W. Wang* 71171 (GH).

In habit and length of leaf, specimens of var. *grandiflora* are generally smaller than those of var. *mairei* to which it is most nearly related. The number of lateral leaflets is fewer and there is a greater tendency to produce leaves without laterals or only with rudimentary ones. In the flower parts, although no hard and fast line may be drawn, var. *grandiflora* is usually larger. It is easily recognized by the nature of its peduncles.

Batalin (Acta Hort. Petrop. xiv, 181: 1895) reduced both *I. bonvaloti* and *I. grandiflora* to synonyms of *I. compacta*. While he was correct in respect of *I. bonvaloti* he was wrong about the latter. Thus in a list of citations (l.c. p. 183) he subdivided the species into forms, e.g. *forma grandiflora foliis integris*, *forma bonvaloti* and *forma longipes* some of which names appear in herbaria. It was perhaps Batalin's paper which prompted Wehrhahn to publish *I. grandiflora*, *bonvaloti* and *brevipes* as varieties of *I. compacta*.

Chinese seed of this variety was first introduced into cultivation in 1895 when seed collected near Tchonn-Kin in E. Szechuan by Farges was sent to M. Maurice de Vilmorin. Although other introductions have been made, plants from Chinese sources are non-existent or very scarce and it would appear that all the plants of this variety in cultivation today are the result of Ludlow and Sheriff introductions. Tibeto-Nepalese plants of this species appear to belong to this variety in that their flowers are solitary, but are somewhat different from those from Western China. Unfortunately, however, the characters which might separate them from the latter are not sufficiently constant to warrant the creation of a separate subspecific category. They may indeed with wider collecting be found to belong to more than one such category.

The characters both constant and inconstant which the East-Himalayan plants show are as follows:

(1) Peduncles strictly 1-flowered.
(2) Leaflets often having distinct petiolules (up to 1 cm. long), but in number of leaflets they are similar to the Chinese plants.
(3) The calyces are usually more indistinctly ribbed than they are elsewhere in the species.
(4) The capsules are often falcate instead of being nearly straight as in the eastern range of the species. In this respect, however, *L. & S.* 17250 shows capsules of both sorts and in cultivation *L. & S.* 15614 produces both curved and straight capsules.
(5) The seeds which have been examined tend to have notched instead of entire seed wings.

The following specimens belong in this group:

S.E. TIBET. Pome Prov. Nambu La, Tongyuk River, 3650 m., *Ludlow, Sherriff & Elliot* 13879 (LE, BM); Nyoto Sama, 4570 m., *L.S. & E.* 15614 (E, BM).

BHUTAN. Chojo Dzong, Upper Pho Chu (Eastern Branch), 4115 m., *Ludlow, Sherriff & Hicks* 16722 (E, BM); Tranza, Gaffoo La, Upper Pho Chu, 3960 m., *L.S. & H.* 17250 (BM).

NEPAL. Barbung Khola, Kaya Khola, 4115 m., *Polunin, Sykes & Williams* 1089 (E, BM); near Rohagaon, Suli Gad, 3750 m., *P.S. & W.* 2160 (E, BM): the same at 3405 m., *P.S. & W.* 3399 (E, BM); Durpa Humla, Karnali, 3352 m., *P.S. & W.* 4306 (E, BM).

The relationship of these with *I. younghusbandii* is to some extent doubtful. The latter remains distinct on account of its smaller size and its elongated narrow corolla bases but it also has crescentic capsules and notched seed-wings. Thus, the possibility that the Himalyan plants of *I. mairei* may be of hybrid origin cannot be ruled out although the absence of sterile pollen grains does not substantiate this view.

From the above collections, the progeny of two distinctive Ludlow & Sherriff gatherings are quite widely grown in gardens and, while it appears at present impossible to categorize the East Himalayan branch of this species, it is possible, and necessary, to distinguish these two gatherings as cultivars.

Incarvillea mairei cv. 'Nyoto Sama'.

Adult leaves ± smooth above. Flowers light pink. Corolla tube 5·5 cm. long. Flowering time: May to early June.

This cultivar is derived from seed of *L. & S.* 15614 (from Nyoto Sama, S.E. Tibet—thus the cultivar name) and has been distributed as "*Incarvillea* sp. Ludlow & Sherriff". It is regularly the earliest *Incarvillea* to flower each season.

Incarvillea mairei cv. 'Frank Ludlow'.

Adult leaves ± bullate above. Flowers rich deep pink. Corolla tube 4·5–5 cm. long. Flowering time: June.

This cultivar is derived from seed of *L. & S.* 17250 and has been distributed both as *I. younghusbandii* and as *I. grandiflora* Ludlow & Sherriff. It is reckoned to be an excellent garden plant (see Lawson in Journ. Scot.

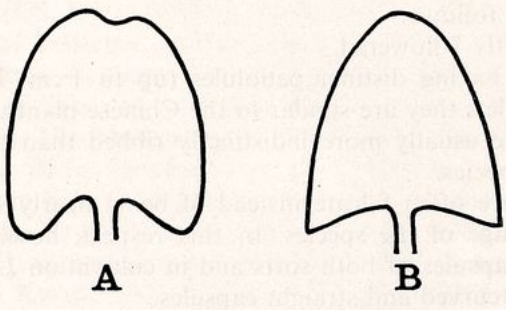

FIG. 13. Cotyledons of *I. mairei* (× ca. 4).
A, cv. 'Frank Ludlow' (L. & S. 17250). B, cv. 'Nyoto Sama' (L. & S. 15614).

Rock Gard. Cl. iv, 232, t. 30: 1959) and generally speaking, flowers a fortnight later than "Nyoto Sama".

Both the above cultivars appear to breed true and, besides the differences recorded above, their seedlings are distinct from the cotyledon stage. Whereas the cotyledons of *L. & S.* 17250 are roughly ovate in outline sharply truncate at the base and rounded or only slightly emarginate at the apex, those of *L. & S.* 15614 tend to be more reniformly ovate, cordate at the base and regularly emarginate at the apex (see fig. 12). The chromosome numbers of both were investigated by Prof. Manton who found them to have 2n = 22, i.e. the complement found in all the other species which have been studied. (For this information the author is indebted to Mr. Ludlow.)

12. **Incarvillea younghusbandii** Sprague in Kew Bull. 1907: 320; Ostenfeld and Paulson, List of Fl. Pl. Inner Asia 42, t. 3 (1922); R.H.S. Dict. Suppl. 246 (1956).

Acaulous perennial herb; rootstock fleshy, little branched, 3–6 mm. broad in the upper part, usually regularly whorled with foliar remains. *Cataphylls* up to 1 cm. long usually present, ligulate, scale-like. *Leaves* pinnate 1·5–2·5 cm. long at flowering time, bullate on the upper surface, prominently veined beneath, increasing to 4–5·5 cm. in fruit and becoming smoother; lateral leaflets 3–7 pairs 0·6–0·9 cm. long 0·4–0·6 cm. broad, ovate or oblong, cordate at the base, obtuse at the apex, margins crisped crenate, puberulent especially on the upper surface; terminal leaflets 0·8–1·5 cm. long 1–2 cm. broad, very broadly ovate or orbicular, cordate at the base, obtuse at the apex, margins crisped crenate. *Flowers* opening as the leaves unfold, solitary peduncles up to 2 cm. long. *Calyx* campanulate, tube 5–9 mm. long inconspicuously ribbed; teeth triangular 2–5 mm. long 3–4 mm. broad at the base, puberulent. *Corolla* purplish pink with white striations in the throat, tube 3–5 cm. long 2–3 mm. broad at the base, level with the apices of the calyx teeth, lobes 1–2 cm. long 1·5–2·5 cm. broad orbicular or oblate covered with shortly stalked glands. *Staminode* 1 mm. long filiform. *Capsule* somewhat woody 2·5–3·5 cm. long 0·8–0·9 cm. broad, curved or crescentic, quadrangular, acute at the apex. *Seeds* greyish-brown 4 mm. long 3 mm. broad; wing 0·5 mm. broad crenulate.

HABITAT. Open gravelly hill slopes. Flowering; May to July.

TIBET. Khamba Jong, 4500 m., *Younghusband* 21 (lectotype E, K), 316 (E); Gyangtze, 3960 m., *Walton* 103 (K, BM); E. Rongbuk glacier *Humphreys* 5059 (E, BM); Lhasa and hills S. of Lhasa, 3655–4570 m., *Ludlow & Sherriff* 9530 (E, BM); Hills N. of Lhasa 4420 m., *L. & S.* 8689 (E, BM); Trigu Dzong, 4875 m., *L. & S.* 12462 (E, BM); Reting, 60 miles N. of Lhasa, 4265 m., *L. & S.* 11015 (E, BM). Also found by Sven Hedin (Ostenfeld & Paulson l.c.) on the shores of Naktsong-tso and the Upper Tsang-po valley between Dongbo & Tuksum.

NEPAL. Mukden Khola, 5840 m., *Polunin, Sykes & Williams* 1395 (BM).

In his original description Sprague cited eight specimens without designating a holotype. It is impossible from his description and from the absence of drawings, notes, etc., to pick out any one of them which he might have used particularly, and therefore, in nominating *Younghusband*

21 as lectotype, a well preserved specimen which is represented in the herbaria of both Kew and Edinburgh has been chosen.

I. younghusbandii is a plant of the Tibetan plateau and, apparently, does not spread to the southern slopes of the Himalayas. Apart from its diminutive stature it remains distinct from *I. mairei* var. *grandiflora* its closest Himalayan relative, in the shape and proportions of its corolla. This is very narrow towards the base, level with the apices of the calyx teeth; from that point is continues upwards almost without broadening from 1–1·5 cm. before widening quite rapidly into the bell of the corolla. In conjunction with this elongated basal tube, the filaments are inserted about 2 cm. from the base proper of the corolla whereas, in other species, they are attached at about 1 cm. from the base and the corolla widens to form the bell from a point beyond the mouth of the calyx tube.

Other features combine to make this plant one of distinctive appearance. The upper part of the rootstock is very narrow and often regularly whorled with foliar remains. The crescentic capsule is otherwise found only in Himalayan plants of *I. mairei* var. *grandiflora* and is smaller than in that species.

The bullate character of the leaves on some herbarium specimens is directly related to the simultaneous production of flower and leaf which takes place in this species immediately the snows of their native hillsides begin to melt. Between flowering and fruiting the leaves lose their crumpled appearance become smooth and attain their full size; thus the foliage has a different appearance at different times of the year. A similar phenomenon occurs in other species but it is less marked than here.

The species is in cultivation but is a rare and, apparently, a difficult one.

13. **Incarvillea delavayi** Bur. et Franch. in Journ. de Bot. v, 138 (1891); Rev. Hort. (1893) 544; Wittmark in Gartenflora xlii, 577 (1893) et xliii, 2, t. 1398 (1894); Journ. Roy. Hort. Soc. Lond. xix, 43 (1896); Hook. f. in Bot. Mag. t. 7462 (1896); Garden liv, 430 (1898); Gard. Chron. III, xxvi, 123 (1899); Garden lviii, 179 (1900); Gartenflora xlix, 451 (1900); Garden lx, 229 (1901); Vilmorin, Hort. Vilm. 238, f. 67 (1906) et Fl. de Plein Terre 526 (1909); Silva Tarouca, Frejland Stauden 126 (1910); 200 (1920); L. H. Bailey, Stand. Cycl. Hortic. iii, 1645 (1917); Cox, Pl. Introd. of R. Farrer 38 (1930); Wehrhahn, Garten-Stauden ii, 947 (1931); L. H. & E. Z. Bailey, Hort. Sec. (1941) 382; L. H. Bailey, Man. Cult. Pl. 905 (1949); R. H. S. Dict. Gard. ii, 1049 (1951) et Suppl. 256 (1956).

Acaulous perennial herb. *Root* fleshy often branched, 5–7 mm. thick in the upper parts, surrounded with foliar remains. *Leaves* 8–25 cm. long, radical, pinnate below pinnatifid above, lateral leaflets (2–)6–11 pairs, 1·3–5 cm. long, 0·5–2·5 cm. broad, lanceolate or narrowly ovate, the lower ones rounded or cuneate at the base, the upper ones decurrent on the rachis and with a second main vein running parallel to the midrib arising independently of it from the rachis, obtuse or acute at the apex, margins crenate or occasionally pinnately divided, glabrous or puberulent on the veins; terminal leaflet 1·5–3·5 cm. long 0·9–2·5 cm. broad, broadly elliptic or obovate, cuneate at the base, distinct or confluent with the uppermost lateral leaflets, obtuse or acute at the apex, margins crenate. *Inflorescence* 2–10 flowered, raceme borne on a peduncle 15–30 cm. long (up to 47 cm. in fruit); pedicels 0·5–1·5 cm. long subtended by a linear bract 1 cm. long

and bearing 2 smaller bracteoles c. 0·5 cm. long close above the bract. *Calyx* tube 1·3–1·6 cm. long; teeth triangular 5–6·5 cm. long 5–7 mm. broad at the base. *Corolla* tube 4·5–6 cm. long, purplish outside on the posterior side, yellow on the anterior, yellow with purple lines on the inside; lobes varying from Mallow Purple (R.H.S. Col. Code $_{6}$30/1) to Cyclamen Purple (R.H.S. Col. Code 30/1), 1·5–2·6 cm. long 1·9–3 cm. broad, orbicular or oblate, emarginate at the apex, covered with shortly stalked glands. *Staminode* 0·2–1 cm. long, usually somewhat broadened at the apex. *Capsule* ligno-coriaceous, brownish 5–7·3 cm. long 0·8–1·5 cm. broad, quadrangular, curved towards the anterior side, acuminate at the apex. *Seeds* greyish-brown, very broadly ovate, plano-convex, glabrous above, puberulent beneath, 5 mm. long 3–3·75 mm. broad; wing entire 1 mm. broad.

HABITAT. Open stony situations among scrub. Flowering May to June.

YUNNAN. Sommet du Hee-chan-men, au-dessus de Lankong, 25 mai 1883, *Delavay* s.n. (P); au pied du Mt. Yang-in-chan, près de Lankong, 1 août 1883, *Delavay* 94 (P); Mt. Hee-chan-men, Lankong, 2 juin 1884, *Delavay* s.n. (P); pâturages de montagnes, Mt. Hee-chan-men (Lankong), 2 juin 1884, *Delavay* 1027 (lecto. P); sur le plateau calcaire du Che-tchu-tze, au dessus de Ta-pin-tze, 27 août 1885, *Delavay* s.n. (P); coteaux calcaires, au pied du Yang-in-chan (Lankong), 2500 m., 7 juin 1886, *Delavay* 2229 (P, GH); Hee-chan-men, 21 mai 1887, *Delavay* s.n. (P); les prairies des terrains sur le Hee-chan-men (Lankong), de 2800 à 3500 m., 27 juin 1885, *Delavay* s.n. (P); Western flank of Tali Range, lat. 25°40′N., 3350 m., *Forrest* 11658 (E); Mt. Chi Tsu, *McLaren's Collector* L1A (E); Pin-chaun Hsien, 2400 m., *H. T. Tsai* 52984 (GH).

SZECHUAN. Inter Yen yuan Hsien et Hunka, 2800 m., *Schneider* 1466 (E, US, GH).

I. delavayi is best distinguished by its radical leaves which bear 6–11 pairs of lateral leaflets, the upper pairs of which are incompletely divided from the rachis and have a second main vein parallel to the midrib. This character is also found in *I. lutea*, a species which has a true stem and seldom has radical leaves. The leaf character also divides *I. delavayi* from *I. mairei* and the terminal leaflet of the latter is always broader than the lateral leaflets so that the leaf tapers from the apex to base; here the opposite is the case (see fig. 11, D). The inflorescence generally bears more flowers than that of *I. mairei*, the calyx appears always to be unspotted and the teeth shorter than they are broad at the base (see fig. 12, C). From *I. compacta* with which it agrees in having a larger number of leaflets, it is distinguished by the venation and attachment of the upper leaflets as well as the absence of a stem.

The confusion, by Bureau and Franchet, of the extremes of *I. delavayi* with *I. mairei* var. *mairei* has already been pointed out (see p. 343) and of the seventeen specimens collected by Delavay which they cite, at least six belong to this taxon. It is impossible to pick out, from their description, any one particular sheet which the original authors might have had before them. In distribution, duplicates of Delavay's material appear to be rare in other herbaria and the specimens, gathering for gathering, do not always match those at Paris. Thus, in choosing *Delavay* 1027 as lectotype, the

selection of the most typical sheet has been the primary consideration.

Cox (1930, p. 38) credits Farrer with collecting *I. delavayi* in Kansu. Unfortunately his herbarium specimen of this plant (No. 268) has not been examined but the field notes ("A beautiful plant of much lower habit and larger flowers than *I. delavayi*. Seed scapes 6–9 in. high, flowering stems much shorter round the crown") make it obvious that the plant was not *I. delavayi* at all but probably *I. compacta* (there is an unlabelled specimen of this among this collection at Edinburgh). Also, if *I. delavayi* does grow in Kansu it would have been recorded by some other collector but it appears to be confined to Yunnan and Szechuan. Thus, *I. delavayi* var. *farreri*, references to which occur in horticultural literature (L. H. & E. Z. Bailey, 1941), is completely erroneous (see p. 325).

This species is perhaps the most popular *Incarvillea* in cultivation not only because of its beauty of flower but also because it is easily adaptable to average garden conditions and individual plants may perennate happily for ten years and more. Seed of it was first introduced by Delavay himself but it was subsequently lost. It was reintroduced by George Forrest acting on behalf of Messrs. Bees Ltd., and is now generally sold under the name 'Bees' Pink' a cultivar that appears to differ from the wild forms only by the light pink colour of its flowers.

Incarvillea subgen. **Niedzwedzkia** (B. Fedtsch.) Grierson **stat. nov.**

Syn.: *Niedzwedzkia* B. Fedtsch. Rastit Turkest. 701 (1915).

14. **Incarvillea semiretschenskia** Grierson, **comb. nov.** (Plate 16).

Syn.: *Niedzwedzkia semiretschenskia* B. Fedtsch. in Bull. Jard. Bot. Pierre Grand xv, 399 (1915) cum ic.; Rastit Turkestan 701 (1915); Vassilczenko in Not. Syst. U.R.S.S. xviii, 219 (1957) et Flora U.S.S.R. xxiii, 5 (1958).

Erect perennial herb, woody at the base 8 mm. thick, branched. *Stems* 20–30 cm. high branched, striated, glabrous. *Leaves* alternate, pinnatisect or bipinnatisect, 1·5–5 cm. long, glabrous; segments 7–9 pairs linear, acute at the apices 0·75–2·5 mm. broad, simple or again divided into 3–5 segments (see fig. 7, E). *Inflorescence* racemose; pedicels 0·5 cm. long in flower, 1·5 cm. long in fruit, borne in the axil of a minutely glandular-puberulent, ovate-elliptic bract 5 mm. long and bearing two smaller bracteoles close above this, the three appearing as a tripartite bract. *Calyx* subpolysepalous, tubular only at base, minutely glandular puberulent 5–7 mm. long; sepals spreading or reflexed in fruit, obovate acuminate with or without membranous horn-like margins (altogether ± cuneate in outline) (see fig. 8, E). *Corolla* deep rose-red, tube 2·5–3 cm. long, lobes 0·75 cm. long rounded. *Staminode* minute. *Capsule* (immature) ovate, 6-winged ligno-coriaceous at least 3 cm. long; wings 0·9 cm. broad at base narrowing above with irregularly crenate margins. Septum bifid at the apex. *Seed* compressed, plano-convex, pale brown, surface minutely rugose, 6 mm. long 5 mm. broad including wing (c. 1 mm. broad).

HABITAT. On mountain slopes in *Artemisia* steppe as well as in valleys and on limestone cliffs.

PLATE 16. Type specimen of *Incarvillea semiretschenskia* (B. Fedtsch.) Grierson.

TURKESTAN (Kasakh) Semiretschensk prov. Basin of Kopal river, 18 May 1909, *Niedzwedzki* s.n. (LE, holo.); Mt. Akrakan, Alma (-Anshu?) towards Kazakstan, 1926, collector unknown (LE); Tian-schan exterior in loco Ajderke, in montibus Tchu-iliensibus, *Joffe & Titov* 446 (E, K).

In several characters this species appears at first sight to belong to the subgenus *Incarvillea*. As Fedtschenko remarked, the habit is very similar to that of *I. olgae* and in its bipinnatisect leaves it agrees with *I. sinensis* but its segments are less divided than they are in that species. The thickish herbaceous sepals with their membranous margins may also be compared with the segments of the tubular campanulate calyx of this subgenus. Apart from its almost polysepalous calyx, however, this species is distinct from the species of the subgenus *Incarvillea* (and from all other species) on account of its ligno-coriaceous 6-winged capsule which appears to be only tardily dehiscent. Correlated perhaps with the development of this fruit, the wings of the seeds have become reduced and, in their somewhat leathery character, resemble those of the subgenus *Pteroscleris* which are also somewhat reduced.

On the type specimen the calyces are composed of unwinged sepals but on *Joffe & Titov* 446 wings may be present or absent whereas on the third specimen (collector unknown) they are regularly present. No explanation is offered for this variability nor do the specimens appear to differ in other respects. The winged state appears to represent a stage in the course of the development of this organ as seen in the other subgenera and particularly in *Incarvillea* wherein the sepals have fused along the lateral margins and the wings have given rise in *I. sinensis* and *I. potaninii* to the membranous bifid teeth which alternate with those formed by the free ends of the sepals and account for these calyces being described as " 10-toothed" (see De-Candolle, Don, etc.). This explanation for the origin of these supplementary teeth given by Bureau (l.c.) is strengthened by the recognition of *I. semiretschenskia*.

According to Vvedensky (Herb. Fl. As. Med. Fasc. 18 (1928) No. 446), Titov was unable to find this plant in its *locus classicus*, in spite of several attempts to do so which led him to suppose that it has been incorrectly noted by Niedzwedzki. It may also indicate that the species is becoming extinct, for Vassilczenko (l.c.) relates that no more material of this remarkable plant has been collected during the last 25 years and that it has now disappeared from its three known localities. Goloskokov (Izvest. Akad. Nauk. Kazak. SSR, No. 74, 4: 1949) in his Materials for a Flora of the Chu-Ili Mountains does not record this species.

The transliteration of the subgeneric name would, according to Busch (Jour. Soc. Bot. Russ. iii, 153: 1918) have been more correct as "*Niedzwieckia*". In its suffix, the specific name does not conform with the recommendation (73d) in the International Rules of Nomenclature for the formation of epithets from geographical names but, as it is neither an orthographic nor a typographic error, it must be retained in its present form.

Fossil Species

Incarvillea pristina E. M. Reid & M. E. J. Chandler, Cat. Cainozoic Pl. (Bembridge Fl.) 130, t. 8, fig. 23 (1926).

This fossil species is based on the impression of the ventral surface of a seed found in the Oligocene beds near Gurnard in the Isle of Wight and is part of the A'Court Smith collection at the British Museum (Natural History).

The authors record that the fossil (V. 17611) is similar to the seeds of both *I. mairei* and *I. compacta* but smaller than the former and differing in the arrangement of cells in the testa in the latter.

Although only one isolated specimen is known, no reason has been brought forward to discredit this determination. No further material has been found in beds of Tertiary age in this country nor has any been recorded from abroad. (For this information the present author is indebted to Dr. K. Chesters of the Palaeontology Section of the British Museum, in collaboration with Miss Chandler.)

Excluded Species

I. argyi Lévl. in Bull. Geogr. Bot. xxiv, 292 (1914); Cat. Illust. et Alph. des Pl. du Sen Tchouen, t. 4 (1918) = *Ipomaea quamoclit* Linn.

I. chinensis Spreng., Syst. ii, 836 (1825); DC., Prod. ix, 237 = *Campsis adrepens* Lour. (See Merrill, Comment. Lour. Fl. Coch.)

I. dubia Wall. MSS.; DC. Prod. ix, 264 = *Lysionotus serratus* D. Don.

I. foliosa Steud., Nom., ed. 2, i, 805 = *Crotalaria medicaginea* Lamk.

I. grandiflora Poir. in Dict. Sci. Nat. xxiii, 53 (1822) = *Tecoma grandiflora* Delaun.

I. grandiflora Spreng., Syst. iii, 836 = *Aeschynanthus grandiflorus* G. Don.

I. oblongifolia Roxb., Hort. Beng. 95; Fl. Ind. iii, 113 = *Chirita oblongifolia* (Roxb.) Sinclair.

I. parasitica Roxb., Pl. Corom. iii, 88, t. 291 (1819); Hort. Beng. 47; Fl. Ind. iii, 112 = *Aeschynanthus parasiticus* (Roxb.) Wall.

I. tomentosa Roxb. ex DC., Prod. ix, 237 = *Paulownia imperialis* Sieb. & Zucc.

I. tomentosa Spreng., Syst. ii, 836 = *Bignonia mollis* Vahl.

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