A reconsideration of the infrageneric classification of Homalium Jacq. (Salicaceae)

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Abstract
APPLEQUIST, W.L. (2016). A reconsideration of the infrageneric classification of Homalium Jacq. (Salicaceae). Candollea 71: 231-256. In English, English and French abstracts. DOI: http://dx.doi.org/10.15553/c2016v712a9

Homalium Jacq. (Salicaceae) is widespread in tropical regions and includes considerable diversity in floral morphology. Its modern infrageneric classification is complex, including two subgenera and nine sections. Morphological variation within the genus is described, and an emended classification including ten sections is proposed. Subgenera have been defined by stamen number: subg. Homalium has stamens in fascicles of two to 12, while subg. Blackwellia (Benth.) Warb. has one stamen per petal. These subgenera are not natural groups; since the relationships of some sections are uncertain, recognition of subgenera may not be of value and is not upheld here. Sect. Eumyriantheia Warb. is polyphyletic; it is herein restricted to Malagasy species, while sect. Polyanthera Warb. is revived for fasciculate-stamened species from Asia to the Pacific region. Also, three Malagasy species formerly placed within sect. Blackwellia Benth. (Homalium brachystylis (Tul.) Baill., Homalium longistaminum H. Perrier, and Homalium planiflorum (Boivin ex Tul.) Baill.) are transferred to sect. Odontolobus Warb. Several problematic species are individually discussed.

Résumé
APPLEQUIST, W.L. (2016). Une révision de la classification infragénérique du genre Homalium Jacq. (Salicaceae). Candollea 71: 231-256. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2016v712a9

Homalium Jacq. (Salicaceae) est un genre très répandu dans les régions tropicales et possède une morphologie florale très variée. Sa classification infragénérique moderne est complexe comprenant deux sous-genres et neuf sections. La variation morphologique du genre est décrite et une classification modifiée comprenant dix sections est proposée. Les sous-genres ont été définis sur la base du nombre d'étamines : le sous-genre Homalium possède des étamines en fascicules de 2 à 12, tandis que le sous-genre Blackwellia (Benth.) Warb. possède une étamine par pétale. Ces sous-genres ne sont pas des groupes naturels, les relations de certaines sections étant incertaines ; la reconnaissance des sous-genres n’est donc pas utile et n’est pas retenue ici. La section Eumyriantheia Warb. est polyphylétique ; elle est ici limitée aux espèces malgaches, tandis que la sect. Polyanthera Warb. est rétablie pour les espèces de l’Asie à la région du Pacifique avec des étamines fasciculées. De plus, trois espèces malgaches anciennement placées dans la sect. Blackwellia Benth. (Homalium brachystylis (Tul.) Baill., Homalium longistaminum H. Perrier, and Homalium planiflorum (Boivin ex Tul.) Baill.) sont transférées à la sect. Odontolobus Warb. Plusieurs espèces problématiques sont discutées individuellement.

Keywords
SALICACEAE – Homalium – Blackwellia – Madagascar – Taxonomy – Sections – Infrageneric classification
Introduction

Homalium Jacq., placed in Salicaceae following the demonstration that Flacourtiaceae were polyphyletic (CHASE et al., 2002) is a pantropical woody genus. As currently circumscribed, Homalium encompasses a broad range of floral diversity; its defining features include two perianth whorls, a semi-inferior ovary, and a single large gland at the base of each sepal, on the adaxial surface. The oppositipetalous stamens may be equal in number to the petals or borne in fascicles of two to several (rarely to 12). SLEUMER (1954) estimated that Homalium included 180 to 200 species worldwide, though a recent literature review (APPLEQUIST, 2013) suggested that fewer than 150 previously published species are recognized in current taxonomic treatments. Regional treatments from all of the geographic regions with substantial representation of Homalium were published by SLEUMER in the 1950s through 1980s (SLEUMER, 1954, 1973, 1974, 1975, 1980, 1985; SLEUMER & BOSSER, 1980). Some of these treatments from the regions of most diversity, notably Madagascar and Malesia, are now obsolete due to the greater volume of specimens now available.

The last overall survey of Homalium as currently circumscribed was by WARBURG (1893), who published a complex classification of two subfamilies distinguished by stamen number (one per petal in subg. Blackwellia (Benth.) Warb., two or more per petal in subg. Homalium [wrongly termed "subg. Myriantheia", nom. inval.]), and nine sections. That classification was heterogeneous. A broader study of floral and fruit morphology, including species from other geographic regions, was therefore undertaken.

Table 1. – Infrageneric classification of Homalium by Warburg (1893) as emended by SLEUMER (1973), with nomenclatural corrections as needed.

| Subgenus/Section | Classical supporting character(s) | Distribution |
|------------------|----------------------------------|-------------|
| Subg. Blackwellia (Benth.) Warb. | | |
| Sect. Antinisa (Tul.) Baill. ex Warb. | Bracts large, reniform | Madagascar |
| Sect. Blackwellia Benth. | Bracts small, sepals and petals similar in size | Asia, Pacific, Africa, Madagascar |
| Sect. Nisa (Noronha ex Thouars) Baill. ex Warb. | Petals much smaller than sepals | Madagascar |
| Sect. Odontolobus Warb. | Sepals highly reduced | Madagascar |
| Sect. Rhodonisa (Tul.) Sleumer | Petals accrescent, much larger than sepals | Madagascar |
| Sect. Symphyostylum Warb. | Sepals and petals differ in size; styles fused | Africa |

| Subg. Homalium | | |
|----------------|-------------------------------|-------------|
| Sect. Eumyriantheia Warb. | Stamens 2-5 per bundle; calyx variable | Asia, Pacific, Madagascar |
| Sect. Homalium | Styles basally fused | Africa, New World |
| Sect. Pierrea (Hance) Warb. | Stamens 6+ per bundle, partly inserted on petals; sepals accrescent | Asia, Pacific |
| Sect. Polypanthera Warb. [= sect. Eumyriantheia Warb.? | Stamens 6+ per bundle; scaly persistent bracts and bracteoles | New Caledonia |

recognized by these authors, with their geographic distribution and classical defining features (cf. Warburg, 1893). In addition, LAI (1994) proposed two sections, Paniculatae S.S. Lai and Racemosae S.S. Lai, which perhaps dubiously separate Asian species traditionally referred to Sect. Blackwellia based on inflorescence morphology, but these names are illegitimate (see Applequist, 2013).

In support of an effort to revise the species of Madagascar, where both subgenera and six sections of Homalium are present, of which four sections are endemic, a re-evaluation of infrageneric classification seemed appropriate. It was questionable whether the subgenera were monophyletic, especially given the possibility that the Malagasy endemic Calantica Jaub. ex Tul. is related to a portion of Homalium as presently circumscribed. Calantica has a superior ovary but otherwise bears a strong resemblance to some species of Homalium. Like Homalium, Calantica may have either single or fasciculate stamens, suggesting that stamen number is relatively labile in this group of genera; this is already seen to be true in Homalium itself, in which fasciculate-stamened species may have from two to 12 stamens per petal. Observation of herbarium material of Malagasy species of Homalium, which include species of sects. Blackwellia Benth. and Eumyriantheia Warb. as well as four endemic single-stamened sections placed within subg. Blackwellia, suggested that species of some of the endemic single-stamened sections bore a much closer overall resemblance to sect. Eumyriantheia than to sect. Blackwellia, and that sect. Blackwellia as circumscribed by SLEUMER (1973) was heterogeneous. A broader study of floral and fruit morphology, including species from other geographic regions, was therefore undertaken.

Table 1. – Infrageneric classification of Homalium by Warburg (1893) as emended by SLEUMER (1973), with nomenclatural corrections as needed.
Because *Homalium* and potentially related genera form a group that is both large and morphologically complicated, a molecular phylogeny would be a very desirable aid to infragenic classification. Available sequence data from this group at this time, however, are not sufficient to provide useful resolution. Moreover, some species and species groups could not be included in a phylogenetic study because they are known only from one or a few, sometimes quite old collections, from which destructive sampling would not be permitted. Thus, any classification in the near future that includes all or most species can only be based on morphology, as is the existing classification accepted in Sleumer’s treatments. A new classification could be acknowledged not to be ultimately definitive, and yet be demonstrably more informative than the previously used classification.

**Material and methods**

All Malagasy specimens of *Homalium* at P and MO were examined to facilitate revisionary treatments of the six sections that occur in Madagascar (Applequist, 2016 and unpubl. data). Based on those observations, characters identified as varying among sections included: bract and bracteole size and persistence; petal and sepal number, shape, and similarity or lack thereof; presence or absence of long cilia on petal and sepal margins; shape of the calyx cup; stamen number, stamen length and anther size and conformation; style length and degree of fusion; shape of the apical part of the ovary in flower and in fruit; presence or absence of trichomes inside the ovary; and, possibly, the number of seeds per fruit. Mature fruits are rarely seen in herbarium material, as entire flowers generally fall as seeds mature; hence flowering characters are of primary importance. Material of species available at MO from other sections and regions outside Madagascar was examined to determine the broader scope of variation within *Homalium*.

Microphotographs of representative examples of each section or morphologically distinctive infrasectional group were made using a Canon Powershot A640 attached to a Nikon SMZ dissecting microscope [all specimens from MO for Fig. 1 to 10]. Most species seen were not photographed, because their floral morphology was broadly similar to that of illustrated relatives.

For some species (mostly from the Asian, Malesian and Pacific regions), no herbarium material was available for study, or the only available material was poor or questionably identifiable. Protologues, type images from JSTOR, and descriptions or illustrations in recent literature (Sleumer, 1954, 1973, 1985; Lescot, 1970, 1980; Craven, 1979; Smith, 1979; Sleumer & Bosser, 1980; Whistler, 2004; Yang & Zmarzty, 2007; Wu et al., 2008; Tagane et al., 2016) were consulted to verify the apparent affinities of these species. Currently recognized species that could not be placed in a section with reasonable confidence were left as incertae sedis; these are discussed individually below.

**Results and discussion**

Morphological examination of species from all recognized sections of *Homalium* reveals that most sections are quite consistent, but one is markedly heterogeneous (sect. *Eumyriantheia*) and another (sect. *Blackwellia*) includes three misplaced species. Further, maintenance of the current circumscription of subgenera is untenable, as both appear heterogeneous. Morphology and possible affinities of each section are discussed below.

**Section Homalium**

Three fasciculate-stamened sections have been recognized in *Homalium* in recent decades, namely sect. *Homalium* itself, sect. *Eumyriantheia*, and sect. *Pierriea* (Hance) Warb. Sect. *Homalium* (Fig. 1A–F), which includes about three species each in the New World and Africa, was putatively distinguished from the large and heterogeneous sect. *Eumyriantheia* by its fused styles. (This character has the potential for confusion, since a slight degree of basal stylar fusion sometimes appears in species of the latter section.) The petals and sepals number 5 to 7, are ovate (or the petals elliptical), and at anthesis often spreading, with the upper part of the hypanthium relatively conspicuous; the petals may be similar to the sepals in size or longer, and both are often moderately accrescent; the calyx cup, which is usually more or less funnelform at anthesis, becomes nearly hemispherical in fruit; the sepals glands are large; the petals may be minutely ciliate or appear so due to the abaxial petal indument but are not strongly long-ciliate.

Anthers of sect. *Homalium* are broadly oblong-elliptical, dorsifixed, with a large connective and oblong-elliptical locules that are usually not much divergent from one another; the slits by which they dehisce are visible on the same face and are often nearly parallel (Fig. 1E). This morphology, which will be termed “*Homalium*-like”, is described in such detail because some subgroups have significantly different morphology. The apical part of the ovary is nearly flat to conical at anthesis, becoming shallowly to conspicuously conical in fruit; there is a fused stylar column, but it is typically short. There are often some short trichomes inside the maturing ovary (Fig. 1B, 1F). Though multiple immature seeds are sometimes seen, fruits may also contain one to two large ellipsoid seeds (also reported for *H. abdessammadii* Aschers. & Schweinf. by Sleumer, 1973); it is possible that most developing ovules usually do not mature.

Size and persistence of bracts and bracteoles varies among sections (as well as to some extent within sections). In sect. *Homalium* the bracts are small, or long and narrow, and
Fig. 1. – Flowers and fruit of Homalium sect. Homalium. A-B. Homalium racemosum Jacq.: flower and fruit longitudinal section; C. Homalium guianense (Aubl.) Oken; D-F. Homalium abdessammadii Asch. & Schweinf.: flower, close-up of anthers and fruit longitudinal section. [A-B: Clarke et al. 6438; C: Del Carpio et al. 1685; D-E: Vandenberghen 5; F: White 1066]
persistent. Flowers are usually pedicellate, and bracteoles are often borne quite high on the pedicel. As is the case in most sections, pedicels, where present, are articulated.

**Section Blackwellia**

The widespread, single-stamened sect. *Blackwellia* and similar fasciculate-stamened species were together recognized at the generic level as *Blackwellia* Lam. (nom. illeg.) in early literature, and present a maximal contrast to the morphology of sect. *Homalium* and allied sections. Species of sect. *Blackwellia* (Fig. 2A–H, 3A–G) have small flowers with usually 7 to 11 (in a few species to 5 or 12, or reportedly aberrantly 15) petals and sepals. In many species the petals and sepals are ligulate to narrowly elliptical (to linear or oblong) and similar in size, while in others the petals are narrowly elliptical to spatulate or oblanceolate (rarely narrowly obovate, oblong-ovate or narrowly deltoid) with the sepals noticeably smaller and narrower with acute apices; rarely, the sepals are tiny. The petals and sepals are usually ciliate, often conspicuously so with very long and/or stiff trichomes, and (as is common in several sections of *Homalium*) often moderately and to a similar degree accrescent in fruit. They are usually erect to ascending at anthesis, sometimes spreading or rarely reflexed in fruit. The sepals and petals are usually small and rounded (proportionate to the narrow sepals), rarely elliptical. The fused portion of the calyx is turbinate to narrowly funnelform or tubular, at least in fruit (though occasionally funnelform or short, especially in very small-flowered species), and is usually conspicuously ridged. Bracts are usually small or narrow and early caducous; bracteoles are usually absent, though the possibility that some species have very small and rapidly caducous bracteoles cannot be excluded.

There is a noticeable diversity of anther morphology in sect. *Blackwellia*. All species from Madagascar and the Mascarenes (Fig. 2A–E) have anthers that are quite small, to 0.2 mm long, with locules that are subglobose, so the anthers’ width exceeds their length, and usually noticeably divergent (Fig. 2D, 2G); the slits by which they dehisce are oriented at a broad angle of separation, sometimes almost opposite one another. This is henceforth termed “Blackwellia-like” anther morphology. The anthers of these species often appear to be basifixed and to dehisce towards the apex, though given the overall shape and appearance of the flowers. Those species with *Blackwellia*-like anthers (Fig. 2A–H) tend to have petals and sepals both ligulate (to narrowly elliptical or oblong) and similar in size, and those with *Homalium*-like anthers (Fig. 3A–G) tend to have petals broadest above the midpoint and markedly smaller, acute sepals. However, there are exceptions. For example, all three African species of sect. *Blackwellia*, whatever their anther morphology, have petals and sepals that are significantly different in shape and/or size.

The ovary in sect. *Blackwellia* is conical, usually narrowly so, at anthesis; the styles are free or fused only at the extreme base. The upper part of the ovary is sometimes narrowly tapering and long enough that it might be assumed to be a conical, fused style base, but the ovary locule extends for almost all of this length (Fig. 2H, 3E–F). In fruit, the calyx tube frequently expands in breadth and the apical portion of the ovary becomes more prominently conical. At least the lower, empty portion of the ovary locule is pubescent, sometimes densely, seldom to glabrate. Immature fruits usually contain several small seeds that are confined to the upper portion of the locule, though it is not clear whether all of these mature.

Three species from Madagascar traditionally placed within this group are excluded from the above description and discussed under sect. *Odontolobus*, below.

Hence, sects. *Homalium* and *Blackwellia* exemplify groups of species that usually differ in several floral characters, in addition to stamen number, and that are readily distinguished by the overall shape and appearance of the flowers.

**Sections Eumyriantheia and Polyanthera**

Sect. *Eumyriantheia* is defined by having fasciculate stamens while lacking probably derived features (fused stylar column, filaments partly inserted on petals, high stamen number combined with persistent bracts and bracteoles; see Table 1) that characterize other fasciculate-stamened sections. It is widespread and distinctly heterogeneous. The Malagasy species of sect. *Eumyriantheia* (Fig. 4A–C, and see Applequist, 2016), including the type of the section, have only 4–5 (rarely to 6) sepals and petals, both broad and often markedly different in shape, ascending to spreading; the petals are often obovate. The calyx cup is usually funnelform, broadening in fruit, and not prominently ridged. Sepal glands are often large and elongated, proportionate to the relatively broad sepal bases. The anthers are large (at least 0.3 mm) and similar to those of sect. *Homalium* in shape. However, the styles are fused only at the extreme base, or are effectively free; the locule of the maturing ovary is glabrous. It appears that at maturity there is usually only one large subglobose seed, though as in sect. *Homalium*,
Fig. 2. – Flowers and fruit of Homalium sect. Blockwellia Benth. from Mauritius, Madagascar, and Africa. A. Homalium paniculatum (Lam.) Benth.; B. Homalium axillare (Lam.) Benth.; C. Homalium erianthum (Tul.) Baill.; D. Homalium myrtifolium Sleumer; E. Homalium viguieri H. Perrier; F-H. Homalium rufescens Benth.: flower, dehiscing anthers, and fruit longitudinal section.
[A: Lorence 1161; B: Antilahimena 8838; C: Randrianasolo et al. 519; D: Thulin & Razafindraibe 11855; E: Rakotonirina 535; F-H: Ogilvie 28864]
Fig. 3. – Flowers and fruit of Homalium sect. Blackwellia Benth. from Asia and Africa. A-B, Homalium napaulense (DC.) Benth.: flower side and top views; C-D, Homalium cochinchinense (Lour.) Druce: flower and close-up of anthers; E, Homalium paniculiflorum F.C. How & W.C. Ko: fruit longitudinal section; F, Homalium tomentosum (Vent.) Benth.: flower and fruit longitudinal section; G, Homalium dentatum (Harv.) Warb.: flowers.

[A-B: Suzuki et al. 9455047; C-D: Liang & Liang 94; E: Chow et al. 78286; F: Raizada s.n.; G: Chase 8113]
multiple small, probably immature seeds are sometimes seen. The ovary is usually shallowly conical (to nearly flat or convex) in flower and in early fruit is moderately conical but not much elongated as in some species of sect. *Homalium*.

By contrast, the examined Asian, Malesian and Pacific species previously placed in sect. *Eumyriantheia* (Fig. 5A-G and 6A-E) are in most ways hardly distinguished from sect. *Blackwellia*, except in having two or more stamens per petal, and it seems obvious that they are related to the latter. (Early authorities implicitly recognized this fact by describing many of them first under *Blackwellia* Lam., nom. illeg.) Both bracts and bracteoles are present and at least the bracts are often persistent. Species from southern Asia and Malesia (Fig. 5A-5G) usually have *Homalium*-like anthers (though small-anthered potential intermediates were seen) and petals usually (but not always) exceeding sepals and broadest above the midpoint. A few of these species have ovaries that remain nearly flat at the apex after anthesis (Fig. 5B, 5G); the apical part of the ovary is narrow in diameter, in proportion to the overall size of the flower (distinguishing these from species in other groups that have nearly flat ovaries whose exposed apical surface is broad) and the calyx tube is usually well-developed. This ovary morphology was not seen in any of the single-stamened species.
The Papuan *H. dentrecteauxcense* Craven (Fig. 5H), from the southeastern extreme of the *Flora Malesiana* region, has *Blackwellia*-like anthers and ligulate sepals and petals with long patent hairs. Almost all species seen from Pacific islands outside the *Flora Malesiana* region (Fig. 6A-E) also have *Blackwellia*-like anthers (though rare individual specimens post-anthesis had apparently somewhat elongated locules). However, *H. circumpinnatum* F.M. Bailey, one of two Australian species seen, has unusually small *Homalium*-like anthers. Most of these species have ligulate to linear petals and sepals. As in sect. *Blackwellia*, the correlations between anther morphology and corolla morphology or geography are imperfect. The fact that similar patterns appear in both subgroups does suggest the possibility that classification by stamen number is artificial, with natural groups being characterized by a common anther shape. Contrarily, Asian and Malagasy species of sect. *Blackwellia* that have different anther types share the probably derived character of rapidly caducous bracts and apparently absent bracteoles.

Warburg (1893) segregated two New Caledonian species, *H. deplanchei* (Vieill.) Warb. and *H. polyandrum* Warb. (= *H. mathieuannum* (Vieill.) Briq.), into sect. *Polyanthera*. These species are not conspicuously different from the Pacific species of sect. *Eumyriantheia* except in having an unusually high number of stamens per fascicle (Fig. 6F-G). Sleumer (1973) therefore lumped sect. *Polyanthera* into sect. *Eumyriantheia*. However, when overall morphology is considered, it is not plausible that the Malagasy species of sect. *Eumyriantheia* and the “*Blackwellia*-like” Asian and Pacific species that have been placed in the same section form a natural group. Since the type of sect. *Eumyriantheia* is the Malagasy *H. laxiflorum* (Tul.) Baill., it is proposed below that sect. *Eumyriantheia* be restricted to the Malagasy species and that sect. *Polyanthera* be revived and expanded to encompass all fasciculate-stamened Asian and Pacific species except those belonging to sect. *Pierrea* (see below).

One atypical Malagasy species of sect. *Eumyriantheia, Homalium trigynum* (Baker) Sleumer (Fig. 7A), bears some resemblance to atypical Asian *Blackwellia*-like species (see for comparison Fig. 5A). As in other species of sect. *Eumyriantheia*, its ovary is only moderately conical; the calyx tube is noticeably distended in fruit, and the locule is glabrous and sometimes contains a single large seed. The ovary often appears to be partly divided by an internal partition or may be almost entirely filled with spongy tissue, perhaps indicating a tendency to abnormal development. The flower has 4-5 sepals, which are sometimes slightly longer than the petals, and the broad sepal glands are sometimes elevated on a short thick stalk, a character that is seen in some other species of *Eumyriantheia* but not normally in *Blackwellia*-like flowers (though see discussion below of the aberrant, ambiguous Philippine species *Homalium palawanense*). Anthers are *Homalium*-like but unusually small. This species is herein considered probably related to the remainder of Malagasy *Eumyriantheia*, but molecular data regarding its relationships would be of interest. Individual specimens believed to represent intersectional hybrids have been observed from Madagascar and Malesia, so it is tempting to speculate that this species could be of hybrid origin, though no solid evidence to that effect exists. It is morphologically fairly consistent over a large geographic range (see *Applequist*, 2016), so specimens certainly are not interpretable as hybrids.

Sleumer (1954) treated *Homalium moultonii* Merr., a species from Sarawak and Brunei, as “anomalous” and did not place it within a section. The species was said to be unique in having very large glands, fused into an almost continuous disk that almost covers the apical surface of the ovary, and about 20 stamens described as “inserted irregularly” on that disk. On specimens now available, the flowers are 10- to 12-merous and the stamens consistently 2 per petal (Fig. 7B-C), a feature Sleumer (1954) reported in several Malesian “*Eumyriantheia*” species. The species’ numerous narrow similar perianth segments, long narrowly funnelform calyx tube, and narrow densely pubescent ovary locule certainly suggest membership in the *Blackwellia* group. The ovary locule is narrow and densely pubescent. Given these features and its geographic origin, it is most reasonably presumed to be an unusual member of sect. *Polyanthera* as herein circumscribed. However, two atypical features should be noted. First, this species is one of the only species seen from the region that has *Blackwellia*-like anthers (though several rare Malesian species were not seen). The filaments are unusually short. Second, the flower has a broad, nearly flat apical ovary surface, though combined with a long calyx tube. These, together with the short petals, suggest potential affinities to the Malagasy single-stamened sect. *Odontolobus* as herein circumscribed.

*Homalium kunstleri* King is a very rare species from the Malay Peninsula (Perak). Sleumer (1954) reported it as having two stamens per petal; in contrast to the other two-stamened species from the region, *H. dasyanthum* (Turcz.) Theob. and *H. foetidum* (Roxb.) Benth. (see Fig. 5C, 5F) it is said to have broad persistent bracts (much larger than bracts of any other species from the region) and 6-merous flowers with a “widely funnelform” calyx and “broadly lanceolate” petals. This raised the question of whether this species might be similar to *H. moultonii*, discussed above, in overall morphology, except for the lack of abnormally large sepal glands, and both might have affinities to the Malagasy *Blackwellia* species herein suggested to be similar to sect. *Odontolobus*. Neither the protologue nor Sleumer’s (1954) description clarify all relevant features (e.g., androecial morphology and ovary shape are not described), and no herbarium material was available for observation by this author. Online images of type and syntype material do not definitively answer the question, largely because the
Fig. 5. – Flowers and fruit of Homalium sect. Eumyriantheia Warb. from Asia and Malesia. A. Homalium caryophylaceum (Zoll. & Moritz) Benth.: flower and ovary longitudinal section; C. Homalium foetidum (Roxb.) Benth.: flower, fruit and longitudinal section; E. Homalium myriandrum Merr., fruit and longitudinal section; F. Homalium dasyanthum (Turcz.) Theob.; G. Homalium bracteatum Benth.; H. Homalium dentrecasteauxense Craven. [A-B: Giesen 115; C: Chung 2678; D: Soejarto et al. 7791; E: Petelot 960 (left) & Hiep 3036 (right); F: Maxwell 86-400; G: Jacobs s.n.; H: Takeuchi & Towati 14876]
Fig. 6. – Flowers and fruit of Homalium sect. Eumyriantheio Warb. from Pacific islands and Australia. A. Homalium decurrens (Vieill.) Briq.: flower and fruit; B. Homalium guillainii (Vieill.) Briq.: fruit and longitudinal section; C. Homalium francii Guillaumin; D. Homalium viitense Benth.; E. Homalium alnifolium Thwaites & F. Muell.; F-G. Homalium deplanchei (Vieill.) Warb. (formerly placed in H. sect. Polyanthera Warb.): top and side views and dehiscing anthers.

[A: MacKee 30488; B: McPherson 3747; C: McPherson 1598; D: Degener 14969; E: Hodge s.n.; F-G: MacKee 37844]
Fig. 7. – Flowers of atypical species of Homalium sect. Eumyriantheia Warb. (A), H. sect. Polyanthera Warb. (B–C), and H. sect. Pierrea (Hance) Warb. (D–F). A. Homalium trigynum (Baker) Sleumer: post-flowering; B–C. Homalium moultonii Merr.: flower, top view, and post-flowering; D–F. Homalium grandiflorum Benth.: pressed-open flower, flower with bract, and post-flowering.
[A: Randrianaivo et al. 833; B: Jawa 36601; C: Dyg. Awa & Othman S47078; D–E: Parkinson 8754; F: Elmer 21686]
consistently erect petals obscure the androecium and ovary. This is not consistent with the “Odontolobus-like” species, which have a broad upper ovary surface and spreading petals. Hence *H. kunstleri* is tentatively retained in sect. *Poyantha*.

When these sections are compared to the previously discussed sections in terms of floral morphology and overall floral appearance, sect. *Eumyriantheia* s.s. clearly has affinities to sect. *Homalium*, whereas the revived and expanded sect. *Polyantha*, including all Asian and Pacific species formerly placed within sect. *Eumyriantheia*, must be closely related to sect. *Blackwellia*. Though no single character unites all the species in the latter group of sections (individual species may have few broad petals, spreading petals, absence of long cilia, short calyces or flat-topped ovaries, etc.), they have as a group a distinctive appearance that leaves little doubt that they form a natural group.

**Section Pierrea**

The last section that has fasciculate stamens is the south Asian to Malesian sect. *Pierrea*, which usually has 6 or more stamens per fascicle, some of which are inserted on the basal portion of the petal itself. Species of sect. *Pierrea* are distinctly different from all other Asian and Pacific species. The flowers are sometimes unusually large, especially in fruit due to perianth accrescence; the sepals are often markedly longer than the petals in flower, in fruit, or both, and the petals may ultimately curve inward over the fruit. Sepals range from oblong to narrowly elliptical, oblanceolate, lanceolate or linear to spatulate, while the petals are lanceolate to ovate or somewhat oblong. In one species, *H. dictyonervum* (Hance) Warb., the perianth is up to 10-merous, although perianth parts are usually less numerous. The calyx cup in sect. *Pierrea* is typically funnelform to hemispherical, and the anthers are large and *Homalium*-like. Bracts and bracteoles are sometimes quite large and persistent. Thus, sect. *Pierrea* seems to have closer affinities with the African/Malagasy and New World sects. *Homalium* and *Eumyriantheia* s.s., and/or with single-stamened sections described below that have unequal and accrescent perianth whorls, than with other Asian and Malesian species.

The only species for which adequate material for study was available was *H. grandiflorum* Benth. (Fig. 7D-F), but protologues, descriptions of species from recent literature (Sleumer, 1954, 1985; Lescot, 1970) and type images available from JSTOR support the placement of others. Species of this section display other unusual features: the stylar branches of some species can number up to 7 or 8 (rarely 9), and the elongated, tubular ovary appeared in some flowers of *H. grandiflorum* to be nearly superior, with the short hypanthium mostly adherent to the ovary rather than truly adnate to it except at the very base.

**Section Odontolobus and species with “Odontolobus-like” morphology**

Sections with one stamen per petal, in addition to the widespread sect. *Blackwellia*, include one that is endemic to Africa (sect. *Symphyostylium* Warb.) and four that are endemic to Madagascar (sects. *Nisa* (Noronha ex Thouars) Baill., *Rhodoma* (Tul.) Sleumer, *Odontolobus* Warb., and *Antinisa* Warb.). It is very common in all of these sections for the sepals and petals to be markedly different in size at some stage of development. Most seem more similar to the fasciculate-stamened sects. *Homalium*, *Eumyriantheia* s.s., and *Pierrea* than to sect. *Blackwellia*; however, the diversity among them is substantial. The Malagasy sects. *Odontolobus* and *Antinisa* are discussed first because they are least similar to sects. *Homalium*, *Eumyriantheia* s.s., and *Pierrea* while the remaining group of three sections includes some intermediates between *Homalium*-like forms and *Odontolobus*-like forms.

The three recognized species of sect. *Odontolobus* have small or even tiny sessile flowers that are usually borne in clusters (Fig. 8A-D). Bracts and bracteoles are thick-textured rather than membranous, and both are often persistent, though the bracteoles are very small and often hidden by flowers. *Homalium lucidum* Scott-Elliot rarely has partly short-pedicellate flowers, in which case the pedicels are not articulated (and may simply be a highly elongated receptacle). The sepals are reduced to minute teeth, so that from above the flower appears to have only one perianth whorl (Fig. 8A-B). Petals are 5 to 7 in number; in one species they are prominently ciliate, and in the other two they are much reduced in size, though still larger than the sepals. The apical part of the ovary is broad and flat to shallowly convex at anthesis. In fruit it becomes convex (not, as in previously discussed sections, conic), while the short, broadly funnelform calyx tube can become nearly hemispherical. The anthers are very small, with locules diverging at a relatively broad angle, hence more *Blackwellia*-like than *Homalium*-like. In these species, the filaments and styles are both very short, and it seems unambiguous that the attachment of the anther is basal and the locules dehisce at the apex (Fig. 8C). The styles are not fused except sometimes at the extreme base; the apical portion of the inner surface of the ovary locule is sparsely pubescent to glabrate. The ovary locule is subglobose (to obovoid in *H. lucidum*) and sometimes contains several small developing ovules, though large single subglobose mature seeds have been seen by the current author in both species.

Three Malagasy species placed within sect. *Blackwellia*, i.e. *Homalium brachystylis* (Tul.) Baill., *H. longistaminum* H. Perrier, and *H. planiflorum* (Boivin ex Tul.) Baill. (see Sleumer, 1973), are herein proposed for transfer to sect. *Odontolobus*. Their sepals are not reduced to teeth, though those of *H. planiflorum* (Fig. 8E-F) are short and both perianth whorls are quite small in *H. longistaminum*; they can have up to...
Fig. 8. – Flowers and fruit of the Malagasy Homalium sect. Odontolobus Warb. (A-D) and atypical Malagasy species until now placed in H. sect. Blackwellia Benth. (E-G). A-B. Homalium lucidum Scott-Elliot: underside of flower and top view; C. Homalium parkeri Baker : flower cluster; D. Homalium moniliforme H. Perrier, flower clusters; E-F. Homalium planiflorum (Boivin ex Tul.) Baill.: flower and longitudinal section of fruit; G. Homalium brachystylis (Tul.) Baill.: flower.

[A: lambana 181; B: Ravelonarivo 2253; C: Skema et al. 54; D: Ludovic et al. 870; E: Rakotovao 4737; F: Nicoll et al. 553; G: Ranaivojaona et al. 365]
8 sepals and petals, which are or appear ciliate, especially in *H. brachystylis* (Fig. 8G). In two species, especially the rare *H. longistaminum*, the styles and filaments are unusually long for sect. *Odontolobus*. Hence, their presumed affinities have been to sect. *Blackwellia*. However, they otherwise more closely resemble the species of sect. *Odontolobus* than the other Malagasy species of sect. *Blackwellia*. The upper surface of the ovary is broad and nearly flat (to hemispherical in *H. longistaminum*) at anthesis, becoming convex, not elongated-conical, in fruit. The locule of the fruit is subglobose and glabrous and usually contains a single large, subglobose maturing seed (Fig. 8F); this fruit morphology sharply contrasts with the typical morphology of sect. *Blackwellia*. The flowers are pedicellate, but in two species borne in clusters. Bracts and bracteoles are present and sometimes thick-textured or the bracteoles even subterete, whereas all other Malagasy species of sect. *Blackwellia* lack bracteoles. These species, plus one undescribed species similar to *H. longistaminum*, are therefore believed to be sister lineages to sect. *Odontolobus* s.s., lacking the synapomorphic character of extreme sepal reduction. Transferring them from sect. *Blackwellia* to sect. *Odontolobus* will reduce the heterogeneity of the former section more than it increases the heterogeneity of the latter.

The enigmatic Indonesian *H. moultonii* (Fig. 7B–C), discussed above, could possibly be a more distant relative of this group, sharing with it features such as a broad, flat upper ovary surface and short stamens and styles, but also possessing features, such as a long calyx tube, elongated pubescent ovary locule, and paired stamens, that are typical of sect. *Polyantha*. No other species representing plausible transitional forms between the *Blackwellia*-like and the *Odontolobus*-like have been seen, though some species have been seen only from type images that do not permit observation of fine detail.

The strong floral reduction in previously recognized species of sect. *Odontolobus* would have made it challenging to identify their affinities with other sections. The relatively few and broad petals, and the broad, single-seeded ovary, could suggest a similarity to sect. *Homalium* and related sections, while the form of the anthers is *Blackwellia*-like, although even more extreme. However, the existence in Madagascar of species that appear intermediate between classic *Blackwellia* and classic *Odontolobus* strongly favors the hypothesis that sect. *Odontolobus* is related to sect. *Blackwellia*, or perhaps even evolved within the latter section as it is presently circumscribed.

**Section Antinisa**

The current treatment of sect. *Antinisa* (Sleumer, 1973) recognizes only one species, *Homalium involucratum* (DC.) O. Hoffm. (Fig. 9A–C), divided into three “forms” that should probably be recognized at least at the varietal level, as modest geographically correlated morphological variation is observable. In this species, the inflorescence is spicate with small sessile flowers usually borne in clusters (often 3-flowered) that are subtended, and usually completely enveloped, by very large persistent reniform bracts (Fig. 9A–B). The flowers and sometimes the paired bracteoles are pubescent; the calyx tube is densely sericeous with very long trichomes. The petals and sepals number 5 to 8 and are more or less lanceolate, with the petals at least slightly exceeding the sepals. Sleumer (1973) states that in fruit the petals are more strongly accrescent and curve over the fruit; this was not conspicuous in this study, but probably no mature fruits were seen. The stamens have short filaments and small anthers (Fig. 9C); the anthers are basifixed and dehisce laterally, and the connective is large and bulbous, more conspicuous than in sect. *Odontolobus* or small-anthered species of sect. *Blackwellia*. The styles are short and free. The upper part of the locule of the ovary is rather densely pubescent, and Sleumer (1973) reports that fruits can be up to 4-seeded.

Another morphology of *H. involucratum* suggests a relationship to the group of sections including *Blackwellia* and *Odontolobus*; however, the very large bracts and well-developed persistent bracteoles suggest otherwise. Molecular data from this species would therefore be desirable to determine its affinities.

**Single-stamened sections with “Homalium-like” morphology and intermediates:** *Nisa, Symphyostylium*, and *Rhodonissa*

The remaining three sections, including *Symphyostylium, Nisa*, and *Rhodonissa*, seem most closely affiliated with the multi-stamened *Homalium*-like sections and/or sect. *Pierrea*, but some characters are inconsistent. Most species of sect. *Nisa* have sepals that are much larger than the petals, as in sect. *Pierrea*, while sects. *Symphyostylium* and *Rhodonissa* have petals that are much larger than the sepals. In all three, the larger perianth whorl is often conspicuously accrescent after anthesis, much more so than the smaller whorl, which in two sections tends to curve inward over the fruit.

Sect. *Nisa* (Fig. 9D–G) has a very short, cup-shaped to broadly funnelform calyx tube and 5–6(-7) broad, variously shaped, accrescent petals and sepals. In one species, *H. louvelianum* H. Perrier, the sepals and petals are of almost equal size and both are often spreading (Fig. 9D–E). In the other three recognized species, the sepals are usually larger than the petals and spreading, while the petals tend to curve over the fruit (Fig. 9F). Anthers are large, with the locules broadly oblong-elliptical and not diverging much, similar to those of sect. *Homalium*. The styles can be relatively short, or long and partly fused. The upper surface of the ovary is usually nearly flat at anthesis, usually becoming prominently conical or hemispherical in fruit (Fig. 9E); the fruit may contain one large subglobose seed or several small immature seeds (which may or may not actually mature). Bracts and bracteoles are large and persistent (Fig. 9G).
Fig. 9. – Flowers and fruit of the Malagasy Homalium sect. Antinisa Warb. (A-C) and H. sect. Nisa (Noronha ex Thouars) Baill. ex Warb. (D-G). A-C. Homalium involucratum (DC.) O. Hoffm.: bract, flower cluster, and flower with anther; D-E. Homalium louvelianum H. Perrier: flower and fruit longitudinal section; F-G. Homalium nudiflorum (DC.) Baill.: flower and bracts.

[A-C: Birkinshaw et al. 1635; D: Dumetz 1237; E: Razakamala & Rabehevitra 649; F-G: Rakotovao et al. 3201]
The relatively speciose African sect. Symphyostylium (Fig. 10A-D) has usually 5-6-merous (rarely to 4- or 8-merous) flowers, typically with oblong to obovate petals and much smaller, lanceolate to ovate, acute sepals. The anthers are similar in shape to those of sects. Homalium, Nisa, etc., though sometimes quite small. The styles are almost always fused into a column for at least half their length, and usually longer, except that in H. stipulaceum Welw. ex Mast. the column is much reduced and the style branches also quite short. The upper surface of the ovary can be nearly flat or column is much reduced and the style branches also quite short. The upper portion of the ovary can be nearly flat or elevated, especially in fruit; the calyx tube is funnel-form to cup-shaped in fruit. Immature seeds often number 10 or more, though occasionally a single large maturing seed is seen. Sleumer (1973) distinguished this section from sects. Nisa, Rhodonisa, and Odontolobus on the basis that the latter three had styles free to the base. While the distinction between the upper portion of a conical ovary and a broad fused style base is not always obvious, it seems evident that some basal fusion of the styles can occur in sects. Nisa and Rhodonisa; indeed it is usual in the latter (see Fig. 10G). Unlike sect. Rhodonisa and other Malagasy sections in this and the previous group, sect. Symphyostylium generally does not have persistent bracts, and has typical Homalium-like anthers.

Species of sect. Rhodonisa (Fig. 10E-H) have usually 5 (to 4 or rarely 6) oblong to obovate petals, which as in sect. Symphyostylium are accrescent and much larger than the sepals, and large sepal glands. The sepals in fruit typically enlarge modestly and curve over the fruit; this morphology very much resembles that of sect. Nisa, except that a different perianth whorl is reduced in size and inward-curving. As in sect. Nisa, broad persistent bracts are common. However, this picture is complicated by contradictory and variable features. While anthers of some taxa are similar to those of Eumyriantheia, Nisa, etc., if usually rather small, there is a continuum of variation with the far extreme represented by H. rubriflorum Sleumer, which has short filaments and anthers with small, subglobose, widely divergent locules, as in Blackwellia or Odontolobus. In most taxa of the H. albi-florum (Boivin ex Tul.) O. Hoffm. complex, which actually encompasses several distinct species (Applequist, unpubl. data), the calyx tube is narrowly funnel-form to tubular and somewhat tapering at anthesis, becoming elongated, tubular and conspicuously ribbed or grooved (to ellipsoidal), with the locule strongly pubescent inside and the visible upper surface of the ovary narrow and often nearly flat except for the conical base of the fused styles (which Sleumer, 1973, considered often to be merely connivent; Fig. 10H). Though this morphology is not identical to that of sects. Blackwellia and Polyanthera, there is a certain resemblance. Short-ciliate petals and/or sepals are common in sect. Rhodonisa, another character that is also seen in sects. Blackwellia, Polyanthera and Odontolobus.

The affinities of sect. Symphyostylium are clearly with the Homalium group, previously indicated to include the fasciculate-stamened sects. Homalium, Eumyriantheia, and Pierrea, demonstrating that stamen number is not fundamental to the circumscription of that group. Sects. Nisa and Rhodonisa by extension also resemble that group more than sect. Blackwellia and allied sections. However, individual Blackwellia-like features appearing in certain species of sect. Rhodonisa complicate this picture. Since Madagascar is the primary center of sectional-level diversity in Homalium, it is possible that groups like Antinisa or Rhodonisa that display unexpected combinations of features are the descendants of ancestral forms intermediate between the ancestors of present-day sections. It is also possible that the species involved originate from intersectional hybridization; intersectional hybrid specimens are known and might be fertile. Genetic data would be desirable.

Criteria and implications for taxon circumscription

The following proposed classification of Homalium makes amendments to the existing classification where it is apparent from morphological evidence that species have previously been misplaced or sections inappropriately circumscribed. In view of the complexity of this group and the possibility that adequate molecular data will eventually be available, it seems best to be conservative in the interpretation of morphological data that are less than definitive. Whilst recognition of doubtfully monophyletic new infrageneric groups is to be avoided, existing groups that are certainly not monophyletic should no longer be recognized without recircumscription. These criteria, which to some extent are in conflict, influence decisions regarding the recognition and definition of subgenera and sections in ways that will be made explicit below.

Most sections appear to be natural groups, or at least not demonstrable by morphology to be otherwise. Two rearrangements of sectional boundaries seem necessary. Three Malagasy species formerly placed in sect. Blackwellia (Homalium brachystylis, H. longistanimum and H. planiflorum) should be moved to sect. Odontolobus, and the Asian and Pacific species now included with Malagasy species in sect. Eumyriantheia should be removed from that section. The latter group of ca. 50 fasciculate-stamened species and the over 40 remaining species of sect. Blackwellia together form a cohesive group. It is not, however, clear how that group should be subdivided: is number of stamens per petal or anther structure more important? If the former is used, in accordance with Warburg’s and following classifications, the simplest approach is to restore sect. Polyanthera and expand it to include all of the fasciculate-stamened species of this group, while all of the species with one stamen per petal remained in sect. Blackwellia. The latter approach would require the resurrection of sect. Pythagorea (Lour.) Kuntze, which was superfluous when published so has hardly ever been used, for the species with Homalium-like anthers.
Fig. 10. – Flowers and fruit of the African Homalium sect. Symphyostylium Warb. (A-D) and the Malagasy H. sect. Rhodonisa (Tul.) Sleumer (E-H). 
A. Homalium africanaum (Hook. f.) Benth.: top, bottom and side views; B. Homalium stipulaceum Welw. ex Mast.: top and bottom views; C. Homalium longistylium Mast.: post-flowering; D. Homalium letestui Pellegr.; E-F. Homalium rubriflorum Sleumer: flower and fruit longitudinal section; G. Homalium albiflorum (Boivin ex Tul.) O. Hoffm. s.l.: flower; H. Homalium leucophloeum (Tul.) Baill.: flower.
[A: Wieringa 3282; B: Louis[?] 8857; C: Ewango 1120; D: de Wilde et al. 9289; E-F: Rakotonandrasana et al. 401; G: Rakotovao et al. 3288; H: Barnett et al. 460]
Anther structure is apparently correlated with corolla morphology and geographic distribution, but the former correlation is imperfect, and both anther morphologies are found in southern Africa and in Australia, the farthest extremes of the group’s range. Contrariwise, single-stamened species tend to have rapidly caducous bracts and absent bracteoles, and fasciculate-stamened species to have persistent bracts and bracteoles, whatever their anther morphology. Thus, pending the availability of molecular phylogenetic data (assuming that the evolutionary history of this group is straightforward enough to be fully and accurately resolved by such data), the evidence in favor of any subdivision of this group will be limited and contradictory. Under these circumstances, it seems better to continue to employ the characters traditionally considered important than to adopt new divisions that contradict existing understanding. Using anther morphology to circumscribe sections would also have practical implications in the portions of the range where both morphologies are found: anthers are often lost after flowering, and without them, it might not be possible reliably to place specimens within a section. Hence, sects. Blackwellia and Polypanthera are treated for convenience as including all single-stamened and all fasciculate-stamened species from this group respectively, though it is acknowledged that one of these subgroups may ultimately prove to be paraphyletic or polyphyletic.

As for subgenera, it is evident that the subgenera as now defined are artificial, as the resurrected sect. Polypanthera is more closely related to sect. Blackwellia than to sects. Homalium and Eumyriantheia s.s. Authors of previous classifications perhaps recognized this but did not consider artificial, even polyphyletic, groups to be unacceptable if they seemed useful. Is it possible to rearrange sectional placement to maintain two subgenera for convenience? Most sections are easily assigned to the Blackwellia or the Homalium group. However, certain Malagasy sections, especially Antinisa and Rhodonia, incorporate features that are typical of both groups, though Rhodonia also seems to have clear affinities to sect. Nisa, which could reasonably be grouped with Homalium. Therefore, maintaining two subgenera would require the recognition of at least one newly circumscribed group whose monophyly was in doubt. Furthermore, both subgenera would be variable enough in floral shape, merosity, anther morphology, and other characters that formal verbal descriptions or keys would depend upon characters whose extreme states overlapped; this would make the classification cumbersome for those who were not familiar with the genus. The alternative of describing one, or possibly two, new subgenera for groups of sections including species with intermediate features is also undesirable due to the significant chance of accidentally promoting the recognition of a new non-monophyletic group. Since this genus is not very large, two levels of infrageneric classification are not necessary to facilitate taxonomic studies or specimen identification.

It is therefore proposed that only sections should be recognized at this time; future authors may recognize subgenera after phylogenetic data have shed light on the preferable means of doing so.

Two other small genera of Salicaeae in Madagascar, Calantica and Bivinia Jaub. ex Tul., have hermaphroditic flowers and single large sepal glands. Calantica, a genus of ten species (Applequist et al., 2014), has flowers that resemble the Eumyriantheia type except that the ovary is fully superior; both singly borne and fasciculate stamens are known in the genus. Bivinia includes the single species B. jalbertii Tul., which also occurs in eastern Africa; it has a superior ovary and lacks petals, and the stamens are much more numerous than in any Malagasy Homalium. In the event that future phylogenetic studies reported Homalium as now defined to be paraphyletic due to the exclusion of these or other recognized genera of Salicaeae, any genera arising within Homalium could be subsumed into that genus as sections or Homalium could be subdivided into multiple genera. This author would favor the latter because Homalium is already exceedingly diverse, and smaller segregate genera would be more cohesive and perhaps more useful. However, in view of the uncertain relationships among major lineages of Homalium, at present it is preferable to maintain the traditional generic circumscription.

### Key to recognized sections of Homalium

1. Stamens in fascicles of 2 or more per petal .......... 2
   1a. Stamens 1 per petal ....................................................... 5

2. Stamens partly inserted on the petals; petals shorter than the sepals in flower and/or fruit (to nearly equal); perianth accrescent, the sepals often more so than the petals ........ ............................................................... 7. Sect. Pierrea
   2a. Stamens all inserted between the sepal glands; petals longer than or equal to the sepals; perianth often moderately accrescent, if so then the petals at least as much so as the sepals ............................................................... 3

3. Calyx tube turbinate to narrowly funnelform or tubular, at least in fruit (rarely funnelform or hardly visible in flower), usually prominently ridged; sepals and petals 5–12(-13), usually ciliate with usually long and/or stiff trichomes; upper surface of ovary usually narrowly conical (rarely nearly flat), the styles free to near base; ovary locule elongated and narrow (rarely to obconical), pubescent; Asia, Maleasia, Pacific ................................................................ 8. Sect. Polypanthera
   3a. Calyx tube broadly funnelform, in fruit becoming convex to cup-shaped or nearly hemispherical (in H. trigynum short-cylindrical or turbinate becoming broadly ellipsoid in fruit), not prominently ridged; sepals and petals 4–7, not ciliate (ciliolate); upper surface of ovary usually broad, nearly flat to conical, in fruit conical to convex, the styles

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### Key to recognized sections of Homalium (Salicaeae) – 249

- **Section 1**: Stamens in fascicles of 2 or more per petal
  - **1a**: Stamens 1 per petal
- **Section 2**: Stamens partly inserted on the petals; petals shorter than the sepals in flower and/or fruit
  - **2a**: Stamens all inserted between the sepal glands; petals longer than or equal to the sepals; perianth often moderately accrescent
- **Section 3**: Calyx tube turbinate to narrowly funnelform or tubular
  - **3a**: Calyx tube broadly funnelform, in fruit becoming convex to cup-shaped or nearly hemispherical
free to near base or fused into a short stylar column; ovary
locule broad, ovoid to ellipsoid or subglobose, pubescent
or glabrous; Africa, Madagascar, Americas................. 4

4. Petals 4-5(-6), ovate to elliptical (to somewhat oblong,
broadly spatulate), moderately accrescent; upper surface
of ovary prominently conical; styles usually fused at base
into a short distinct column (free to near base, fused for
most of length); locule of fruit ellipsoid with a shallowly
to strongly conical apex, more or less pubescent; Central
and South America, Africa ................... 1. Sect. Homalium

4a. Petals 5-7, obovate to oblanceolate (in *H. trigynum*
to spatulate), little accrescent; upper surface of ovary nearly
flat to shallowly (moderately) conical in flower, in fruit
moderately conical to convex; styles free to near base;
locule of fruit subglobose, glabrous (in *H. trigynum*
ellipsoid, partly divided or filled with spongy tissue, sparsely
pubescent); Madagascar................... 4. Sect. Eumyriantheia

5. Bracts very large, reniform, persistent, enfolding and com-
pletely or almost completely concealing flowers............... 6

5a. Bracts variable in size and persistence, not large enough to
cover flowers .......................................................... 2. Sect. Antinisa

6. Stipules fused opposite petiole (in *H. intercedens* free and
axillary); sepals longer than (in *H. loxostachium* about equal
to) petals .................................................. 5. Sect. Nisa

6a. Stipules free, axillary; sepals shorter than or about equal to
petals.............................................................. 7

7. Sepals reduced to minute deltoid teeth or small and ligu-
late to lanceolate-oblong; petals small, ovate to transversely
ovate or narrowly oblong-lanceolate to oblong-elliptical,
not or very little accrescent; styles free to base, often short;
upper surface of ovary broad and nearly flat (to convex) in
flower, becoming convex in fruit ...... 6. Sect. Odontolobus

7a. Sepals variable in relative size, not minute; petals usually
broadest above the midpoint or ligulate to narrowly ellipti-
cal or oblong (rarely to linear, oblong-ovate, or narrowly
deltoid), at least modestly accrescent; styles free, with ovary
conical in flower, or lower portion of styles usually fused,
with ovary nearly flat to moderately conical or convex in
flower, in fruit usually becoming conical to convex unless
apical surface is very narrow............................... 8

8. Bracteoles usually absent; calyx tube turbinate to nar-
rowly funnelform or tubular (seldom short, funnelform),
usually prominently ridged; perianth 5-12(-15)-merous,
usually ciliate, usually with long and/or stiff trichomes;
upper surface of ovary conical in flower, usually promi-
ently so in fruit; styles free (though upper part of nar-
rowly conical ovary may resemble a stylar column)......... 3. Sect. Blackwellia

8a. Bracteoles present, caducous or persistent; calyx tube
broadly funnelform, in fruit convex to nearly hemispheri-
cal (in a few species cylindrical and ridged or grooved);
perianth 4-5-6(-8)-merous, not ciliate or ciliate with soft,
often short trichomes; upper surface of ovary nearly flat
(to shallowly convex or conical) at anthesis, in fruit convex
or conical (or remaining nearly flat); styles usually partly
fused (seldom quite short)....................................... 9

9. Bracts and bracteoles usually small and caducous; calyx
tube funnelform, in fruit cup-shaped, not prominently
ridged; sepals acute, often little accrescent, not strongly
curved over fruit; Africa.................. 10. Sect. Symphyostylium

9a. Bracts broad, bracts and bracteoles persistent; calyx tube
tubular to funnelform, in fruit tubular to cup-shaped or
ellipsoid and often ridged or grooved; sepals accrescent,
usually broad to apex, tending to curve over the fruit;
Madagascar...................................................... 9. Sect. Rhodonisa

Taxonomic treatment

*Homalium* Jacq., Enum. Syst. Pl.: 5. 1760.

Typus: *Homalium racemosum* Jacq.

1. *Homalium* sect. *Homalium*

   = Racoubea Aubl., Hist. Pl. Guiane 1: 589, tab. 236. 1775.
   = *Homalium* sect. Racoubea (Aubl.) C.B. Clarke in
     Hooker, Fl. Brit. India 2: 597. 1879. *Typus*: *Homalium*
     guianense (Aubl.) Oken. (= Racoubea guianensis Aubl.).

   = Napimoga Aubl., Hist. Pl. Guiane 1: 592, tab. 237. 1775.
   *Typus*: *Napimoga guianensis* Aubl.

   *Stipules* axillary, free. *Inflorescences* racemose (to spiccate)
or paniculate; bracts small or narrow, usually persistent, bract-
ole small, usually borne high on pedicel. *Flowers* pedicellate
to subsessile (in part sessile), with pedicels articulated, 5-7-
merous. *Sepals* ovate (to somewhat oblong or oblong-lanceo-
late), often moderately accrescent; calyx tube funnelform, in
fruit to nearly hemispherical or broadly turbinate; sepal glands
quite large, rounded to oblong-elliptic. *Petals* ovate to ellipti-
cal (to somewhat oblong, in *H. fulviflorum* Sleumer broadly
spatulate), similar to sepals in size or longer, usually spread-
ing at anthesis, often moderately accrescent; sepals and petals
not ciliate or minutely ciliate. *Stamens* (2-)3-7(-8) per petal,
inserted between glands; anthers dorsifixed, broadly oblong-
elliptical with oblong-elliptical locules and a large connect-
tive, the slits of dehiscence nearly parallel. Upper surface of
*ovary* conical (to nearly flat) in flower, conical (sometimes very
prominently) in fruit; styles fused basally into a short column
(less often free to near base, or fused for most of length), the
branches 3-4(-5). *Locule of fruit* ovoid to ellipsoid, apically
conical, pubescent; seeds where known 1-2 per fruit, often
ellipsoid, mostly filling the locule (sometimes several immature seeds present, possibly not maturing).

Distribution. – Africa, Central and South America.

Species included. – Homalium abdessammadii, H. angustifolium Sm., H. fulviflorum, H. guianense, H. racemosum, H. senarium Moç. & Sessé ex DC.

2. Homalium sect. Antinisa Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a) : 35. 1893.

= Nisa Noronha ex Thouars [unranked] Antinisa Tul. in Ann. Sci. Nat., Bot. ser. 4, 8 : 73. 1857. = Homalium [unranked as §] Antinisa (Tul.) Baill. in Bull. Mens. Soc. Linn. Paris 1 : 576. 1886.

Typus: Homalium involucratum (DC.) O. Hoffm. (= Nisa involucrata DC.).

Stipules axillary, free. Inflorescences spicate with flowers mostly in few-flowered clusters; bracts very large, reniform and usually completely concealing flowers, persistent; bracteoles 2 per flower, broad, ciliate, persistent. Flowers sessile; perianth 5-8-merous. Sepals lanceolate to narrowly lanceolate, modestly accrescent; calyx tube broad-based funnelform, densely sericeous; sepal glands irregularly rounded, usually prominent. Petals lanceolate, becoming longer than sepal after anthesis, erect or nearly so, more accrescent than sepals and sometimes curving over fruit; sepals and petals ciliate in conjunction with surface pubescence. Stamens 1 per petal, inserted between glands; anthers basifixed, the locules very small, attached by a deep bulbous connective (hence anther inserted between glands); anthers dorsifixed, the locules very large, ribbed; calyx tube turbinate to narrowly funnelform or tubular, at least in fruit (seldom much reduced), usually accrescent; calyx tube tubinate to narrowly funnelform or tubular, at least in fruit; sepals and petals moderately accrescent; sepal glands usually small and rounded, rarely elliptical. Petals similar in shape and size to sepals or narrowly elliptical to spatulate or oblanceolate (narrowly obovate, oblong-ovate, narrowly deltoid) and markedly longer than sepals, ascending to spreading (usually only in a few flowers at one time), usually modestly accrescent; sepal and petals usually ciliate, usually with long and/or stiff trichomes. Stamens 1 per petal, inserted between glands; anthers dorsifixated, broadly oblong-elliptical with oblong-elliptical locules and a large connective, the slits of dehiscence nearly parallel, or broader than long, usually

3. Homalium sect. Blackwellia Bent in J. Proc. Linn. Soc., Bot. 4 : 33. 1859.

= Homalium subg. Blackwellia (Benth.) Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a) : 35. 1893. = Blakwellia Comm. ex Lam., Encycl. 1 : 428. 1785 [nom. illeg.] [non Blakwellia Scop.].

Typus: Homalium paniculatum (Lam.) Benth. (= Blakwellia paniculata Lam.) (designated by Sleumer, 1954 : 52).

= Astranthus Loure., Fl. Cochinch. 1 : 221. 1790. Typus: Homalium cochinchenisis (Lour.) Druce. (= Astranthus cochinchenisis Loure.).

= Pythagorea Loure., Fl. Cochinch. 1 : 243. 1790. = Homalium sect. Pythagorea (Lour.) Kuntze in Post & Kuntze, Lex. Gen. Phan., Prop. : 285. 1903. = Homalium subg. Pythagorea (Lour.) Sleumer, Fl. Males., ser. 1, 5 : 52. 1954. Typus: Pythagorea cochinchenisis Loure.

= Homalium sect. Eublackwellia Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a) : 35, 36. 1893. Lectotypus (designated here): Homalium paniculatum (Lam.) Benth. (= Blakwellia paniculata Lam.).

= Homalium sect. Paniculata S.S. Lai [as Paniculatae], Bull. Bot. Res., Harbin 14 : 222. 1994 [nom. illeg.] [non Homalium [unranked] Paniculata Benth.]. Typus: Homalium planerophlebium F.C. How & W.C. Ko.

= Homalium sect. Racemosa S.S. Lai [as Racemosae], Bull. Bot. Res., Harbin 14 : 223. 1994 [nom. illeg.] [non Homalium [unranked] Racemosae Benth.]. Typus: Homalium ceylanicum (Gardner) Benth. (= Blackwellia ceylanica Gardner).

Stipules axillary, free. Inflorescences racemose (to spicate) or paniculate; bracts usually small or narrow, caducous, bracteoles absent (sometimes possibly very small and rapidly caducous). Flowers pedicellate to subsessile (sessile) with pedicels usually short; articulated at least post-anthesis; perianth 5-12-(15)-merous. Sepals ligulate to narrowly elliptical (linear, oblong; seldom much reduced), usually modestly accrescent; calyx tube tubinate to narrowly funnelform or tubular, at least in fruit (seldom short, funnelform), usually prominently ridged; sepal glands usually small and rounded, rarely elliptical. Petals similar in shape and size to sepals or narrowly elliptical to spatulate or oblanceolate (narrowly obovate, oblong-ovate, narrowly deltoid) and markedly longer than sepals, ascending to spreading (usually only in a few flowers at one time), usually modestly accrescent; sepal and petals usually ciliate, usually with long and/or stiff trichomes. Stamens 1 per petal, inserted between glands; anthers dorsifixated, broadly oblong-elliptical with oblong-elliptical locules and a large connective, the slits of dehiscence nearly parallel, or broader than long, usually
small, with subglobose locules diverging at a broad angle, slits of dehiscence often toward the apex; Upper surface of ovary conical, usually narrowly, in flower, more prominently so in fruit; styles (2-)3-5(-6, or reportedly 7 in H. barandae), free to near base. Locule of fruit usually elongated (rarely to subglobose in very short-flowered species), conical above, pubescent (to glabrate) at least on lower portion; seeds usually several per fruit, small, confined to apical portion of ovary.

**Distribution.** – Asia, Malesia, Pacific to Australia, Madagascar, Mascarenes, South Africa.

**Species included.** – *Homalium acutissimum* Gilg, H. axillare (Lam.) Benth., *H. barandae* S. Vidal ex Fern.-Vill., *H. bismarckianum* Craven, *H. brachyrhachis* Sleumer, *H. brevidens* (F. Muell.) F. Muell., *H. breviflorum* Gagnep., *H. breviroacemosum* F.C. How & W.C. Ko, *H. capitatus-avis* Craven, *H. caudiflorum* H. Perrier, *H. ceylanicum* & W.C. Ko, *H. coelanicum* H. Perrier, *H. dentatum* H. erianthum (Tul.) Baill., *H. glandulosum* Tagana & V.H. Nguyen, *H. integrifolium* (Lam.) Baill., *H. kainantense* Masam., *H. kwangsiense* Kainantense Masam., *H. lense* H. Perrier, *H. micranthum* Merr., *H. nobile* Sleumer, *H. paniculatum* H. Perrier, *H. phanerophlebium* Sleumer, *H. Perrieri* Sleumer, *H. petaloides* Merr., *H. phanerophlebium* H. Reductum Craven, *H. retivenium* Sleumer, *H. rufescens* H. Sabifolium F.C. How & W.C. Ko, *H. laberi* Merr., *H. longifolium* Benth., *H. micranthum* (Bovin ex Tul.) O. Hoffm., *H. microphyllum* O. Hoffm., *H. mollissimum* Merr., *H. multiformum* Merr., *H. myrtifolium* Sleumer, *H. napaulense* (DC.) Benth., *H. parayanum* H. Panicalatum, *H. paniculiflorum* F.C. How & W.C. Ko, *H. peninsulare* Sleumer, *H. petelotii* Merr., *H. phanerophlebium* H. Reductum Craven, *H. retivenium* Sleumer, *H. rufescens* H. Sabifolium F.C. How & W.C. Ko, *H. serratum* Guillaumin, *H. sleumerianum* Lescot, *H. stenophyllum* Merr. & Chun, *H. thuaranium* (Tul.) Baill., *H. tomentosum* (Vent.) Benth., *H. viguieri* H. Perrier

**Notes.** – *Homalium* sect. *Blackwellia* was intended to be based upon Lamarck’s (1785: 428) genus *Blackwellia*, but as the generic name is an illegitimate later homonym, Bentham (1859) alone is credited with the name. The later-published *Eublackwellia* is not a nomenclatural synonym of sect. *Blackwellia*, but because the name has not been used, it has never been typified. The type designated for sect. *Eublackwellia* above is chosen to ensure that it will be a synonym of sect. *Blackwellia*, as it has always been considered to be.

At least two of three African species are distinctly unusual. The petals of *Homalium boinense* from Zimbabwe can be as few as in number as 5, at most short-ciliate, and unusually different in shape from the sepals. Specimens were not seen, but online images make it appear that the calyx tube is funnel-shaped to relatively short turbinate, and the perianth parts are strongly reflexed after anthesis, which is quite unusual. *Homalium dentatum* has a very short calyx cup and short-ciliate petals, appears likely to have rapidly caducous bracteoles or unusually plentiful bracts, and sometimes is reported to have a single large seed (Sleumer, 1973). The latter species is observed to have *Homalium*-like anthers, whereas the southern African *H. rufescens* and all Malagasy species of sect. *Blackwellia* have small anthers with subglobose locules. These species occur in the region overlapping the strictly southern distribution of *H. rufescens* and the usually more northerly distribution of species of sect. *Symphyostylum*, and seem in some ways morphologically intermediate.

**4. Homalium sect. Eumyriantheia** Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a) : 36. 1893.

≡ *Myriantheia* Thouars, Gen. Nov. Madagasc.: 21. 1806.
≡ *Homalium* [unranked as §] *Myriantheia* (Thouars) Baill., Bull. Mens. Soc. Linn. Paris 1 : 576. 1886 [as *Myriantheia*]. = *Homalium* sect. *Myriantheia* (Thouars) kuntze in Post & Kuntze, Lex. Gen. Phan., Prop.: 285. 1903 [as *Myriantheia*].

**Typus:** *Homalium laxiflorum* (Tul.) Baill. (= *Myriantheia laxiflora* Tul.) (designated by Sleumer, 1973: 315).

Stipules axillary, free. Inflorescences racemose or paniculate; bracts ovate to deltoid, sometimes broadly, of small to moderate size; bracteoles usually 2 per flower, often borne on pedicel (1 per flower, or absent or rapidly caducous). Flowers pedicellate with pedicels articulated (in *H. trigynum* sessile or short-pedicellate); perianth 4–5(–6)–merous. Sepals oblong to elliptical, ovate or obovate, sometimes narrowly (oblancoate), very little accrescent; calyx tube funnelform, in fruit becoming convex to cup-shaped or nearly hemispherical (in *H. trigynum* short-cylindrical or turbinate becoming broadly ellipsoid in fruit); sepal glands usually large, oblong to elliptical or irregularly trapezoid (semicircular), sometimes elevated. Petals obvate to oblancoate (in *H. trigynum* to spatulate), similar to sepals in length or up to twice as long, spreading or ascending at anthesis, very little accrescent; sepal and petals not ciliate (appearing ciliolate in conjunction with overall surface indument). Stamens 3 (aberrantly 4, in *H. boinense* H. Perrier 5) per petal, inserted between glands; anthers dorsifixed, broadly oblong-elliptical with oblong-elliptical locules and a large connecting, the slits of dehiscence nearly parallel. Upper surface of ovary conical, usually shallowly, to nearly flat in flower, in fruit sometimes becoming convex; styles 3–5, free to base or near base. Locule of fruit subglobose (in *H. trigynum* ellipsoid and partly filled with spongy tissue), glabrous (sparsely pubescent); seeds sometimes 1 (to 2) per fruit, large and subglobose to ellipsoid (possibly at least 4 in *H. nobile* Baill.).

**Distribution.** – Madagascar.

**Species included.** – *Homalium boinense*, *H. brevipediculatum* Scott-Elliott, *H. capuronii* Sleumer, *H. dorrill Appleg.,* *H. graciliflorum* Sleumer, *H. laxiflorum*, *H. maringiera* H. Perrier, *H. nobile*, *H. oppositifolium* (Tul.) Baill., *H. pseudoboinense*
Appleq., *H. pulchrum* Sleumer, *H. randrianasoloi* Appleq., *H. ranomafanicum* Appleq., *H. schatzii* Appleq., *H. trigynum*.

**Notes.** – Sleumer (1973) wrongly corrected the name of *Homalium* sect. *Eumyriantheia* to ‘sect. *Myriantheia*’ and presumed it to have been based upon Thouars’ *Myriantheia*. The two were not nomenclatural synonyms, but because he explicitly treated them as such, he effectively designated the same type for both simultaneously.

*Homalium trigynum* has some unusual features that are similar to features common in sect. *Blackwellia*, which also occurs in Madagascar (see discussion above); molecular data regarding its relationships would be of interest. A recent revision describes five new species in the section (Applequist, 2016).

5. *Homalium* sect. *Nisa* (Noronha ex Thouars) Baill. ex Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a): 36. 1893.

   = *Nisa* Noronha ex Thouars, Gen. Nov. Madagasc.: 24. 1806. = *Homalium* [unranked as §] *Nisa* (Noronha ex Thouars) Baill. in Bull. Mens. Soc. Linn. Paris 1: 575. 1886.

   **Typus:** *Homalium nudiflorum* (DC.) Baill. (= *Nisa nudiflora* DC.) (designated by Sleumer, 1973: 295).

   **Stipules** opposite the petiole base and fused (in *H. intercedens* Sleumer axillary, free). **Inflorescences** spicate; bract and bracteoles large, broad, thick-textured, persistent. **Flowers** sessile (rarely subsessile); perianth 5–6(-7)-merous. **Sepals** obovate to oblongate (to nearly ligulate), oblongate-oblong or narrowly elliptical, or ovate to oblong-ovate), spreading, accrescent; calyx tube short, broadly funnelform to cup-shaped, or in fruit hemispherical; sepal glands large, elliptical to elongated oblong-elliptical or roughly trapezoid. **Petals** ovate to oblong, usually smaller than sepals and curving over fruit (in *H. lucidum* similar in size and spreading), accrescent; sepals and petals not ciliate or ciliolate in conjunction with overall surface pubescence). **Stamens** 1 per petal, inserted between glands; anthers basifixated, broadly oblong-elliptical with oblong-elliptical locules and a large connective, the slits of dehiscence nearly parallel. Upper surface of **ovary** often nearly flat in flower, in fruit becoming hemispherical or broadly conical; styles fused basally into a short but distinct column (rarely fused for most of length), the branches 3–4. **Locule of fruit** subglobose or vertically compressed, glabrous (short-pubescent); seeds 1 per fruit, subglobose, largely filling the locule (or several small immature seeds).

   **Distribution.** – Madagascar.  

   **Species included.** – *Homalium intercedens*, *H. lucidum*, *H. nudiflorum*, *H. stelliferum* H. Perrier.

6. *Homalium* sect. *Odontolobus* Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a): 35, 36. 1893.

   **Typus:** *Homalium parkeri* Baker (designated by Sleumer, 1973: 306).

   **Stipules** axillary, free. **Inflorescences** spicate to racemose (in part panicles with racemoid branches) with most flowers borne in small clusters or glomerules (singly in *H. brachystylis*); bracts small, often broad, usually persistent; bracteoles minute to broad and larger than bracts, thick-textured, caducous or persistent. **Leaves** alternate (partly opposite or subopposite), glabrous (occasionally glabrate with a few hairs on midrib). **Flowers** sessile or short-pedicellate, pedicels not articulated; perianth 5–8-merous. **Sepals** reduced to minute deltoid teeth or small and ligulate to lanceolate-oblong, not at all accrescent; calyx tube short and broadly funnelform (to narrowly in *H. lucidum*), in fruit becoming nearly hemispherical. **Sepals** ovate, sometimes broadly to transversely, or narrowly oblong-lanceolate to oblong-elliptical, sometimes quite small but larger than sepals, spreading, not or very little accrescent; sepals and petals not ciliate (in minute-sepaled species) or ciliate with sometimes long, wavy, fine trichomes (in small-sepaled species); sepal glands large, rounded (to elliptical), densely pubescent (to sparsely so, usually with age). **Stamens** 1 per petal, inserted between glands (filaments usually short); anthers basifixated, broader than long, very small, with subglobose locules diverging at a broad angle, slits of dehiscence short and at or near the apex. Upper surface of **ovary** broad and nearly flat (to convex) in flower, in fruit becoming convex to hemispherical; styles 2–4(-5), free, usually quite short. **Locule of fruit** subglobose to obovoid, sparsely pubescent to glabrate; seeds 1 per fruit, subglobose, occupying entire locule (several-seeded, seeds possibly not mature).

   **Distribution.** – Madagascar.

   **Species included.** – *Homalium brachystylis*, *H. longistaminum*, *H. lucidum*, *H. moniliforme* H. Perrier, *H. parkeri*, *H. planiflorum*.

7. *Homalium* sect. *Pierrea* (Hance) Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a): 36. 1893.

   = *Pierrea* Hance in J. Bot. 15: 339. 1877.

   **Typus:** *Homalium dictyoneurum* (Hance) Warb. (= *Pierrea dictyoneura* Hance).

   **Stipules** axillary, free. **Inflorescences** racemose to spicate or paniculate; bracts often large and broad, sometimes small, caducous or moderately persistent, bracteoles variable in size, caducous. **Flowers** pedicellate, with pedicels articulated
or paniculate (usually short-branched); bracts usually small and ovate to subsessile or sessile; perianth 5-12(-13)-merous. \textbf{Flowers} pedicellate with pedicels articulating past anthesis. \textbf{Sepals} lanceolate to ovate or oblong, usually shorter than sepal in flower, fruit or both (nearly equal), accrescent and sometimes curving over the fruit; sepal and petals not ciliate (often pubescent overall). \textbf{Stamens} (4-)5-10(-12) per petal, inserted between glands; anthers dorsifixed, broadly oblong-elliptical with oblong-elliptical locules and a large (sometimes crested) connective, the slits of dehiscence nearly parallel. Upper surface of \textit{ovary} conical (in flower and fruit; in a few species, nearly flat and narrow, the ovary almost entirely inferior); styles 3-5(-7), free to near base. \textit{Locule of fruit} much taller than broad, apex shaped like that of the ovary, pubescent at least in lower portion; seeds usually several per fruit, small, confined to apical portion of ovary.

\textbf{Distribution.} – Southern Asia, Malesia, Pacific to Australia.

\textbf{Species included.} – \textit{Homalium acuminatum} Cheeseman, \textit{H. anilifolium} Thwaites & F. Muell., \textit{H. aneitense} Guillain, \textit{H. australondonicum} Seem., \textit{H. betulifolium} Däniker, \textit{H. bracteatum} Benth., \textit{H. buxifolium} Däniker, \textit{H. caryophyllaceum} (Zoll. & Moritz) Benth., \textit{H. celebicicum} Koord., \textit{H. circuminnatum}, \textit{H. dayanthum}, \textit{H. deplanchei} (Vieill.) Briq., \textit{H. dentrecaustoeuenze} (Vieill.) Briq., \textit{H. deplanchei}, \textit{H. foetidum}, \textit{H. franci} Guillain, \textit{H. guillainii} (Vieill.) Briq., \textit{H. intermedium} (Vieill.) Briq., \textit{H. jainii} (Vieill.) Briq., \textit{H. kunstleri} Craven, \textit{H. kanaliense} (Vieill.) Briq., \textit{H. lambertii}, \textit{H. laurifolium} A.C. Sm., \textit{H. letratorum} Guillain, \textit{H. laurifolium} Craven, \textit{H. mathieuanum}, \textit{H. mottii} H. St. John, \textit{H. mouo} (Vieill.) Briq., \textit{H. myriandrum} Sleumer, \textit{H. myriandrum} Sleumer, \textit{H. nitens} Merr., \textit{H. obovatum} Craven, \textit{H. oblongifolium} (Burr.) Benth., \textit{H. pallidum} A.C. Sm., \textit{H. polyandrum} (Vieill.) Briq., \textit{H. protectum} Sleumer, \textit{H. rubiginosum} (Vieill.) Briq., \textit{H. rubrocostatum} Sleumer, \textit{H. samarense} Merr., \textit{H. schleichii} Kurz, \textit{H. spatulatum} Ridl., \textit{H. streimannii} Craven, \textit{H. subcordatum} Craven, \textit{H. tatambense} Sleumer, \textit{H. taypau} H. St. John, \textit{H. tongaense} H. St. John, \textit{H. travancoricum} Bedd., \textit{H. undulatum} King, \textit{H. velutinum} Craven, \textit{H. villarianum} S. Vidal, \textit{H. vitiense} Benth., \textit{H. whitmeeanum} H. St. John.

\textbf{Notes.} – The original publication of \textit{Homalium sect. Polyantha} did not designate a type, and included two species, \textit{Homalium deplanchei} and \textit{H. polyandrum} Warb. Because \textit{H. polyandrum} is now considered to be a junior synonym of \textit{H. mathieuanum} (Sleumer, 1974; Lescot, 1980), \textit{H. deplanchei} is preferred as type. Some species-level taxonomic problems exist in this group, perhaps especially in the Pacific island taxa most recently dealt with by St. John (1977). Whistler (2004) tentatively treats \textit{H. tongaense} as a synonym of \textit{H. whitmeeanum} (described from Samoa) and implies that \textit{H. taypau} and \textit{H. mottii} are likely to be synonymous with \textit{H. acuminatum} and \textit{H. mottii} respectively.

\textit{Notes.} – Little herbarium material of \textit{Homalium sect. Pierrea} was seen, so the sectional description relies heavily on previously published species descriptions (Sleumer, 1953, 1985; Lescot, 1970) and type images.

\textbf{8. Homalium sect. Polyantha} Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a): 35, 36. 1893.

\textbf{Lectotypus} (designated here): \textit{Homalium deplanchei} (Vieill.) Warb. (= \textit{Blackwellia deplanchei} Vieill.)

\textbf{Stipules} axillary, free. \textbf{Inflorescences} racemose (to spicate) or paniculate (usually short-branched); bracts usually small or narrow, bracteoles small, at least the bracts usually persistent past anthesis. \textbf{Flowers} pedicellate with pedicels articulated to subsessile or sessile; perianth 5-12(-13)-merous. \textbf{Sepals} ligulate to linear or narrowly elliptical (ovate to lanceolate, narrowly oblong; seldom much reduced), usually modestly accrescent; calyx tube turbinate to narrowly funneled or tubular, at least in fruit (rarely funneled in flower), usually prominently ridged; sepal glands usually small and round, rarely broad. \textbf{Petals} similar in size and shape to sepal or narrowly elliptical to spatulate, oblongate or obovate, rarely deltoid) and markedly longer than sepal, ascending to partly spreading (seldom nearly erect or reflexed after anthesis), usually modestly accrescent; sepal and petals usually ciliate, usually with long and/or stiff trichomes. \textbf{Stamens} 2-10(-12) per petal, inserted between glands; anthers dorsifixed, broadly oblong-elliptical with oblong-elliptical locules and a large (sometimes crested) connective, the slits of dehiscence nearly parallel, or broader than long, usually very small, with subglobose locules diverging at a broad angle, slits of dehiscence often toward the apex. Upper surface of \textit{ovary} conical in flower and fruit (in a few species, nearly flat and narrow, the ovary almost entirely inferior); styles 3-5(-7), free to near base. \textit{Locule of fruit} much taller than broad, apex shaped like that of the ovary, pubescent at least in lower portion; seeds usually several per fruit, small, confined to apical portion of ovary.

\textbf{Distribution.} – Southern Asia, Malesia, Pacific to Australia.

\textbf{Species included.} – \textit{Homalium anilifolium} Thwaites & F. Muell., \textit{H. aneitense} Guillain, \textit{H. australondonicum} Seem., \textit{H. betulifolium} Däniker, \textit{H. bracteatum} Benth., \textit{H. buxifolium} Däniker, \textit{H. caryophyllaceum} (Zoll. & Moritz) Benth., \textit{H. celebicicum} Koord., \textit{H. circuminnatum}, \textit{H. dayanthum}, \textit{H. deplanchei} (Vieill.) Briq., \textit{H. dentrecaustoeuenze} (Vieill.) Briq., \textit{H. deplanchei}, \textit{H. foetidum}, \textit{H. franci} Guillain, \textit{H. guillainii} (Vieill.) Briq., \textit{H. intermedium} (Vieill.) Briq., \textit{H. jainii} (Vieill.) Briq., \textit{H. kunstleri} Craven, \textit{H. kanaliense} (Vieill.) Briq., \textit{H. lambertii}, \textit{H. laurifolium} A.C. Sm., \textit{H. letratorum} Guillain, \textit{H. laurifolium} Craven, \textit{H. mathieuanum}, \textit{H. mottii} H. St. John, \textit{H. mouo} (Vieill.) Briq., \textit{H. myriandrum} Merr., \textit{H. nitens} Turrill, \textit{H. obovatum} Craven, \textit{H. pallidum} A.C. Sm., \textit{H. polyandrum} (Vieill.) Briq., \textit{H. protectum} Sleumer, \textit{H. ramossi} Merr., \textit{H. rivulare} (Vieill.) Briq., \textit{H. rubiginosum} (Vieill.) Briq., \textit{H. rubrocostatum} Sleumer, \textit{H. samarense} Merr., \textit{H. schleichii} Kurz, \textit{H. spatulatum} Ridl., \textit{H. streimannii} Craven, \textit{H. subcordatum} Craven, \textit{H. tatambense} Sleumer, \textit{H. taypau} H. St. John, \textit{H. tongaense} H. St. John, \textit{H. travancoricum} Bedd., \textit{H. undulatum} King, \textit{H. velutinum} Craven, \textit{H. villarianum} S. Vidal, \textit{H. vitiense} Benth., \textit{H. whitmeeanum} H. St. John.
9. Homalium sect. Rhodonisa (Tul.) Sleumer in Bull. Jard. Bot. Natl. Belg. 43: 300. 1973.

= Nisa [unranked] Rhodonisa Tul. in Ann. Sci. Nat., Bot. ser. 4, 8: 70. 1857 [as Rhodoniae].

Typus: Homalium sanguineum (Boivin ex Tul.) Baill. (= Nisa sanguinea Boivin ex Tul.) (designated by Sleumer, 1973: 300).

Stipules axillary, free. Inflorescences spiciform to paniculate; bracts broad (sometimes rather short), bracts and bracteoles persistent. Flowers short–pedicellate, with pedicels articulated usually just below the receptacle, to sub sessile or sessile; perianth (4-)5(-6)-merous. Sepals oblong, sometimes broadly or narrowly, to somewhat obovate, ovate, or elliptical (seldom to obo lanceolate or lanceolate), moderately accrescent and usually curving over the fruit; calyx tube tubular with a narrow base, often visibly ridged or grooved, to funnelform, in fruit tubular to turbinate or ellipsoid; sepal glands of moderate size, broadly elliptical to rounded (somewhat oblong or trapezoid). Petals obo lanceolate to obovate, much longer than sepals, ascending (spreading), accrescent; sepals and petals ciliate, usually shortly, or not. Stamens 1 per petal, inserted between glands; anthers varying from broadly oblong–elliptical with oblong–elliptical locules, the slits of dehiscence nearly parallel, to small, broader than long with small subglobose locules, widely separated lateral slits towards apex (sometimes apparently or nearly basified with connective not prominent). Upper surface of ovary sometimes quite narrow, nearly flat to shallowly conical in flower, in fruit convex to conical (or little expanded in narrow–ovari ed species); styles usually fused into a column (or connivent) for at least half of length (sometimes quite short), the branches 4–5. Locule of fruit narrowly cylindrical or ellipsoid (to narrowly obovate), pubescent throughout; seeds 2–4 per fruit, small (possibly no mature seeds seen).

Distribution. – Madagascar.

Species included. – Homalium albiflorum, H. baillonii Scott-Elliot, H. leucophloeum (Tul.) Baill., H. rubriflorum, H. sanguineum.

Notes. – The most recent treatment of Malagasy Homalium (Sleumer, 1973) recognized only three species in sect. Rhodonisa, with Homalium leucophloeum and H. baillonii synonymized under H. albiflorum var. leucophloeum (Tul.) Baill. ex H. Perrier. Preliminary study of the H. albiflorum complex (Applequist, unpubl. data) suggests that it encompasses several distinct species and that H. leucophloeum and H. baillonii should be resurrected for two of these.

10. Homalium sect. Symphyostylum Warb. in Engler & Prantl, Nat. Pflanzenfam. III(6a): 35. 1893.

Typus: Homalium africanum (Hook. f.) Benth. (designated by Sleumer, 1973: 265).

Stipules axillary, free. Inflorescences racemose (to spicate) or paniculate; bracts generally small and caducous (rarely large or small but persistent), bracteoles usually very small (rarely broad), rapidly caducous. Flowers pedicellate, with pedicels usually short and articulate, to sub sessile; perianth (4–)5–6(--8)–merous. Sepals small, narrowly deltoid to lanceolate, ovate, or subulate, acute, very little to moderately accrescent; calyx tube funnelform, in fruit cup–shaped; sepal glands elliptical (or irregularly oblong–elliptical, sometimes shallowly bilobed, or nearly orbicular). Petals obo lanceolate to obovate, usually much larger than sepals, ascending to spreading, at least moderately accrescent; sepals and petals not ciliate or ciliolate in conjunction with similar overall surface pubescence. Stamens 1 per petal, inserted between glands; anthers dorsifixed, broadly oblong–elliptical (sometimes quite small) with oblong–elliptical locules and a large connective, the slits of dehiscence nearly parallel. Upper surface of ovary nearly flat to modestly conical or convex, especially in fruit; styles fused into a column for usually more than half of length (in H. stipulaceum free to near base and short), the branches 3–5 (abnormally to 6 in H. stipulaceum). Locule of fruit broadly ellipsoid (to somewhat rhomboid in longitudinal section), sparsely to moderately pubescent; immature seeds usually 10 or more per fruit, small (3–4-seeded or occasionally 1 seed largely filling locule; it is not clear whether all seeds in many-seeded fruits may mature).

Distribution. – Africa.

Species included. – Homalium africanum, H. dalziellii Hutch., H. deweveri De Wild. & T. Durand, H. elegantulum Sleumer, H. gracilipes Sleumer, H. henriquesii Gilg, H. hypolasi um Mildbr., H. lastoursvillense Pellegr., H. letestui Pellegr., H. longistylium Mast., H. ogouense Pellegr., H. oubaguienne Tisser., H. snythei Hutch. & Dalziel, H. stipulaceum, H. viridiflorum Exell.

Species incertae sedis
Homalium dewitii Kosterm., from Sri Lanka, was described from a single specimen that seems to be mostly but not entirely consistent with H. sect. Polyanthera. The ovary is described as being almost completely inferior (which rarely does occur in that section, e.g., Homalium carophyllaceum). The inflorescence is a terminal panicle with spiciform branches and the sessile flowers are said to be subtended by two pairs of tiny, decussate, suborbicular bracts (whereas Homalium normally has only one bract per flower or flower cluster and,
usually, one pair of bracteoles per flower). KOSTERMANS (1980) observed that the specimen seemed in some ways intermediate between a known Homalium species from the region and Osmelia gardneri Thwaites. Though he did not explicitly suggest that the specimen might be an intergeneric hybrid, this might be a possibility.

Homalium palawanense Regalado, Soejarto & Madulid, from the Philippines, has small flowers with stamens that were repeatedly said to be solitary and depicted as such, but also once stated to be twice as numerous as the petals (the publication is inconsistent on this point; REGALADO et al., 2000). It may thus be presumed to be affiliated with sect. Blackwellia (or possibly sect. Polyanthera). However, it is certainly unusual within that group: it is described as having sometimes only 4 petals that lack ciliate margins, large clavate sepal glands, relatively large anthers, and a short obconic calyx tube. (Some small-flowered species of sect. Blackwellia do sometimes have reduced calyx tubes, and the figure does depict the calyx as becoming turbinate.) REGALADO et al. (2000) reported seeing only two collections; additional specimens might help to clarify the status of this taxon and ensure that it is not of hybrid origin.

Acknowledgements
I thank the Museum national d’Histoire naturelle for permitting study of collections at P; Sovannmoly Hul, Peter Phil- lipson, Simon Verlynde, and Jacques Florence for assistance during my visit and helpful discussions; Matthieu Berthod for editing the pictures; and Martin Callmander and an anonymous reviewer for helpful comments and editing.

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