A REDEFINITION OF GASTONIA AND RELATED GENERA (ARALIACEAE)

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SUMMARY

The six genera *Gastonia, Tetraplasandra, Reynoldsia, Munroidendron, Peekeliopanax*, and *Indokingia* form a natural complex distributed from East Africa to the Marquesas and the Hawaiian Islands. The characters which have been thought useful in distinguishing these genera are re-examined. The distinction between *Gastonia* and *Tetraplasandra* is redefined, emphasis being placed on the radiating stigmatic arms in the fruit rather than on pleiomery of the stamens. On this basis *Tetraplasandra* is confined to the Hawaiian group. The monotypic genera *Peekeliopanax* and *Indokingia* are reduced to synonymy under *Gastonia*, which thus comprises all species of the complex west of Samoa.

INTRODUCTION

Araliads with imparipinnate leaves and pedicels with no articulation between the pedicel and the flower form a clearly defined group with a nearly continuous distribution from East Africa, through the islands of the Indian Ocean and Malesia, to the Solomons, Samoa, the Society Islands, the Marquesas, and the Hawaiian group. Generic limits within this natural group of species have always been confused, and this is especially true in the Malesian area. Here, at the centre of the range, species have been referred to genera characteristic of the Pacific or the Indian Ocean according to the characters available in the material being studied.

The reason underlying much of this confusion is undoubtedly that the fruit of *Gastonia* Comm. *ex* Lamk is distinctive, having radiating stigmatic arms, and that the flower found in many species of *Tetraplasandra* A. Gray is also distinctive, having numerous stamens. In the Malesian and some other species these two features occur together. This has resulted in fruiting material being described as species of *Gastonia*. *G. papuana* Miq., *G. winkleri* Harms, and *G. boridiana* Harms were all described from specimens lacking floral parts. On the other hand, flowering material (with the exception of *G. eupteronoides* Teysm. & Binn.) has been described either as *Tetraplasandra* (*T. paucidens* Miq., *T. philippinensis* Merr., *T. solomonensis* Philipson, and *T. koordersii* Harms) or as the new monotypic genus *Peekeliopanax* Harms. Indeed, Miquel described flowering and fruiting material of the same species as a *Tetraplasandra* and a *Gastonia* on consecutive pages and Harms described another species as *Peekeliopanax* from flowering material, and several years later described a fruiting specimen of the same species as a *Gastonia*.

In the present study the characters which have been used to diagnose the genera within this complex of species have been re-examined. The species are currently placed in six genera, three of moderate size and three monotypic. These are set out in Table 1. The remarks included in the last column of Table 1 are intended to indicate some of the characters at present used to delimit the genera. These and other characters will be discussed in the following account. For purposes of presentation of data, the genus *Tetraplasandra* has been regarded as confined to the Hawaiian Islands. This practice is justifiable because all the Malesian *Tetraplasandra* can be referred to existing species of *Gastonia*. This course in no way prejudices any decisions on generic limits that may be drawn after the data have been presented.

TABLE 1. GENERA CURRENTLY RECOGNIZED

Genus	Number of spp.	Distribution	Remarks
Gastonia	7	East Africa, Madagascar, Seychelles, Mascarenes, Malesia, Solomons.	At present defined by the radiating stigmatic arms in the fruit, and the stamens (supposedly) equal in number to the corolla segments.
Tetraplasandra	19	Hawaiian group (Malesian and Solomons spp. excluded - see text).	Stigmatic arms not radiate in fruit, some spp. with pleiomery of the stamens, ovary cells rather few (10--)5--2, and leaflets entire.
Reynoldsia	17	Hawaiian group, Marquesas, Society Islands, Samoa.	Stigmatic arms not radiate in fruit, stamens equal in number to petals, ovary cells rather numerous (6--)10--24, leaves rarely without some denticulations.
Munroidendron	1	Hawaiian group.	Stigmas not radiate in fruit, stamens not more than corolla ribs, ovary cells about 13, inflorescence branches long--racemose.
Peekeliopanax	1	New Britain, New Guinea, Solomons.	Radiating stigmatic arms (unknown when described), corolla calyptrate, stamens numerous.
Indokingia	1	Seychelles.	Radiating stigmatic arms with cleft tips, corolla calyptrate, stamens numerous.

DESCRIPTION OF THE CHARACTERS

Vegetative morphology

All the species are trees with imparipinnate exstipulate leaves clustered at the ends of thick branches. The majority are glabrous but the single species of *Peekeliopanax* Harms and *Munroidendron* Sherff have indumentum as do *Tetraplasandra hawaiiensis* A. Gray, *T. kauaiensis* (H. Mann) Sherff, and *T. turbans* Sherff. The margin of the leaflets is entire in *Tetraplasandra* A. Gray, *Munroidendron* Sherff, and also in most *Gastonias*. *G. papuana* varies from entire to strongly crenate, both conditions occurring at the two extremes of its wide range. In *Peekeliopanax* the leaflets are crenate, usually strongly so. The leaflets of the Hawaiian species of *Reynoldsia* A. Gray are distinctive, being borne on long petioles with the lamina papery in texture when dry, somewhat rhomboidal in shape, and with an undulate and dentate margin. The southern species of *Reynoldsia* have more varied leaflets, ranging from those similar to the Hawaiian type to leaflets approaching those found in the other genera of the complex (e.g. *R. pleiosperma* A. Gray).

The inflorescence

The inflorescences terminate the leafy shoots. They may take four main forms: 1) The principal branches may be strictly umbellate, as in species of *Tetraplasandra* with twice or thrice umbellate inflorescences (fig. 1) and this character recurs in *Reynoldsia verrucosa* Seem. (Society Islands). 2) A more common arrangement in these genera is for the main branches (rhachids) to be umbellately arranged, but for the ultimate umbellules to be borne along them in a racemose or subverticillate manner (fig. 2). Such inflorescences also occur in *Peekeliopanax* and *Indokingia* Hemsl. 3) Internodes may develop between the nodes bearing the main branches (fig. 3), giving a paniculate inflorescence (e.g. *Gastonia papuana*). 4) Finally, internodes may develop between all, or at least the outer (lower) pedicels of the ultimate flower clusters, so that these are not umbellules but are more or less distinctly racemose (fig. 4). This character appears in a few species of *Tetraplasandra* and *Reynoldsia*. In *Munroidendron* the long pendulous rhachids bear very striking racemosely arranged flowers.

The pedicel

One important character that distinguishes this group of genera from *Polyscias* Forst. and its allies is the lack of a constriction between the flower and the top of the pedicel. In *Polyscias* there is an articulation below the flower which is clearly visible in fresh material of young flowers and fruits. In fresh material of the genera being considered no such articulation is visible. However, in dried material of flowers of a few species a constriction occurs at the top of the pedicel. This is due to the drying of the fleshy tissue at the base of the hypanthium. In fruiting material these tissues become stronger and the constriction no longer develops on drying. This artifact can become so noticeable in some species [e.g. *Tetraplasandra waialealea* Rock, *T. meiandra* (Hillebr.) Harms and *T. kauaiensis*] that incorrect identifications may occur.

The calyx

The calyx may consist of a rim with the margin entire and straight or irregularly undulate. In most species of *Tetraplasandra*, if not all, the undulations form more regular lobes, usually alternating with the petals, and each bearing a minute apical tooth. In *Reynoldsia* any suggestion of lobing or toothing of the calyx rim is even more obscure and irregular. In *Gastonia* and *Peekeliopanax* undulations of the calyx rim, when present, are irregular. I have been unable to check this feature in *Indokingia*.

The corolla

The general features of the corolla are similar throughout the group, being those typical of the *Scheffllereae*. Those features which are variable, and which will be considered here, are the number of petals and the degree of their separation.

Table 2 indicates the range of merism observed in the genera. The numbers of petals relate either to the free petals or to the more or less united segments of the corolla.

Complete fusion occurs in *Indokingia* Hemsl. In *Peekeliopanax* the corolla is also calyptrate, but sutures which do not reach the outer surface of the cap are clearly developed. The petals of *Munroidendron* are variously free or united into groups. The petals of

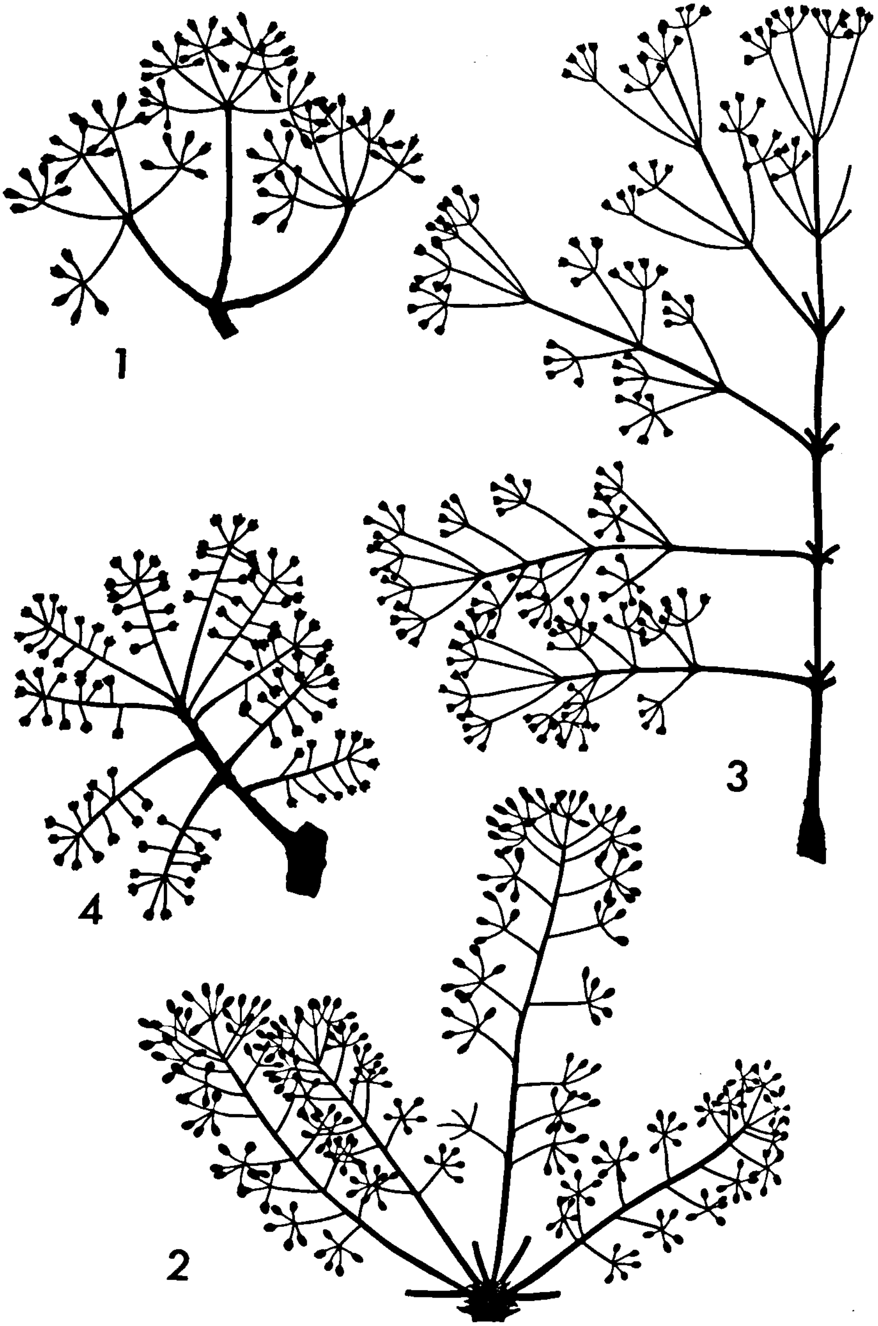

Fig. 1—4. Inflorescence types. — 1. *Tetraplasandra meiandra*, compound umbel. — 2. *Peekeliopanax spectabilis*, an umbellate arrangement of racemes of umbels. — 3. *Gastonia papuana*, panicle. — 4. *Reynoldsia sandwicensis*, ultimate branches.

TABLE 2. MERISTIC VARIATION IN GENERA ALLIED TO GASTONIA

Genus	Petals or corolla segments	Stamens	Ovary cells
Gastonia	5—13	7—55	7—12
Tetraplasandra	5—9	5—60	2—10
Reynoldsia	8—12	8—12	6—24
Munroidendron	16—20	5—20	12—14
Peekeliopanax	6—12	25—66	6—22
Indokingia	6	93	13

Gastonia, Tetraplasandra and *Reynoldsia* do not appear to be united organically, but frequently fail to separate completely.

The number of stamens

In *Reynoldsia* stamens equal the petals in number and alternate regularly with them (Table 2), as they do also in some species of *Gastonia* (e.g. *G. cutispongia* Lamk) and *Tetraplasandra* (e.g. spp. 14—19 in Sherff, 1955). In other species of these two genera the androecium is pleiomerous (e.g. *Gastonia seychellarum* Baker has five petals and eighteen stamens and *G. papuana* is extremely variable, with 7 to 55 stamens).

Peekeliopanax is equally variable with 25—66. It has been possible to make only one count of the stamens in *Indokingia*, the result being 93. The stamens in *Munroidendron* are equal to, or fewer than, the number of petal ribs evident in the corolla. Since these are irregularly united into lobes of varying size, the stamens outnumber the free portions of the corolla.

The hypanthium

As in the family generally, the ovary is inferior, though, as in several other genera throughout the family, the disk and stylopodium may be so well developed that the insertion of the calyx, corolla, and stamens is well below the summit of the ovary. In that case ovary cells and placentae extend well above the level of insertion of the perianth (e.g. *Tetraplasandra kauaiensis*) and this feature becomes emphasized as the fruit develops. In two species, *T. gymnocarpa* (Hillebr.) Sherff and *T. turbans*, the ovary is completely superior (Eyde & Tseng, 1969), a feature unknown elsewhere in the family.

Number of ovary cells

The observed range (Table 2) is considerable in all the genera (except for *Indokingia* where few counts were possible). Most species of *Tetraplasandra* have five or fewer cells, the higher numbers occurring in *T. hawaiiensis* and *T. waimeae* Wawra. The species of *Reynoldsia* exhibit an interesting geographical variation in the number of ovary cells.

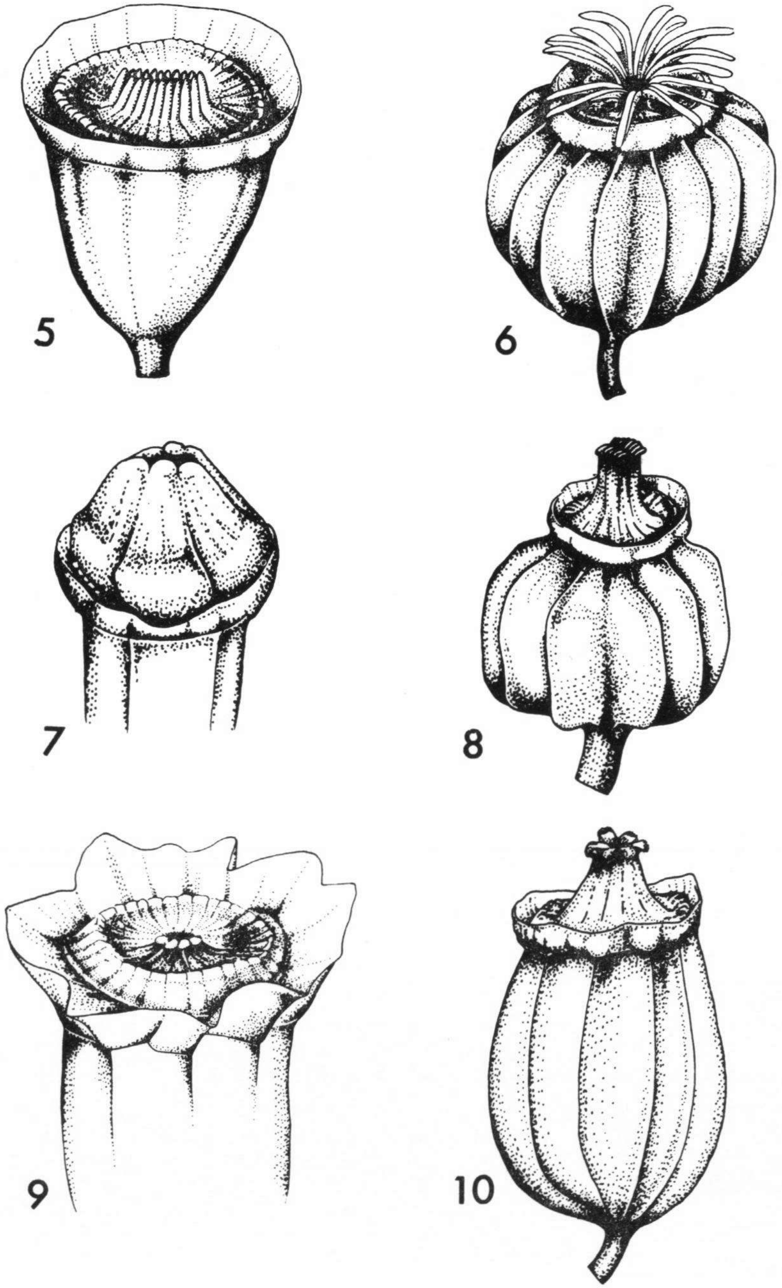

Fig. 5—10. Stylopodia of flowers and fruits. — 5. *Peekeliopanax spectabilis*, at anthesis. — 6. Ditto, in fruit. — 7. *Reynoldsia venusta*, at anthesis. — 8. *Reynoldsia pleiosperma*, in fruit. — 9. *Tetraplasandra lihuensis*, at anthesis. — 10. *Tetraplasandra pupukeensis*, in fruit.

At one end of their range (Samoa) gynoecia with nearly twenty or more cells occur whereas ten or fewer are found in the Hawaiian species. The species of the Society Islands and the Marquesas are intermediate in this character.

The nature of the styles

In *Gastonia*, *Peekeliopanax*, and *Indokingia* the styles, at anthesis, consist of free finger-like processes radiating inwards from the centre of the usually rather flat disk, to roof over a central cavity above the loculi. They are arranged in an ellipse or in two parallel rows, and may be almost flat or be raised into a more or less prominent double ridge (fig. 5). As the fruit develops, these rays curve outwards to form radiating free arms (fig. 6). The styles of the *Reynoldsias* of the South Pacific are similar, there being a double ridge of short projections at the centre of a rather flat disk, but the projections are shorter, resembling crenulations rather than processes. In some Hawaiian species of *Reynoldsia* the disk forms a hemispherical dome at the centre of which a pore is surrounded by the very short lobes of the styles (fig. 7). Mature fruits of *Reynoldsia* bear a hollow column (stylopodium) capped by a rim of stylar bulges. These do not separate or project as free radiating arms. In *Tetraplasandra* and *Munroidendron* the centre of the disk may be raised as a ridge or as a cone with a central slit or pore having a slightly crenulate margin (fig. 9). The fruit in these two genera bears a conical stylopodium tipped with the usually few stylar bulges. Only in *Tetraplasandra pupukeensis* Skottsb. do these show a very slight development of radiating arms (fig. 10).

Harms (1926) comments on the shortly bifid stigma of *Indokingia*. In all the genera the stigmatic surface forms two lines, one along each margin of the stigmatic arm or bulge. The presence in *Indokingia* of a terminal cleft can be regarded as a development of these two stigmatic lines.

Vascular system of the flower

No attempt has been made to study the complete range of variability in the pattern of the floral vascular system in these genera, but serial sections have been examined of flowers of the three monotypic genera and also of three species of *Gastonia*, six species of *Tetraplasandra*, and two of *Reynoldsia*.

The vasculature conforms to the pattern characteristic of the family (Philipson, 1970). Variation in detail is considerable in view of the great meristic variation in and between whorls of floral members. In all species of these genera examined the dorsals are independent for the greater part of their course and several carpellary bundles may occur between these and the ventrals. The ventrals sometimes run as two or more separate bundles for most of their course (e.g. *Indokingia*) or more usually a single ventral runs opposite the septa until near the top of the loculus, when it divides to provide branches to the ovule, the reduced ovule, and to the disk.

The peripheral system of bundles supplies the calyx, corolla, and androecium. In addition at the summit of the ovary it is linked to the carpellary system of bundles and supplies bundles to the disk. In flowers with few stamens there are distinct staminal bundles in the peripheral system of the ovary wall (e.g. *Gastonia cutispongia*). When the stamens are rather more numerous the number of peripheral bundles is approximately equal to the number of stamens and all contribute to the androecium. This was the case in flowers of *Gastonia papuana*, *Tetraplasandra hawaiiensis*, and *Peekeloipanax* in which the number of stamens did not exceed 18, 20, and 37 respectively. In flowers with more numerous stamens, the bundles of the peripheral system divide as they approach the apex of the hypanthium. The vascular system of *Peekeliopanax* is distinctive in that the peripheral system forms two separate rings of bundles in the ovary wall.

DISCUSSION

To recognize generic limits within this assemblage of species it is necessary to consider combinations of the characters described above, and also the geographical areas occupied by these combinations. Much importance has been given to pleiomery of the androecium, but this character occurs in species whose position in *Tetraplasandra* or in *Gastonia* has never been questioned. Similarly species occur in both these genera with the stamens equal in number to the petals. The recognition that the same species has been placed in *Tetraplasandra* or *Gastonia* on androecial and fruit characters respectively places further doubt on the value of stamen number as a generic character.

A second character to which importance has been attributed is the nature of the style in the fruit. The fruit of *Gastonia* is highly characteristic because of the radiating style arms combined with a calyx rim without any regular or clearly defined lobes. This type of fruit is found in all members of the complex from the Solomon Islands westwards. No Pacific Ocean members of the complex have fruits of this kind. The fruits of *Tetraplasandra* and *Munroidendron* terminate in a hollow conical stylopodium bearing at its apex a number of stigmatic bosses which only rarely form minute radiating projections. In *Reynoldsia*, especially in the southern species, the stigmatic processes at anthesis can be similar to those of *Gastonia*, but in the fruit they develop into structures essentially like those of *Tetraplasandra* and *Munroidendron*.

This division of the complex into a Pacific group and an Indian Ocean-Malesian group, using the character of the style in the fruit, can be supported to some extent by subsidiary characters. The calyx shows some indication of regular lobes, however faintly, in *Tetraplasandra* and in most species of *Reynoldsia*, but not in the western group (*Indokingia* possibly excepted). The character of flowers in racemes is also confined to the Pacific, but occurs even there in only a minority of the species. Some other characters, such as a calyptrate corolla or a superior ovary, occur in only one of these geographical groups but are too occasional to provide additional basis for their separation.

There can be no doubt that all the groups within the complex are very closely related and could well be regarded as a single genus. However, this would result in rather a large unit, and since geographical distribution corresponds to a difference in fruit character it appears advisable to recognize a subdivision into genera. The Pacific group of species is currently divided into three genera, *Munroidendron*, *Tetraplasandra*, and *Reynoldsia*. The first comprises a single species with such a distinct inflorescence and corolla that it can well claim generic status. The distinction between *Tetraplasandra* and *Reynoldsia* is difficult to define. In general terms, *Tetraplasandra* contains species with relatively few ovary cells, leaflets with entire margin, and often pleiomerous stamens. It is true that *T. kauaiensis*, for example, has isomerous androecium and may have only one fewer ovary cell than some *Reynoldsia* species, but its leaves are entire. On the other hand, species of *Reynoldsia* which have leaflets with entire margin, or nearly so, have a much higher number of carpels than any *Tetraplasandra*. Such complex distinctions, based on the presence of a majority of several variable characters, appear unsatisfactory as a basis for generic separation. This is especially so when, as here, the ranges of the two genera overlap.

The Indian Ocean-Malesian group also comprises several genera as understood at the present time. Several species of *Tetraplasandra* have been described from this area, namely *T. paucidens*, *T. philippinensis*, *T. koordersii*, and *T. solomonensis*. These four names are here considered to be synonymous. Three other names have been applied to this widespread species in the genus *Gastonia*, namely *G. eupteronoides*, *G. winkleri*, and *G. papuana*. This species is regarded as a *Gastonia*, because its fruit characters are typical of that genus.

The presence of numerous stamens has resulted in its being placed in *Tetraplasandra* but other *Gastonia* species share this character.

All the species from the Solomon Islands westwards to Madagascar and East Africa, therefore, possess a fruit with radiating style arms. Within this area, two species have been singled out to form monotypic genera, namely *Indokingia* (Seychelles) and *Peekeliopanax* (New Britain, New Guinea, and the Solomons). The latter genus was described by Harms and was based on flowering specimens from New Britain. When fruiting material reached Harms from New Guinea he recognized them as a *Gastonia* and named it *G. boridiana*, without realizing that it was conspecific with *Peekeliopanax*. There can be no doubt that this genus is superfluous. Harms compared its flowers with those of *Gastonia* but was not at that time aware that the androecia of other *Gastonia* species could exhibit almost as high pleiomery as *Peekeliopanax*. It is true that the corolla sutures of *Peekeliopanax* do not entirely separate the petals and that the peripheral vasculature of the ovary is distinctive, but these do not appear sufficient to warrant the maintenance of a separate genus within the geographical range of *Gastonia*.

When describing *Indokingia* from the Seychelles, Hemsley remarked on its similarity to *Gastonia cutispongia*. At that time the occurrence of pleiomery of the androecium was not recognized, so that its extreme form in *Indokingia* seemed ample justification for a new genus. Harms (1926) remarked on the similarity between *Indokingia* and both *Peekeliopanax* and *Tetraplasandra*. Its calyptrate corolla is similar to *Peekeliopanax*, from which genus he distinguished it on the slightly cleft stigmas and details of the leaflet and of inflorescence branching. Since similar leaves, inflorescences, and stamen numbers can be found in species of *Gastonia*, the only basis for maintaining *Indokingia* is the slightly cleft arms of the stigma, a character scarcely justifying generic status, especially as the genus *Gastonia* is represented in the Seychelles.

For these reasons it is proposed that *Peekeliopanax* and *Indokingia* be united with *Gastonia*, which thus becomes the sole genus representing this complex west of Samoa. The description of the genus requires amending by increasing the possible number of stamens up to approximately one hundred and several times more numerous than the petals. Such a change was required in any event to accommodate species already in *Gastonia* since *G. seychellarum* may have more than three times as many stamens as petals and *G. papuana* may have up to sixty six stamens. The generic description should also be amended to allow for indumentum and a calyptrate corolla imperfectly divided into its constituent petals.

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