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REVISION OF HAPLOSTICHANTHUS (ANNONACEAE)

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SUMMARY

In the present revision six species are recognized within *Haplostichanthus* F. Muell. (Annonaceae), which now includes the genus *Papualthia* Diels. Four new combinations are made: *Haplostichanthus gamopetala, H. heteropetala, H. lanceolata,* and *H. longirostris*. One new species from New Britain is described: *H. stellatus*.

INTRODUCTION

The present paper deals with the revision of the genera *Haplostichanthus* F. Muell. and *Papualthia* Diels. When studying the flower morphology of Annonaceae (Van Heusden, 1992), I found indications that the genus delimitation of *Papualthia* was problematic in three ways: 1) the Philippine species differ in their flowers from the species from New Guinea; 2) some specimens of the Australian genus *Haplostichanthus* so closely resembled certain specimens of *Papualthia* from New Guinea and New Britain that I suspected these specimens to be conspecific, and, consequently, that *Haplostichanthus* and *Papualthia* are congeneric; 3) the delimitation from *Polyalthia,* and especially the position of *Polyalthia celebica,* which closely resembles the *Papualthia* from New Guinea except for its free petals. Therefore, a revision of *Haplostichanthus* and *Papualthia* is carried out to examine the genus delimitations.

Haplostichanthus and *Papualthia* are both recognized by their flowers with connate petals (Fig. 1), two or more lateral ovules per carpel, and leaves with a distinct reticulate venation (in larger-leaved specimens). The two genera differ in the arrangement of the six petals: in one whorl in *Haplostichanthus* and in two whorls in *Papualthia.* A comparable situation is found in the African genus *Monanthotaxis* sensu Verdcourt (1971) (Annonaceae). Verdcourt included in *Monanthotaxis* Baill. the former genus *Enneastemon* Exell and the African species of *Popowia* Endl. In the latter *Popowia* species the petals are placed in two whorls. In flower buds of *Enneastemon* the petals are placed in one whorl but overlap in two series at the apex. In *Monanthotaxis,* in its original sense, the petals from base to apex are placed in a single whorl. In other characters these genera were highly similar.

The flowers of the Philippine species of *Papualthia* look in their flowers quite different from the species from New Guinea, but their leaves show a great overall similarity. The Philippine species have mostly solitary, middle-sized flowers with long petal-lobes, usually long pedicels, whereas the position of the inflorescence is vari-

able. In contrast, the flowers of the New Guinean species are small, with relatively short petal-lobes and usually short pedicels. The inflorescence is mainly axillary and often several-flowered. Specimens with closed flower buds are rarely collected in the Philippines, whereas collections from New Guinea mainly consist of flower buds and only few open flowers. Flower buds in the Philippine species open very early in their development. This type of flower bud development is also common in some other Annonaceae, e.g., *Desmopsis, Polyalthia, Sapranthus,* and *Stenanona* (Van Heusden, 1992).

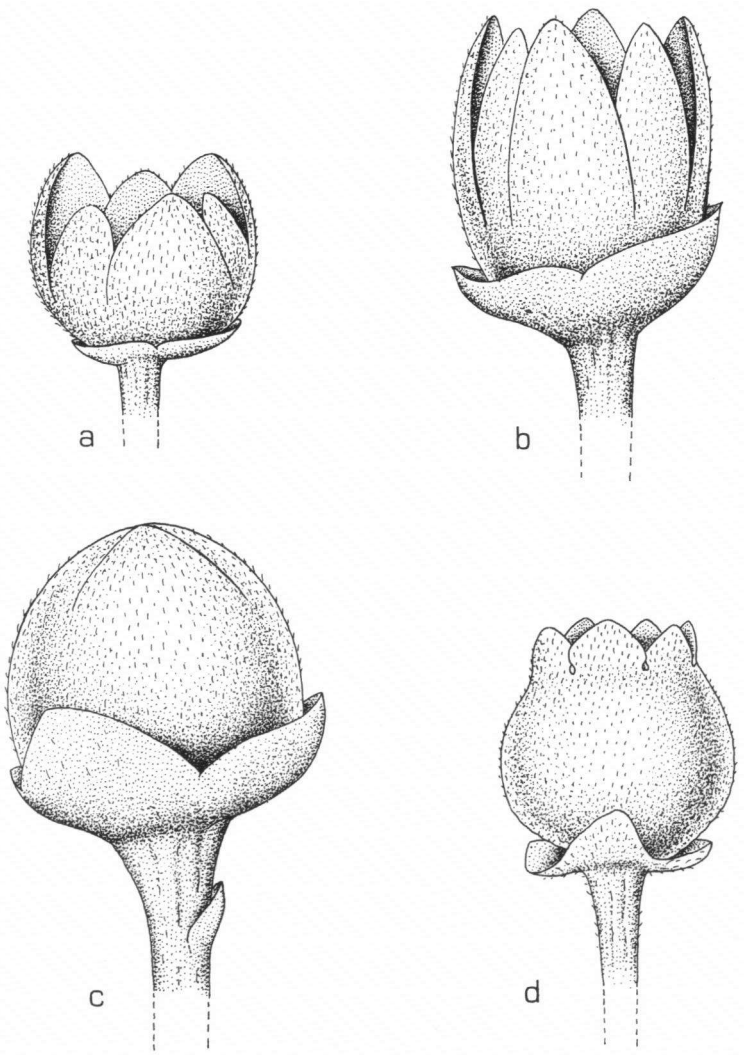

Fig. 1. Various degrees of fusion of petals in species of the genus *Haplostichanthus*. — a. *H. johnsonii* F. Muell.; b. *H. lanceolata* (Vidal) Heusden; c, d. *H. longirostris* (Scheff.) Heusden; all × 6 (a: *Jessup 748*; b: *Ramos 17417*; c: *NGF 7136*; d: *Pullen 8324*).

Polyalthia celebica has an intermediate position between *Polyalthia* and *Haplostichanthus*. Diels (1912), when describing the genus *Papualthia*, already suggested to transfer *Polyalthia celebica* to *Papualthia*. *Polyalthia celebica* agrees with *Haplostichanthus* by the presence of closed flower buds and a relatively low number of stamens and carpels. It differs from *Haplostichanthus* in the free petals. In the original description, *Papualthia* included species with connate as well as with free petals, due to the inclusion of two species now included in *Pseuduvaria*.

CLADISTIC ANALYSIS

After examination of all material, it was still difficult to make decisions about the genus delimitation. Therefore, a cladistic analysis was carried out to be able to make a more thoroughly based taxonomic decision. The program used is HENNIG86 (Farris, 1988). The ie-option was used to calculate the most parsimonious tree. The 'ccode -,.' command was given to make the character states unordered. HENNIG86 needs an outgroup for which some *Polyalthia*-species were selected. The character states of the outgroup(s) are automatically considered as the most primitive.

CIRCUMSCRIPTION OF TAXA

The taxa listed below are examined in the cladistic analysis. The data of the *Polyalthia* species are taken from the specimens available in the herbarium of Leiden. The cladistic analysis was carried out after the decisions about species delimitation were taken.

As outgroups were taken *Polyalthia longipes, P. subcordata, P. tenuipes,* and *P. minutiflora*. These are *Polyalthia* species which more or less seem to be related to *Papualthia,* but definitively belong to *Polyalthia*. They share the unequal leaf bases and the glabrous inner side of the petals, whereas texture and venation of the leaves is quite close to those of *Papualthia*. Most of the species have relatively long pedicels. *Polyalthia minutiflora* is found on Mindoro in the Philippines and is possibly conspecific with *P. mindorensis* from the same island and *P. palawanensis* from Palawan. The material of the latter two species in the herbarium of Leiden was incomplete. The remaining species are found in Borneo, Java, and/or Sumatra. These species are included in the datamatrix to bring more clarity in the generic position of *Papualthia lanceolata*.

Polyalthia obliqua — This species from the Malay Peninsula and Borneo closely resembles *Papualthia* in vegetative aspects and more or less in its fruits. In at least some of the specimens from Borneo the petals are connate and tend to become smaller like in New Guinean *Papualthias*. The petals of the Malayan specimens are free. Similar to *Papualthia* the petals are glabrous inside with a more or less verrucose surface. The very high number of stamens and carpels is typical of *Polyalthia*, however.

Polyalthia celebica — This species from Sulawesi closely resembles the New Guinean specimens of *Papualthia* except that its petals are free; the small flower buds are somewhat conical towards the apex whereas in the New Guinean *Papualthias* the apex is rounded. The single ovule may be basally or laterally attached.

Polyalthia gamopetala — This is an obscure species from Sulawesi which has conspicuously connate petals and closely resembles the Philippine *Papualthias*. Its petals are unequal and the indument of the petals is denser than in the Philippine specimens of *Papualthia*. The large leaves resemble those of *Papualthia longirostris*, notably the specimens from West New Guinea.

Papualthia lanceolata — This species from the Philippines includes all but one of the former Philippine species of *Papualthia*. It shares with *Polyalthia* the flowers which open very early (closed buds are rarely available) and the relatively long petals. Its petals are connate, unlike in *Polyalthia*.

Papualthia heteropetala — This species from the Philippines is close to *P. lanceolata*, but differs from it in the smaller and more slender flowers with unequal petals.

Papualthia longirostris — This species includes all former New Guinean species of *Papualthia*, except two which are transferred to *Pseuduvaria* (Sinclair, 1956, and present paper).

Haplostichanthus johnsonii — This Australian species resembles *Papualthia longirostris* but differs from that species, among others, by the unequal petals arranged in one whorl.

Haplostichanthus spec. nov. — In some collections from New Britain flowers with very slightly connate petals were found, which seem to belong either to *Haplostichanthus* or to *Polyalthia*. The petals are arranged in one whorl as in *Haplostichanthus johnsonii*.

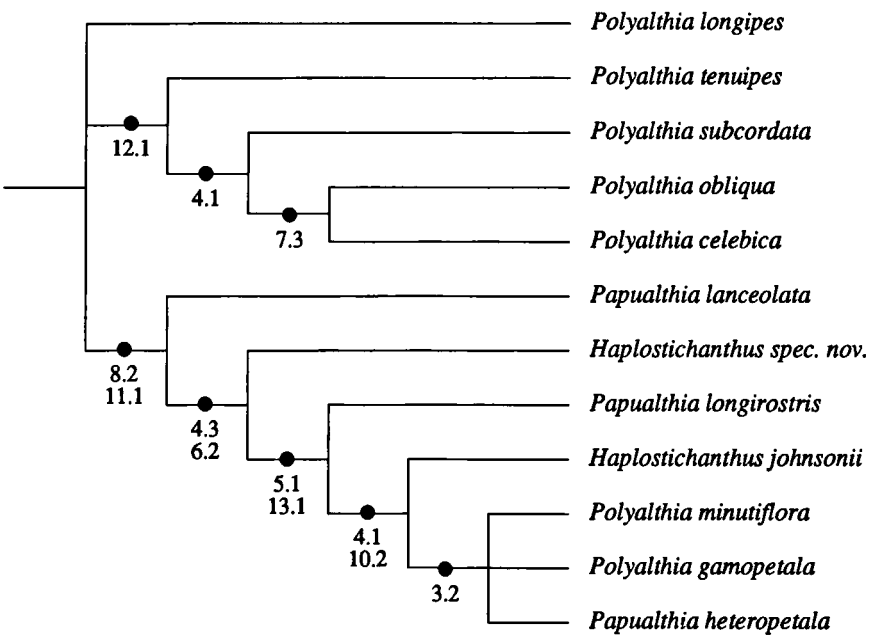

Fig. 2. The tree generated with ie-option. The numbers in the tree refer to the character states listed in Table 2.

Table 1. The datamatrix used in the cladistic analysis.

Taxon / Character	1	2	3	4	5	6	7	8	9	10	11	12	13
Polyalthia longipes	2	1	1	2	2	1	1	1	1	1	2	2	3
subcordata	2	1	3	1	2	1	1	1	1	1	2	1	1
tenuipes	2	1	2	2	2	1	1	1	1	1	2	1	3
minutiflora	2	1	2	1	?	2	1	1	1	2	1	2	1
obliqua	2	1	1	1	2	1	3	3	1	1	2	1	1
celebica	2	1	1	1	1	2	3	1	1	1	1	1	3
gamopetala	1	1	2	2	?	2	1	2	1	2	1	?	?
Papualthia lanceolata	2	2	3	2	2	1	1	2	1	1	1	2	1
heteropetala	2	1	2	1	1	2	1	2	1	2	1	?	1
longirostris	3	2	1	3	1	2	2	2	1	1	1	2	1
Haplostichanthus johnsonii	2	1	1	1	1	2	1	2	2	2	1	2	2
H. spec. nov.	2	1	1	3	2	2	1	2	2	1	1	2	3

Table 2. The character states used in the datamatrix.

1. *Leaf-base*
   1. equal
   2. unequal
   3. both conditions present
2. *Upper side of the leaves*
   1. glabrous
   2. occasionally hairy
3. *Position of the inflorescence*
   1. axillary, ramiflorous
   2. leaf opposed, extra-axillary
   3. both conditions present
4. *Length of the pedicel*
   1. generally short (c. 1 cm)
   2. usually very long, often slender
   3. both conditions present
5. *Buds*
   1. commonly present, subglobose
   2. rarely present, flowers open very early
6. *Flower size*
   1. usually medium-sized
   2. usually small (< 1 cm)
   3. both conditions common
7. *Number of flowers*
   1. solitary
   2. one to several
   3. several
8. *Fusion of the petals*
   1. free
   2. conspicuously connate
   3. both conditions present
9. *Number of petal-whorls*
   1. 2 whorls of 3 petals
   2. 1 whorl of 6 petals
10. *Relative size of the whorls*
    1. (sub)equal
    2. inner whorl longer
11. *Number of stamens and carpels*
    1. not very numerous
    2. very numerous
12. *Ovules*
    1. also basal ovules present
    2. 1–5, lateral
13. *Colour of the fruits*
    1. red
    2. black
    3. green (other data not available)

RESULTS

With the ie-option only one tree is generated (Fig. 2). One subtree contains most of the *Polyalthia* species. The other subtree contains the *Papualthia* species and the *Haplostichanthus* species as well as *Polyalthia gamopetala* and *P. minutiflora. Polyalthia obliqua* and *P. celebica* are both placed in the '*Polyalthia*-subtree'. The tree is not very consistent regarding the geographic distribution of the species: the Philippine *Papualthia lanceolata* is found at the base of the second subtree, whereas two other Philippine species, *Polyalthia minutiflora* and *Papualthia heteropetala,* are found in the final positions of the subtree. In this tree the latter species evolved from the Australian *Haplostichanthus johnsonii.*

CONCLUSION

The main conclusion is that *Haplostichanthus* and *Papualthia* (New Guinean and Philippine species) are monophyletic and consequently are congeneric, so the two genera are united, with *Haplostichanthus* being the older name. *Polyalthia gamopetala* has to be transferred to *Haplostichanthus. Haplostichanthus* spec. nov. also belongs to the latter genus and will be described in the present paper as *H. stellatus. Polyalthia minutiflora,* according to the tree, should be transferred to *Haplostichanthus* as well. As this species has free petals and a slightly different venation pattern of the leaves, I hesitate to consider this as a species of *Haplostichanthus*. For the time being, I prefer to keep this species in *Polyalthia.*

Polyalthia celebica and *P. obliqua,* according the tree, are not monophyletic with the *Haplostichanthus* species. Therefore, it is decided to keep *P. celebica* and *P. obliqua* in *Polyalthia. Haplostichanthus* in its new sense is separated from *Polyalthia* by the sympetalous corolla. Although the difference between *Polyalthia* and *Haplostichanthus* is very small, for the time being *Haplostichanthus* will be regarded as a separate genus. In a future revision of the large genus *Polyalthia* (c. 160 species) the generic status of *Haplostichanthus* may be reconsidered, if necessary.

RELATIONSHIPS WITH OTHER GENERA

In general, *Haplostichanthus* (in its new sense) is one of the many Asian genera which are more or less related to *Polyalthia* (e.g., Van Heusden, 1992; Van Setten & Koek-Noorman, 1992). Studies on pollen morphology and chromosome numbers point out that *Haplostichanthus* (in its original sense) is more closely related to the Australian genera *Ancana* F. Muell. (now included in *Meiogyne* Miq. by Van Heusden, 1994) and *Fitzalania* F. Muell., and to the Central American genus *Sapranthus* Seem. (Morawetz, 1988; Waha & Morawetz, 1988). The chromosome number of *Haplostichanthus* is 2n = 18. This chromosome number is, beside the three genera just mentioned, also found in *Polyalthia* This number is very common in the Asian Annonaceae (Okada, 1987). The pollen of *Haplostichanthus* is disulcate (Waha & Morawetz, 1988), whereas the former Philippine *Papualthia* species have inaper-

Table 3. The taxonomic situation before (a) and after (b) the present revision.

(a)	(b)
Haplostichanthus johnsonii	*Haplostichanthus johnsonii*
Papualthia auriculata	*Haplostichanthus longirostris*
Papualthia grandifolia	"
Papualthia longirostris	"
Papualthia micrantha	"
Papualthia pilosa	"
Papualthia roemeri	"
Papualthia rudolphii	"
Papualthia boholensis	*Haplostichanthus lanceolata*
Papualthia lanceolata	"
Papualthia loheri	"
Papualthia longipes	"
Papualthia reticulata	"
Papualthia romblonensis	"
Papualthia samarensis	"
Papualthia sympetala	"
Papualthia urdanetensis	"
Papualthia heteropetala	*Haplostichanthus heteropetala*
Polyalthia gamopetala	*Haplostichanthus gamopetala*
undescribed	*Haplostichanthus stellatus*
Papualthia bracteata	excluded
Papualthia tenuipes	dubious species

turate pollen, like most *Polyalthia* species (Walker, 1971). *Haplostichanthus, Ancana,* and *Fitzalania* resemble each other also in the seeds (Van Setten & Koek-Noorman, 1992). In its flower morphology *Haplostichanthus* is different from *Ancana, Fitzalania,* and *Sapranthus* (Van Heusden, 1992).

Connate petals are also found in *Oreomitra* Diels, a monotypic genus from New Guinea. The only collection available of *Oreomitra bullata, Schlechter 17655* (holo B; iso BR), is reminiscent of *Haplostichanthus longirostris*. The leaves, however, are much smaller than in bullate-leaved specimens of *H. longirostris*. The inflorescence is leaf-opposed, contrary to *H. longirostris*. The flowering material is incomplete and dissected, so the proper generic status cannot be determined. *Oreomitra* has thus far not been recollected.

DISTRIBUTION

The distribution of *Haplostichanthus* (Figs. 3–5) is mainly East Malesian, including Sulawesi, New Guinea, Philippines, Australia, and a number of more or less adjacent islands. The genus inhabits primary lowland and lower montane rain forests, mainly up to 700 m altitude; some populations of *H. longirostris* in Papua New Guinea can be found up to 2000 m altitude. Most species have a restricted distribution. *Haplostichanthus gamopetala* is endemic in Sulawesi; *H. lanceolata* and *H.heteropetala* are found in the Philippines, the latter species only in Luzon; *H. johnsonii* is endemic in Queensland (Australia). *Haplostichanthus longirostris* shows the widest distribution, occurring in New Guinea, Rossel Island, the Solomon Islands, and probably also Halmahera, New Britain, and Australia. The species delimitation of *H. longirostris,* however, is not very clear; a narrower species concept may reduce the size of its distribution area to New Guinea and the Solomon Islands, and add several endemic species restricted to very small areas in SE New Guinea and to the islands mentioned. *Haplostichanthus stellatus* is restricted to New Britain.

HAPLOSTICHANTHUS

Haplostichanthus F. Muell., Vict. Natural. 7 (Mar. 1891) 180. — Type species: *Haplostichanthus johnsonii* F. Muell. (as *'johnsoni'*).

Papualthia Diels, Bot. Jahrb. 49 (1912) 138. — Lectotype species: *Papualthia pilosa* Diels (see Fries, 1959); syn. nov.

Trees up to 30 m high or shrubs. Young twigs sparsely to densely hairy, hairs simple, older twigs generally glabrous, sometimes lenticels present. *Leaves* membranous to subcoriaceous, rarely coriaceous or chartaceous, glabrous or sometimes hairy above, sparsely to densely hairy or glabrous beneath, occasionally more or less bullate, oblong to elliptic or to (narrowly) (ob)ovate, rarely lanceolate, 2.5–50 cm long, 0.8–16 cm wide, base rounded to obtuse, sometimes cordate or acute, often unequal, apex (tapering to) acute, acuminate, or caudate, rarely obtuse, rounded, or retuse, midrib (very) slightly sunken above, glabrous or sometimes hairy, prominent beneath, sparsely to densely hairy or rarely glabrous, secondary veins prominent to faint, smaller veins often reticulate. Petiole 0.5–9 mm long, 0.5–5 mm thick, sparsely to densely hairy or sometimes glabrous. *Inflorescence* axillary, extra-axillary, ramiflorous, cauliflorous, terminal, or rarely leaf-opposed, 1–several-flowered. Bracts 1–3, up to 5(–7) mm long. Pedicel up to 140 mm long, sometimes very slender, (sparsely) pubescent, (almost) glabrous, or rarely densely hirsute. Bud, if present, broadly to depressed(-triangular)-ovoid, rarely subglobose or obovoid, 1.5–9 mm long. *Sepals* connate or rarely free, (very) broadly triangular-ovate (c.q. ovate or triangular), rarely oblong, 1–7 mm long, 1–6 mm wide, sparsely to densely pubescent or rarely hirsute outside, glabrous inside, apex acute to rounded or acuminate. *Petals* valvate (or rarely imbricate?) if buds are available, connate over a variable length, arranged in 2 whorls of 3 or in 1 whorl of 6 (best noticed in open flowers), equal to unequal in length, 2–36 mm long, hairy outside or inner whorl hairy along midrib and/or towards the apex, otherwise glabrous, glabrous and verruculose inside, apex acute, obtuse, or rounded, lobes (very) (broadly) (triangular-)ovate to elliptic, 1.5–

10 mm wide, or outer whorl (very) (broadly) triangular to broadly ovate, 2–4 mm wide, inner whorl (narrowly) oblong to elliptic or very broadly triangular-ovate, 1.5–4 mm wide. *Stamens* numerous, 0.5–3 mm long, anther extrorse, apex shield-like, glabrous or rarely hairy. Receptacle shortly cylindrical or conical, flat-topped. *Carpels* 3–20, free, 0.9–2.8 mm long, ovary densely hairy, stigma globose, discoid, or obovoid, hairy when immature; ovules 2–6, 1-seriate, lateral. Fruiting pedicel 2–130 mm long. *Monocarps* 1–14(–20), free, subglobose, shortly cylindrical, ellipsoid, oblong, or (ob)ovoid, sometimes oblique, (5–)6–30(–45) mm long, (5–)6–25(–28) mm in diameter, pubescent or sometimes hirsute, verruculose to verrucose, stalk 0–12(–33) mm long. *Seeds* 1–5, discoid, sometimes surface very irregular.

Distribution – Sulawesi, the Philippines, New Guinea, New Britain, the Solomon Islands, Australia, and probably the Talaud Islands and Halmahera.

Habitat & Ecology – In primary lowland or montane rain forests or sometimes in dry forests, up to 2000 m altitude (most frequent up to 700 m).

KEYS TO THE SPECIES
(flowering specimens)

1a. Petals in open flowers unequal in length (inner petals longer) 2
b. Petals in open flowers (sub)equal in length 4
2a. Inflorescences axillary; pedicel 2–6 mm long ..... **3. H. johnsonii**
b. Inflorescences extra-axillary; pedicel 6–45 mm long 3
3a. Leaves up to 11 cm long; petiole c. 0.7 mm thick; outer petals c. 4 mm long, inner petals 5–7 mm long ..... **2. H. heteropetala**
b. Leaves much longer than 11 cm; petiole 1.5–3 mm thick; outer petals 5–7 mm long, inner petals 7–10 mm long ..... **1. H. gamopetala**
4a. Petals arranged in 1 whorl of 6 petals (best visible in mature flowers), only shortly connate ..... **6. H. stellatus**
b. Petals arranged in 2 whorls of 3 petals, conspicuously connate 5
5a. Flower buds open very early in their development; petal-lobes usually oblong; pedicel 10–140 mm long ..... **4. H. lanceolata**
b. Flower buds open at maturity, generally depressed-ovoid; petal-lobes usually broadly ovoid; pedicel 0--25 mm long (very rarely up to 45 mm long) **5. H. longirostris**

(fruiting specimens; fruit unknown in two species)

1a. Stalks (2–)6–12(–32) mm long; fruiting pedicel 15–130 mm long **4. H. lanceolata**
b. Stalks 0–5 mm long; fruiting pedicel 2–25 mm long 2
2a. Fruiting pedicel very slender, 11–16 mm long; monocarps 5–9 mm long **6. H. stellatus**
b. Fruiting pedicel not very slender, 2–20 mm long; monocarps 8–30(–47) mm long 3
3a. Ripe fruits in vivo black; monocarps 8–12 mm long ..... **3. H. johnsonii**
b. Ripe fruits in vivo red, yellow, or brown; monocarps 8–30(–47) mm long **5. H. longirostris**

1. Haplostichanthus gamopetala (Boerl. ex Koord.) Heusden, *comb. nov.*

Polyalthia gamopetala Boerl. ex Koord., Meded. Lands Plantent. 19 (1898) 338. — Lectotype (designated here): *Koorders 15994* (lecto L; iso BO, n.v.).

Young and older twigs glabrous. *Leaves* (sub)coriaceous, oblong to elliptic, more or less bullate, sparsely pubescent beneath, glabrous above, at least 21–31 cm long, 3–10 cm wide, base rounded to obtuse, apex not seen, midrib above slightly sunken, glabrous, beneath prominent, sparsely hairy, secondary veins more or less prominent. Petiole 0–5 mm long, 1.5–3 mm thick, (sparsely) hairy. *Inflorescence* extra-axillary, flower solitary (or one flower at a time). Bracts not seen. Pedicel c. 13–45 mm long, slender, sparsely puberulent. Bud not seen. *Sepals* connate, depressed triangular-ovate, 2–3 mm long, 3.5 mm wide, sparsely pubescent outside, glabrous inside, apex slightly acuminate. *Petals* connate, unequal, outer whorl broadly triangular, 5–7 mm long, 3–4 mm wide, inner whorl probably elliptic, 7–10 mm long, 2.5–4 mm wide, pubescent outside, glabrous inside, apex acute. *Stamens* numerous. *Carpels* several, stigmas hairy when immature. Fruit not seen.

Distribution – NE Sulawesi (2 coll.). Fig. 3.

2. Haplostichanthus heteropetala (Merr.) Heusden, *comb. nov.*

Papualthia heteropetala Merr., Philipp. J. Sci. 14 (1919) 389. — Lectotype (designated here): *Ramos BS 32853* (holo PNH †; lecto K), Philippines, Luzon, Ilocos Norte Prov., Burgos, 26-vii-1918.

Shrub up to 3 m high. Young twigs pubescent, older twigs glabrous, sometimes numerous lenticels present. *Leaves* membranous to subcoriaceous, elliptic-ovate to oblong, glabrous above, glabrous or pubescent beneath, 5.5–11 cm long, 1.5–3.5 cm wide, base more or less obtuse, slightly unequal, apex (tapering to) acute or slightly acuminate, midrib above slightly sunken, glabrous, beneath prominent, glabrous or pubescent, secondary veins faint to slightly prominent. Petiole 1–3 mm long, c. 0.7 mm thick, pubescent. *Inflorescence* extra-axillary, flower solitary. Bract 2.5–3.5 mm long. Pedicel 6–15 mm long, very slender, pubescent to almost glabrous. Bud depressed-triangular-ovoid, 2 mm long. *Sepals* connate or free, broadly triangular or (very) broadly triangular-ovate, 1.5–3 mm long, 2 mm wide, (sparsely) pubescent outside, glabrous inside, apex acute or acuminate. *Petals* valvate (inner ones) in bud, connate, unequal, 'outer' lobes triangular, 4 mm long, 'inner' lobes oblong, 5–7 mm long, 1.5–2 mm wide, pubescent outside, glabrous inside, apex acute. *Stamens* numerous. Receptacle shortly cylindrical. *Carpels* 4, 0.9 mm long, ovary hairy. Fruit not seen.

Distribution – Philippines (Luzon). Fig. 3.

Habitat & Ecology – In dry forests at low altitudes; on riverbank in forest.

Field notes – Flower red, fruit green to red.

3. Haplostichanthus johnsonii F. Muell. — Fig. 1a

Haplostichanthus johnsonii F. Muell., Vict. Natural. 7 (Mar. 1891) 180. (as *'johnsoni'*). — Type: *S. Johnson s.n.* (holo MEL, n.v.; iso BRI, K), Australia, Mount Bartle-Frere.

Shrub or treelet up to 7 m high. Young twigs sparsely to densely pubescent (often with brownish hairs), older twigs glabrous, sometimes numerous lenticels present. *Leaves* membranous, glabrous above, sparsely pubescent beneath, oblong to elliptic-oblong, (narrowly) obovate-oblong, or ovate, 2.5–19 cm long, 1–5.5 cm wide, base rounded, unequal, apex (tapering to) acute, obtuse, acuminate, midrib above slightly sunken, glabrous, beneath prominent, (sparsely) pubescent or rarely hirsute, secondary veins faint or slightly prominent. Petiole 0–2 mm long, 0.5–1.5 mm thick, sparsely to densely pubescent, rarely hirsute. *Inflorescence* axillary, flower solitary, sometimes 2-flowered. Bracts 2 or 3, 0.5–4 mm long, pubescent. Pedicel 2–6 mm long, pubescent. Bud very broadly to depressed-ovoid, 2–3.5 mm long. *Sepals* connate, very broadly triangular-ovate, 1.5–3 mm long and 1–4 mm wide,

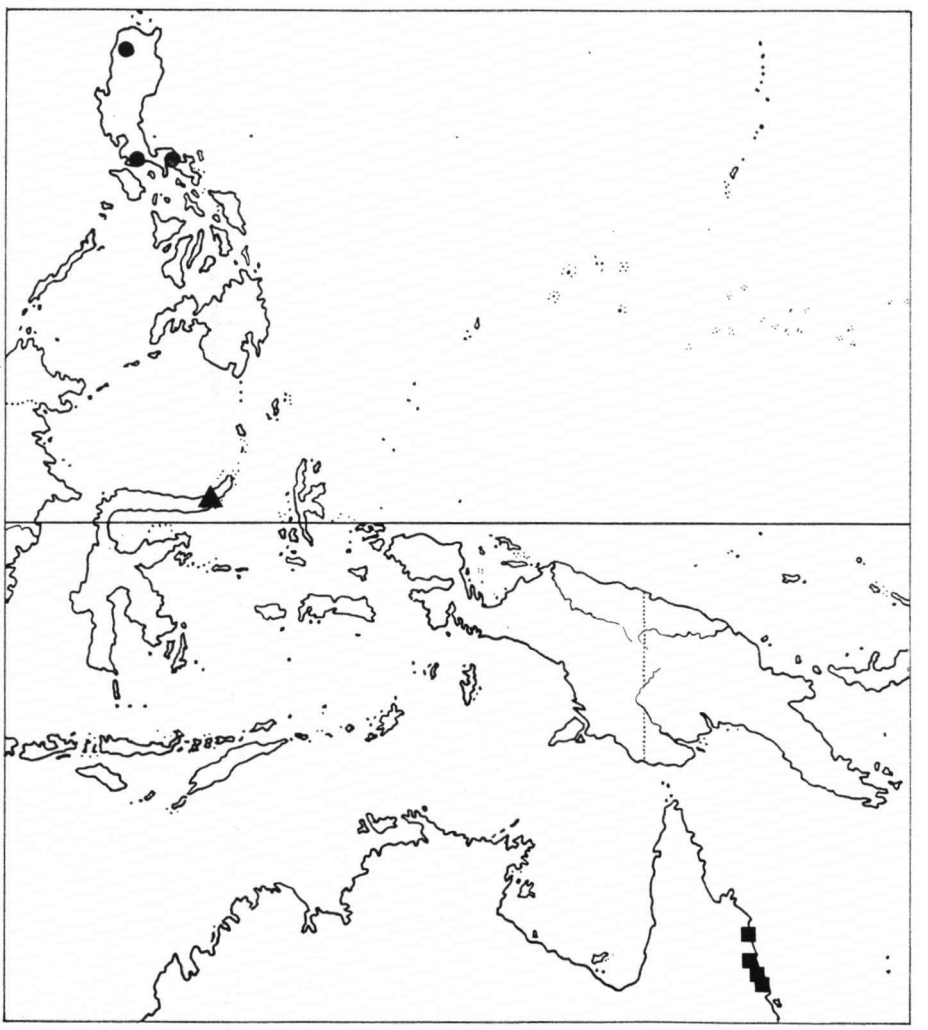

Fig. 3. Distribution of *Haplostichanthus gamopetala* (Boerl. ex Koord.) Heusden (triangle); *H. heteropetala* (Merr.) Heusden (dots), and *H. johnsonii* F. Muell. (squares).

pubescent outside, glabrous inside, apex acute. *Petals* connate, valvate (sometimes imbricate?) in bud, unequal, inner whorl first cohering, later both whorls spreading and in one plane when fully open, outer whorl (very) broadly triangular to (broadly) ovate, 2–5 mm long, 2–3.5 mm wide, pubescent outside, glabrous inside, apex acute to rounded, inner whorl (narrowly) oblong, 2–6 mm long, 1.5–2.5 mm wide, (partially) glabrous outside, glabrous inside, apex broadly acute to obtuse. *Stamens* numerous, 1–1.2 mm long. Receptacle shortly cylindrical or conical, flat-topped. *Carpels* 3–7, c. 1.3 mm long, ovary densely hairy; ovules 2–4. Fruiting pedicel 2–10 mm long. Monocarps 1–4, subglobose to shortly cylindrical, sometimes more or less apiculate, oblique, 8–12 mm long, 7–11 mm in diameter, (very) sparsely pubescent, verrucose to verruculose, stalk 1–3 mm long. *Seeds* 1 or 2, discoid.

Distribution – Australia (Queensland: Cook District). Fig. 3.

Habitat & Ecology – In rain forest or complex mesophyll vine forest, up to 80 (–700) m altitude.

Field notes – Buds olive-cream. Flowers cream or creamy white with red inside near the base of the 'inner' whorl. Ripe fruit black, sometimes purple red, or reddish brown, immature fruit green.

Note – *Haplostichanthus johnsonii* is diverse in its morphology, varying with altitude. The collections *Hyland 7142* and *Smith 3799* differ from the other specimens in the subsessile flowers and the larger bracts and sepals. The specimen *Hyland 7142* is found at 700 m altitude, whereas the other specimens are collected at altitudes up to 80 m. The label of the isotype from K reports an altitude of 5000 feet. This seems doubtful because all other specimens which closely resemble the type are found at or below 80 m altitude. There are no other records of *H. johnsonii* available from such a high altitude.

4. **Haplostichanthus lanceolata** (Vidal) Heusden, *comb. nov.* — Fig. 1b

Polyalthia lanceolata Vidal, Phan. Cuming. Philipp. (1885) 170. — *Papualthia lanceolata* (Vidal) Merr., Philipp. J. Sci., Bot. 10 (1915) 242. — Type: *Cuming 450* (holo K; iso G, L, MO, NY fragm.).

Polyalthia reticulata Elmer, Leafl. Philipp. Bot. 1 (1908) 292. — *Papualthia reticulata* (Elmer) Merr., Philipp. J. Sci., Bot. 10 (1915) 242, syn. nov. — Lectotype (designated here): *Elmer 7272* (holo PNH †; lecto NY), Philippines, Leyte, Palo, i-1906.

Unona sympetala C.B. Rob., Philipp. J. Sci., Bot. 6 (1911) 203. — *Papualthia sympetala* (C.B. Rob.) Merr., Philipp. J. Sci., Bot. 10 (1915) 242, syn. nov. — Lectotype (designated here): *McGregor BS 10352* (holo PNH †; lecto B), Polillo.

Polyalthia loheri Merr., Philipp. J. Sci., Bot. 7 (1912) 268. — *Papualthia loheri* (Merr.) Merr., Philipp. J. Sci., Bot. 10 (1915) 242, syn. nov. — Type: *Alvarez FB 18437* (holo PNH †), Philippines, Luzon, Culasing Mt, in dipterocarp forest, 22-ii-1909.

Polyalthia loheri Merr. var. *cagayensis* Merr., Philipp. J. Sci., Bot. 7 (1912) 269. — Lectotype (designated here): *Ramos BS 13948* (holo PNH †; lecto B), Philippines, Luzon, Cagayan Prov., Abulug R., near Dabba, in forest, a tree c. 5 m high with yellow flowers, 2-ii-1912.

Polyalthia romblonensis Elmer, Leafl. Philipp. Bot. 5 (1913) 1729. — Lectotype (designated here): *Elmer 12170* (holo PNH †; lecto L; iso NY), Philippines, Romblon, Capiz Prov., iii-1910.

Polyalthia urdanetensis Elmer, Leafl. Philipp. Bot. 5 (1913) 1738. — *Papualthia urdanetensis* (Elmer) Merr., Philipp. J. Sci., Bot. 10 (1915) 243, syn. nov. — Lectotype (designated here): *Elmer 13931* (holo PNH †; lecto L; iso B, G, K, NY), Philippines, Mindanao, Agusan Prov., Cabadbaran (Mt Urdaneta), ix-1912.

Papualthia samarensis Merr., Philipp. J. Sci., Bot. 9 (1916) 180, syn. nov. — Lectotype (designated here): *Ramos BS 24180* (holo PNH †; lecto K; iso A), Philippines, Samar, Catubig R. at Camaniwan, in damp forest at low altitudes, 3-ii-1916.

Papualthia bakeri Elmer, Leafl. Philipp. Bot. 8 (1919) 3069. — Lectotype (designated here): *Elmer 17775* (holo PNH †; lecto L; iso A, F, G, K, MO, NY, U, US), Philippines, Luzon, Prov. Laguna, Los Baños (Mt Maquiling), vi/vii-1917.

Papualthia boholensis Merr., Philipp. J. Sci. 29 (1926) 479, syn. nov. — Lectotype (designated here): *Ramos BS 43095* (holo PNH †; lecto K ; iso A, G), Philippines, Bohol, Valencia, damp forest, alt. 300–600 m, x-1923.

Papualthia longipes Quisumb., Philipp. J. Sci. 41 (1930) 323, syn. nov. — Lectotype: *Ramos & Edaño BS 45281* (holo PNH †; lecto NY), Philippines, Luzon, Tayabas Prov., Casiguran (Cabulig R.), in damp forest at low altitudes, 28-v-1925.

Treelet or shrub up to 7 m high. Young twigs pubescent, usually with long adpressed hairs or with dense brown indument, older twigs glabrous, sometimes numerous lenticels present. *Leaves* subcoriaceous or membranous, glabrous to pubescent above, densely pubescent to glabrous beneath, lamina narrowly oblong to elliptic, sometimes to (ob)ovate, 4–50 cm long, 1.5–15 cm wide, base obtuse to rounded to cordate, sometimes to acute, unequal, apex acuminate, caudate, (tapering to) acute, or sometimes retuse, midrib slightly sunken above, glabrous or hairy, prominent beneath, (densely) hairy, secondary veins more or less faint to prominent beneath. Petiole 0–8 mm long, 0.5–5 mm thick, densely hairy to almost glabrous. *Inflorescence* terminal, axillary, extra-axillary, ramiflorous, or cauliflorous, rarely leaf-opposed, usually one flower at a time. Bracts 1 or 2, 1.5–4 mm long, pubescent outside. Pedicel 10–140 mm long, pubescent to glabrous, sometimes very slender. Bud rarely present, ovoid, 5–9 mm long. *Sepals* connate, broadly triangular to very broadly ovate, 2–7 mm long, 3–5 mm wide, sparsely pubescent outside, glabrous inside, apex (broadly) acute, rarely acuminate. *Petals* (sub)equal, connate, 5–36 mm long, petal-lobes (broadly to narrowly) ovate, (narrowly) (elliptic-)oblong, or obovate-oblong, 4–33 mm long, 2–10 mm wide, (sparsely) pubescent outside, glabrous inside, apex (broadly) acute. *Stamens* numerous, 1.3–2 mm long. Receptacle conical, flat-topped, or shortly cylindrical. *Carpels* 4–14, 1.3–1.8 mm long, stigma globose, hairy when immature. Fruiting pedicel 15–130 mm long. *Monocarps* 1–14 (–20), subglobose, ellipsoid, oblong, or ovoid, (5–)9–25 mm long, (5–)8–17 mm in diameter, sparsely pubescent, verruculose to verrucose, stalks (2–)6–12(–33) mm long. *Seeds* 1–4, discoid.

Distribution – Philippines (Alabat Island, Bohol, Catanduanes, Leyte, Luzon, Mindanao, Polillo, Romblon, Samar, and Siargao). Fig. 4.

Habitat & Ecology – In primary forest, up to 600 m altitude.

Field notes – Flowers cream to white, sometimes with a touch of pink and pink near the base inside. Fruits red or shiny vermillion red, green, or blue.

Notes – 1. In Mindanao sterile specimens of *H. lanceolata* can be confused easily with those of *Polyalthia obliqua*. Fruiting specimens can be distinguished by the length of the fruiting pedicel: *P. obliqua* has a short pedicel (c. 1 cm) whereas specimens of *H. lanceolata* from Mindanao have a very long pedicel. The fruits of *P. obliqua* are much more rugose than those of *H. lanceolata*. The flowers can be distinguished by the free (*P. obliqua*) or connate (*H. lanceolata*) petals.

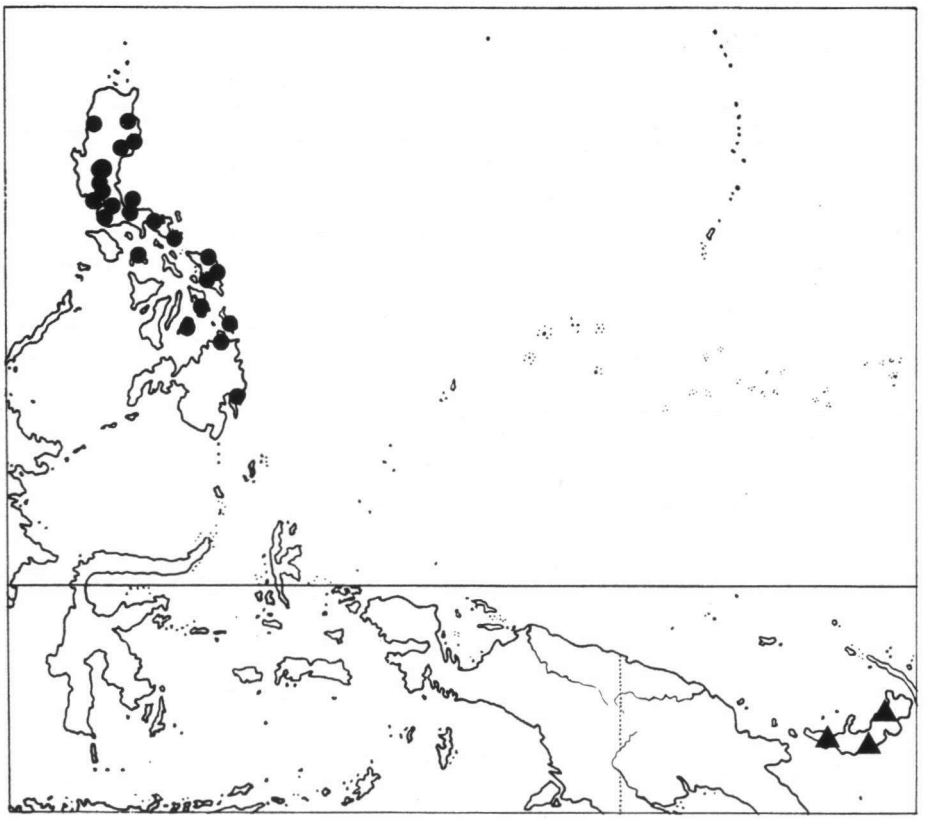

Fig. 4. Distribution of *Haplostichanthus lanceolatus* (Vidal) Heusden (dots) and *H. stellatus* Heusden (triangles).

2. The type of *Polyalthia* (*Papualthia*) *loheri* has not been seen, but Merrill (1912) mentions a number of collections which he refers to this species in his original description. These specimens, except for the generally longer leaves, do not really differ from *Papualthia lanceolata.*

5. Haplostichanthus longirostris (Scheff.) Heusden, *comb. nov.* — Fig. 1c, d

Goniothalamus longirostris Scheff., Ann. Jard. Bot. Buitenzorg 1 (1876) 4. — *Trivalvaria? longirostris* Becc. ex Scheff., Ann. Jard. Bot. Buitenzorg 2 (1885) 28. — *Papualthia longirostris* (Scheff.) Diels, Bot. Jahrb. 49 (1912) 140. — Type: *Teijsmann s.n.* (holo BO, n.v.), W New Guinea, Doré, fr.

Melodorum micranthum Warb., Bot. Jahrb. 18 (1893) 190. — Type: *Hellwig 370* (holo B, n.v.), Finschhafen, fl., 15-ii-1889.

Cyathostemma grandifolium Laut. & K. Schum., Fl. Schutzgeb. Südsee (1901) 318. — *Papualthia grandifolia* (Laut. & K. Schum.) Diels, Bot. Jahrb. 49 (1912) 139, syn. nov. — Type: *Rodatz & Klink 26* (holo B), NE New Guinea, Ramu Station, fl., 22-vi-1899.

Goniothalamus inaequilatera K. Schum. & Laut., Fl. Schutzgeb. Südsee (1901) 322. — Lectotype (designated here): *Lauterbach 1374* (lecto B), New Guinea, Finschhafen, fl., 3-i-1890.

Goniothalamus auriculatus Burck, Nova Guinea 8, 3 (1911) 432. — *Papualthia auriculata* (Burck) Diels, Bot. Jahrb. 49 (1912) 139, syn. nov. — Lectotype (designated here): *Versteeg 1038* (lecto U; iso A fragm., B, L), Irian Jaya, Lorentz R. near Bivak I., fl. & fr., 9-v-1907.

Papualthia rudolphi Diels, Bot. Jahrb. 49 (1912) 139, syn. nov. — Type: *Schlechter 17138* (holo B), NE New Guinea, Kani Mts, forest, alt. c. 1100 m, fl., 4-i-1908.

Papualthia roemeri Diels, Bot. Jahrb. 49 (1912) 141, syn. nov. — Type: *von Römer 465* (holo U, n.v.; iso B, L), SW New Guinea, Lorentz River, lowland forest, fr., 7-x-1909 (see Diels, 1912).

Papualthia pilosa Diels, Bot. Jahrb. 49 (1912) 141, syn. nov. — Type: *Schlechter 16988* (holo B), NE New Guinea, Gati Mts, in forest, alt. c. 600 m, fl., 17-xii-1907.

Papualthia micrantha Diels, Bot. Jahrb. 52 (1915) 182, syn. nov. — Type: *Ledermann 7349* (holo B; iso K), Papua New Guinea, Sepik Prov., fl., v-1912.

Tree up to 30 m high or shrub. Young twigs pubescent or densely covered with brown indument, rarely hirsute, older twigs glabrous or glabrescent, sometimes numerous lenticels present. *Leaves* (thinly) membranous to subcoriaceous, occasionally bullate, glabrous or rarely hairy above, densely pubescent or rarely hirsute to glabrous beneath, lamina oblong, (narrowly) obovate, (broadly) elliptic, or sometimes narrowly ovate, 4.5–42 cm long, 1.5–16 cm wide, base obtuse, acute, rounded, or (slightly) cordate, unequal or sometimes equal, apex acuminate, (tapering to) acute, caudate, rounded, or sometimes obtuse, mucronate, or retuse, midrib slightly (rarely not) sunken above, glabrous or rarely hairy, prominent beneath, (densely) pubescent, rarely glabrous or hirsute, secondary veins prominent to faint beneath. Petiole 1.5–10 mm long, 0.5–5 mm thick, densely hairy to glabrous. *Inflorescence* axillary, ramiflorous or cauliflorous, rarely terminal, more rarely extra-axillary or leaf-opposed, usually several-flowered, sometimes flowers solitary. Bracts 1–3, 1–5(–7) mm long, pubescent or rarely with dense brown indument outside. Pedicel 0–25(–45) mm long, pubescent, sometimes with dense brown indument or rarely hirsute. Bud broadly to depressed-ovoid or subglobose, rarely obovoid, 1.5–8 mm long. *Sepals* valvate in bud, connate, (very) broadly (triangular-)ovate, 1.5–6 mm long, 1.5–6 mm wide, sparsely or densely pubescent or rarely hirsute outside, glabrous inside, apex (broadly) acute, sometimes acuminate or rounded. *Petals* valvate in bud, connate over a variable length, arranged in 2 (sub)equal whorls, 2.5–15 mm long, (densely) pubescent outside, sometimes inner whorl glabrous outside except along the midrib and towards the apex, glabrous inside, apex (very) (broadly) acute to obtuse, occasionally rounded, lobes of the outer whorl (very) broadly ovate, sometimes elliptic, broadly oblong, or broadly triangular-ovate, (1–)2–8 mm wide, lobes of inner whorl (broadly) oblong to obovate, sometimes elliptic or very broadly ovate, 1.5–6 mm wide. *Stamens* numerous, 1–3 mm long, apex shield-like, fleshy, glabrous or rarely hairy. Receptacle shortly cylindrical or conical, flat-topped. *Carpels* 3–20, ovary densely hairy, stigma globose or cushion-shaped; ovules 2–6, 1-seriate. Fruiting pedicel 3–20(–50) mm long. Monocarps 1–8, subglobose, oblong, obovoid, or shortly cylindrical, often oblique, 8–30(–47) mm long, 7–26 mm in diameter, sparsely pubescent to glabrous or pubescent and glabrescent, rarely hirsute, verruculose to verrucose, stalk 0–5 mm long. *Seeds* 1–5, discoid, surface sometimes very irregular.

Distribution – New Guinea, Rossel Island, Solomon Islands; probably also Halmahera, New Britain, and Australia. Fig. 5.

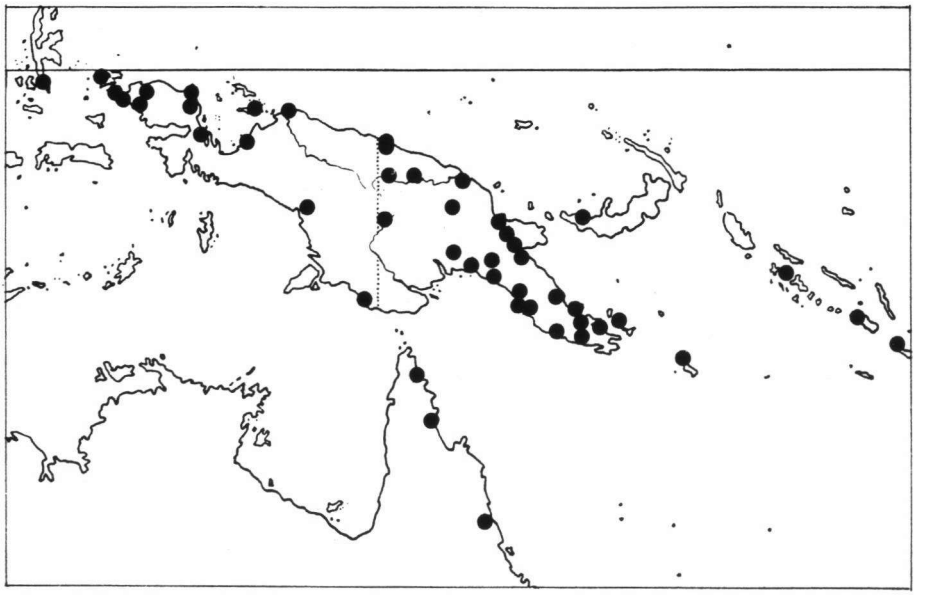

Fig. 5. Distribution of *Haplostichanthus longirostris* (Scheff.) Heusden.

Habitat & Ecology – In lowland rain forest or lower montane forest, up to 2000 m altitude.

Field notes – Buds yellowish, pink, or cream. Flowers cream, white, yellowish, brown, pinkish, (light) green, purplish yellow, purplish brown, or orange, sometimes inside red, sometimes waxy. Fruit light to dark green or yellow-green becoming bright red, yellow, or brown when ripe. Lower side of the leaves lighter green than the upper side.

Notes – 1. *Haplostichanthus longirostris* is morphologically diverse, varying both with geographical distribution and altitude. In W New Guinea the species is relatively uniform, but in E New Guinea *H. longirostris* differentiates into several local races. The intermediates between these races make further distinction into species impossible. Also the very low number of collections of some of these races make it difficult to decide whether a new species is involved or not. Therefore, a wider species concept is preferred. Moreover, some collections show some characters which are more typical of *Polyalthia*. This makes identification of fruiting or sterile specimens very difficult and uncertain. Some of these races and some collections from outside New Guinea are briefly discussed below.

2. In some collections from Papua New Guinea the petals are connate over nearly the whole length (Fig. 1). These flowers have only a small opening near the apex which is surrounded by rudimentary lobes.

3. In SE New Guinea and Rossel Island specimens with small leaves and very small flowers are found. In contrast, in central Papua New Guinea there are specimens with relatively 'big' flowers.

4. A number of collections show dense (sometimes hirsute) indument on all parts. This indument can be found on organs which are normally glabrous in *H. longirostris*, e.g., the upper side of the leaves and the apices of the stamens. Their leaves are somewhat reddish brown. These collections are found in S New Guinea, W New Britain, and Australia (petals in 2 whorls). The specimen from New Britain (*Frodin NGF 26547*) deviates in the very long and slender pedicels and, pro parte, the extra-axillary inflorescences.

5. Two fruiting collections are available from N Queensland, the leaves are reminiscent of *Haplostichanthus*. The fruits are red like in *H. longirostris* and not black as in *H. johnsonii*. Flowers are not available, so the proper species (and also genus, notably *Polyalthia*) cannot be identified with certainty. Also Jessup (1990) refers to some undescribed *Haplostichanthus* species from localities in N Queensland.

6. From Halmahera (Moluccas, Indonesia) a sterile collection of *Haplostichanthus* (*de Vogel 4364*) is available. Based upon the geographic distribution this specimen is expected to belong to *H. longirostris*. Another sterile specimen from the Talaud Islands (*Lam 2820*) is impossible to identify. The leaves remind of those of *Polyalthia celebica* (Sulawesi), *Haplostichanthus lanceolata* (Philippines), and *H. longirostris* (New Guinea). In vegetative characters these species cannot be distinguished. The Talaud Islands are found midway between Sulawesi and the Philippine island Mindanao.

7. The type of *Goniothalamus longirostris* was not available for the present study. The diagnosis of Scheffer (1876) is incomplete regarding the flowers and, to a lesser extent, the fruits. The description may both apply to *Papualthia* and to some *Polyalthia* species. Only the New Guinean origin makes *Papualthia* more likely. In 1885 Scheffer received two collections of *Beccari* (*578* and *976*) on which he based a more extensive description of the flowers of *G. longirostris* which he then transferred to *Trivalvaria* despite the different ovule number. Only a duplicate of *Beccari 976* (K) was available for the present study; this specimen certainly belongs to *Papualthia*.

6. **Haplostichanthus stellatus** Heusden, *spec. nov.* — Fig. 8

Haplostichantho johnsonii similis, in pedicello longiore, corolla ad instar stellae, petalis aequilongis differt. — Typus: *E. E. Henty & Y. Lelean NGF 49486* (holo LAE; iso L), W New Britain, Kombe Subdistr., near Linga Linga, alt. 500 m, 5° 50' S, 149° 50' E, forest on ridge, fl., fr., 29-v-1973.

Shrub or treelet up to 2.5 m high. Young twigs pubescent, older twigs glabrous or glabrescent. *Leaves* membranous, glabrous above, (sparsely) pubescent beneath, verruculose beneath, lamina lanceolate, ovate, or (narrowly) elliptic, 3–13 cm long, 0.8–4 cm wide, base obtuse to rounded, unequal, apex tapering to acute, acuminate, or caudate, midrib slightly sunken above, glabrous or rarely pubescent, prominent beneath, pubescent, secondary veins faint to prominent beneath. Petiole up to 1 mm long, c. 1 mm thick, densely hairy. *Inflorescence* axillary or rarely ramiflorous, 1- or 2-flowered. *Bract* 1 or 2, minute. Pedicel 10–23 mm long, very slender, pubescent. Bud (very) broadly ovoid, 2–2.5 mm long. *Sepals* connate, very broadly triangular-ovate to ovate, 1–1.5 mm long, 1.5–2.5 mm wide, pubescent outside, glabrous inside, apex (broadly) acute to rounded. *Petals* shortly connate near the base, in 1 whorl

Fig. 6. *Haplostichanthus stellatus* Heusden. a. Habit, × 0.7; b. flower, × 5 (*NGF 49486*).

and spreading when mature, forming a stellate corolla, equal in length, 3–6 mm long, petal-lobes 1.5–3 mm wide, 'inner' usually narrower, 'outer' whorl pubescent outside, 'inner' whorl pubescent along the midrib, otherwise glabrous, glabrous inside, apex acute or obtuse. *Stamens* numerous, 1.2–1.5 mm long, apex fleshy. Receptacle cylindrical. *Carpels* 1–4, ovary hairy, stigma globose, obovoid, or 4-lobed, fleshy. Fruiting pedicel 11–16 mm long, very slender, sepals sometimes persistent. *Monocarps* 1 or 2, globose to oblong or transversely ellipsoid, 5–9 mm long, 6–7 mm in diameter, sparsely pubescent, verruculose, stalk 0.5–1.5 mm long. *Seeds* 1–4?

Distribution – New Britain. Fig. 4.

Habitat & Ecology – Lowland rain forest or forest on ridge, up to 500 m altitude.

Field notes – Flowers white, cream, or yellow. Fruits green (immature?).

DUBIOUS SPECIES

Papualthia tenuipes (Merr.) Merr., Philipp. J. Sci., Bot. 10 (1915) 243.

Polyalthia tenuipes Merr., Philipp. J. Sci., Bot. 7 (1912) 269. — Type: *Foxworthy & Ramos BS 13472* (holo PNH †, n.v.), Philippines, Luzon, Tayabas, in forest at low altitudes, non *Polyalthia tenuipes* Merr. (1922) from Borneo.

Note – No material identified as this species nor its type could be traced.

EXCLUDED SPECIES

Papualthia bracteata Diels in Laut., Beitr. Fl. Papuasien 1, 8 (1913) 142. — Type: *Schlechter 16379* (holo B), NE New Guinea, forest, c. 200 m alt., fl., 24-ix-1907 = **Pseuduvaria mollis** (Warb.) J. Sinclair, Gard. Bull. Sing. 15 (1956) 9.

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LIST OF COLLECTIONS

Haplostichanthus F. Muell.
1 = *H. gamopetala* (Boerl. ex Koord.) Heusden
2 = *H. heteropetala* (Merr.) Heusden
3 = *H. johnsonii* F. Muell.
4 = *H. lanceolata* (Vidal) Heusden
5 = *H. longirostris* (Scheff.) Heusden
6 = *H. stellatus* Heusden

Ahern's collector 1103: 4.

Beccari 976: 5 — Brass 1436, 24038, 24039: 5; 25876: 5?; 28448, 28914: 5 — BSIP series (Mauriasi et al.) 8490, 8635, (Gafui et al.) 8738, 8867, 8987, 9248, (Powell et al.) 19428: 5 — BW series (Schram) 6001, (Iwanggin) 9233, (Schram) 12299: 5.

Carr 11648, 11733, 12453, 14022, 15755, 16349: 5 — Cenabre et al. 28549: 4 — Clemens 8045: 5 — Conn et al. 26: 5 — Corner 37: 5 — Craven & Schodde 737: 5 — Cuming 450, 1346, 1715, 1729: 4 — Curran 10191: 4.

Edaño 37135: 4 — Elmer 7272, 12170, 13931, 15166, 16045, 17775, 18327: 4.

Fénix 28413: 4 — Fox 9033: 4 — Frodin & students 6550: 5.

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