

ON THE DELIMITATION OF THE GENUS GAHNIA
(CYPERACEAE)

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Although the Hawaiian *Morelotia gahniaeformis* Gaudich. and the New Zealand *Lampocarya affinis* Brongn. are extremely similar in habit and also agree in numerous details, they were maintained as distinct, though closely related species by most authors of the last century. To be sure, KUNTH (1837) had only seen specimens of the *Morelotia* species, STEUDEL (1855, p. 164) suspected the two to be but varietally distinct, and HOOKER (1867) combined them under the binomial *Gahnia arenaria* Hook. f. On the other hand, BOECKELER (1874, p. 351-352) drew up two accurate descriptions especially pointing out the distinct and specifically different characters of their fruit. Kunth referred the species to *Lampocarya* R. Brown; Steudel, Hooker, and Boeckeler, who did not recognize this genus of Brown, classified them in *Gahnia* J. R. & G. Forst. Unfortunately most subsequent authors did not follow Boeckeler, but shared Hooker's opinion.

Some twenty years ago two monographs on the genus *Gahnia* were published. Both BENL (1940, p. 165-169, f. 6) and KÜKENTHAL (1943, p. 86) ignored Boeckeler's clear exposition of the differentiating characters. Benl found only a negligible difference between the two in the length of the inflorescence, and in Kükenthal's opinion the New Zealand specimens do not differ from the Hawaiian ones except for their paler leaf-sheaths and slightly more ciliate glumes. Therefore both authors referred *Morelotia gahniaeformis* and *Lampocarya affinis* again to the synonymy of *Gahnia gahniaeformis* (Gaudich.) Heller.

Recently St. JOHN (1958) reestablished *Lampocarya affinis* as a clearly distinct species, for which he accepted the binomial *Gahnia affinis* (Brongn.) Steud. He found several additional constant differences with *Gahnia gahniaeformis* overlooked by Boeckeler and others.

My attention was drawn to these species by a splendid collection of *Gahniae* from the Hawaiian Islands presented to the Rijksherbarium by Dr. O. Degener.

I agree with St. John that specific separation of the two is fully justified. When nevertheless I revert to the subject it is because I am convinced that the species were misplaced in *Gahnia* and that by their removal the circumscription of this genus will become more satisfactory.

For a better understanding of the following discussion the history of *Gahnia* as given by KÜKENTHAL (1943, p. 59) needs some corrections.

J. R. & G. FORSTER (1776) based the genus on a single species, *Gahnia procera*, which therefore is the type species by monotypy (KERN,

1957). ROBERT BROWN (1810) created a new genus, *Lampocarya*, of which his new species, *L. aspera* R. Br., must be considered the type, as the second species, *L. hexandra* R. Br., based on *Gahnia trifida* Labill., was only tentatively transferred to it. *Lampocarya* was said to be intermediate between *Cladium* Browne and *Gahnia*, differing from the former by its filaments elongated after anthesis, and from the latter by the smooth surface of the seed, in *Gahnia* proper the seed being transversely rugose. Although most authors of the early part of the last century followed Brown, it was soon realized that by application of his system closely related species had to be placed in different genera, and that newly discovered species were difficult to classify. STEUDEL (1855) united *Lampocarya* and *Gahnia*, but at the same time he created the genus *Syziganthus* for *Gahnia javanica* Mor., a species certainly belonging in *Gahnia* as circumscribed by himself. Besides, those species which Brown had wrongly placed in *Cladium* were not transferred to *Gahnia*. BOECKELER (1874) had the same arrangement except for the reduction of *Syziganthus* to *Gahnia*.

BENTHAM (1878) was the first to discuss amply the circumscription of *Cladium* and *Gahnia*, after F. VON MÜLLER (1875) had united them. Against Von Müller's procedure he objected that if the species are properly placed, there do exist two groups sufficiently distinct to entitle them to generic rank. He pointed out that when the spikelets in *Cladium* are two-flowered the lower flower is fertile and the glumes of the flowers are as long as or even longer than the outer empty ones, whereas in such spikelets in *Gahnia* the upper flower is fertile and the flower-bearing glumes are shorter than the outer empty ones; in *Cladium* there are three stamens, in *Gahnia* three to six. It was emphasized that in *Cladium* there is almost always a small glume either empty or with an imperfect flower, which flower is lacking in *Gahnia*, although "in the section *Lampocarya*, including the Sandwich Island *Morelotia*, Gaudich., . . . there is sometimes a small empty glume above the flower." This assertion is much weakened by Bentham's description of *Gahnia trifida*, in which species there is "rarely a small additional glume with a second imperfect flower." In the spikelets of that species investigated by me, I always found this vestigial flower.

By including in *Gahnia* those species which R. Brown had described under *Cladium* solely on account of the filaments not elongated after anthesis, but which belong in *Gahnia* on account of several more important characters showing their close relationship with the other representatives of the latter, Bentham gave a much better circumscription of the two genera. Apart from some disputed cases he has been unanimously followed to this very day.

Yet it appears from the discussions in Benl's and Kükenthal's monographs that the drawing of a dividing line between *Cladium* and *Gahnia* (both in Bentham's circumscription) is far from easy. BENL (1940, p. 156-157) pointed out that the characters taken from the leaves, the position of the fertile flower in two-flowered spikelets, the number of stamens, the relative length of the flower-bearing glumes, and the attachment of the ripe fruits to the persistent filaments,

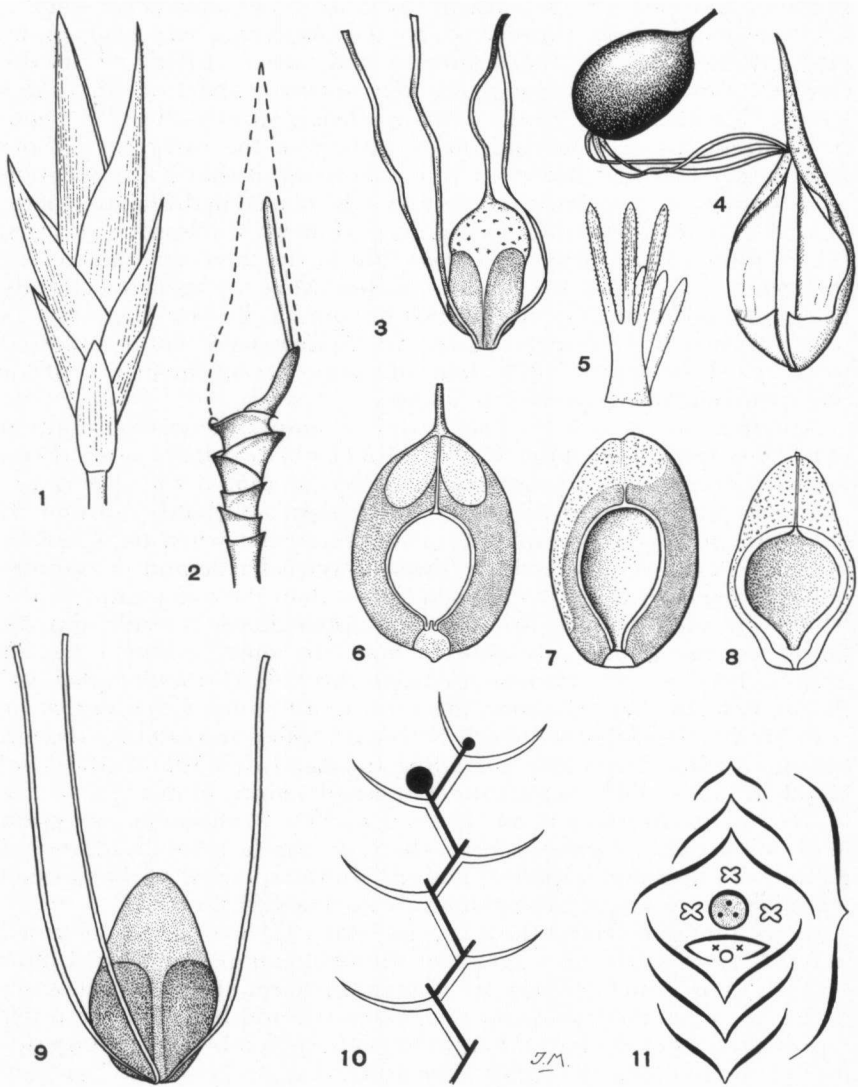


Fig. 1. *Machaerina gahniaeformis* (Gaudich.) Kern — 1: spikelet, $\times 6$; 2: rhachilla and glume embracing sterile flower, $\times 6$; 3: defforate flower, $\times 6$; 4: fixing mechanism, $\times 6$; 5: sterile flower, $\times 40$; 6-7: longitudinal sections of fruit, $\times 10$. *Machaerina affinis* (Brongn.) Kern — 8: longitudinal section of fruit, $\times 10$; 9: fruit, $\times 10$; 10-11: diagrams of spikelet.

let one down in many cases. In his opinion the best differentiating character is afforded by the strongly enlarged style-base in *Cladium* more or less distinctly set off even in the fruits. Also KÜKENTHAL (1943, p. 57) held the view that the discrimination between *Cladium* and *Gahnia* will remain arbitrary as it cannot be based on any constant character, and that there will always be some "borderline-species" linking up the two.

Which of the properties according to Bentham, Benl, and Kükenthal characteristic to a certain extent of *Gahnia* are found in *Gahnia affinis* and *G. gahniaeformis*?

1. The stems in *Gahnia* are always terete (KÜKENTHAL, 1943, p. 57), those of the two species under discussion, however, are rightly described as being trigonous (l.c., p. 86).

2. Kükenthal himself points to the fact that the margins of the leaves in *Gahnia affinis* and *G. gahniaeformis* are strongly revolute, this in contradistinction to all other *Gahniae*, which have involute leaf-margins.

3. The flower-bearing glumes in *Gahnia* are as a rule shorter than the surrounding empty ones, ovate, obtuse, conchiform, but in *G. affinis* and *G. gahniaeformis* they are longer than the outer empty ones, ovate-lanceolate, and very acute. Here it should be remarked that in several other members of the genus the conchiform glumes are not well-developed either.

4. More important is that in *Gahnia gahniaeformis* and in *G. affinis* the glumes are exactly distichous (Fig. I, 11), whereas in the generic descriptions they are always — and rightly — defined as imbricate all round. I cannot understand why they should be called *subdistichous* in the specific descriptions both by Benl and Kükenthal. The transverse position of the lateral spikelets with respect to the subtending bract and/or prophyll may have misled them.

5. I have already pointed to the fact that in *Gahnia* the spikelet is not always terminated by the fertile flower, and that therefore the presence, respectively absence, of an imperfect flower above the perfect one cannot be used as a character absolutely discriminating between *Cladium* and *Gahnia*. The spikelets of *Gahnia microstachya* Benth. I dissected (Fig. II, 9–11) are even more instructive in this respect than those of *G. trifida*. I found them to be three-flowered, the lowest flower functionally male (with vestigial pistil), the next one bisexual and fertile, the topmost one imperfect (both stamens and pistil vestigial). However, imperfect uppermost flowers are exceptional in *Gahnia*, whereas they are a rule in *Cladium*. They are never lacking in *Gahnia gahniaeformis* and *G. affinis* (Fig. I, 5). BENL's assertion (1940, p. 169) corroborated by KÜKENTHAL (1943, p. 87) that Boeckeler was wrong in ascribing two-flowered spikelets to *G. affinis* is due to inaccurate observation. BOECKELER's description (1874) "spiculis bifloris, utroque flore hermaphrodito, sed altero (supremo) compressione sterili" leaves nothing to be desired (Fig. I, 10–11).

Kükenthal, who holds the view that the so-called spikelets are in

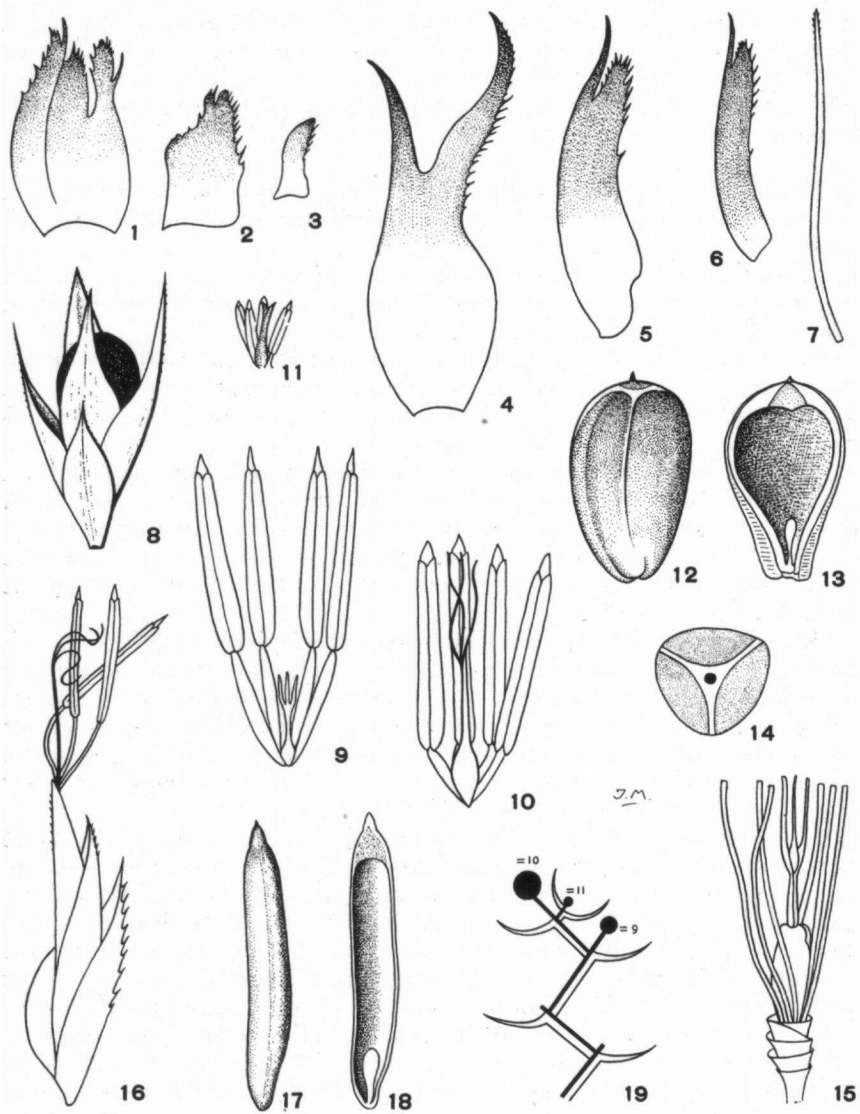


Fig. 2. *Gahnia aspera* Spreng. var. *globosa* (Mann) Benl. 1-3: perigonal scales, $\times 10$. *Gahnia beecheyi* Mann. 4-7: perigonal scales, $\times 20$. *Gahnia trifida* Labill. 8: spikelet, $\times 10$. *Gahnia microstachya* Benth. 9-11: flowers, $\times 20$; 19: diagram of spikelet. *Gahnia hystrix* J. M. Black. 12: nut, $\times 10$; 13: id., longitudinal section, $\times 10$; 14: nut seen from above, $\times 10$; 15: deflores flower, $\times 6$. *Gahnia filum* (Labill.) F.v.M. 16: spikelet, $\times 6$; 17: nut, $\times 6$; 18: id., longitudinal section, $\times 6$.

fact sympodia and even goes so far as to replace "spikelet" consistently by pseudo-spikelet, rhipidium, or 'Fächer', nevertheless applies the terms 'upper' and 'lower' to the relative position of the flowers. Although I have followed him in this, these terms are sometimes misleading. In rhipidia the primary flower-bearing axis is terminated by the 'lower' flower, the secondary one by the 'upper' flower. However, if this subordinate axis is very short and therefore does not overtop its mother-axis, the imperfect flower is seemingly placed lower than the fertile one (Fig. II, 19). With a few exceptions the so-called spikelets in *Gahnia* are either one-flowered without a trace of another flower, or two-flowered with the primary flower functionally male and the secondary one fertile, whereas in *Cladium* there is never a male primary flower and almost always an imperfect flower subordinate to the perfect one.

In my opinion another misinterpretation in Kükenthal's monograph also needs correction. *Gahnia aspera* Spreng. var. *globosa* (Mann) Benl — which endemic of the Hawaiian Islands may better be treated as a subspecies — differs from typical *Gahnia aspera* mainly in having a few irregularly shaped, glume-like organs tightly appressed to the nut (Fig. II, 1-3). In the related *Gahnia beecheyi* Mann similar glumes are found, but here with gradual transitions to hypogynous bristles (Fig. II, 4-7). HILLEBRAND (1888) interpreted them as the remnants of the perianth to the base of which the stamens are affixed, and I think he was right. The homology of hypogynous scales and bristles is demonstrated here once more. Unfortunately Hillebrand now also mistook the glume in *Gahnia gahniaeformis*, which backs the fertile flower and so clearly belongs to the imperfect flower which it embraces, for a perigonal scale. To make matters worse KÜKENTHAL (1943, p. 52) concluded to the reverse in mistaking the perianth in *Gahnia aspera* var. *globosa* for the remnants of a flower.

6. The number of stamens both in *Gahnia gahniaeformis* and *G. affinis* is always three, even in the imperfect flower. In the other representatives of the genus it is often four to six.

7. BOECKELER's very accurate description of the nut in *Gahnia affinis* (1874, p. 353) runs as follows: "caryopsi(s) abbreviato-ovata ima basi attenuata, costis tribus prominentibus, lacunulosa rufa, *styli basi crassa subpyramidalis sulcata lacunosa pallidiore coronata*" (italics partly mine).

It is surprising that none of the authors cited above ever realized that a species in which the nut is crowned by the much thickened corky style-base must be misplaced in *Gahnia* (Fig. I, 9). The equally large style-base in *Gahnia gahniaeformis* can easily be seen in the ovary and in very young fruits (Fig. I, 3); in ripe fruits it is only visible in longitudinal section (Fig. I, 6). In suitable sections the style-base is to be seen as decurrent on the little-pronounced angles of the nut (Fig. I, 7), just like in *Gahnia affinis* (Fig. I, 8). When Kükenthal says that Boeckeler's description only applies to young fruits, he must have compared young fruits of *Gahnia gahniaeformis* with the description of the ripe nuts of *G. affinis*.

8. Fruit dispersal by means of fixing mechanism ("Klemmechanismus") and braiding mechanism ("Flechtmechanismus") is not restricted to the genus *Gahnia*, but is also found in several *Cladium* species. The fact that in *Gahnia gahniaeformis* and *G. affinis* the fixing mechanism is well pronounced (Fig. I, 4), was the reason why Kükenthal placed these species in his section *Inclusae* (correct name: sect. *Lampocarya*), along with unrelated species such as *G. javanica* Mor., *G. aspera* Spreng., *G. schoenoides* G. Forst., and *G. tristis* Nees.

However, species with the same type of fruit dispersal need not be closely allied. BENL (1937), who was the first to distinguish between the various means of fruit dispersal in *Gahnia*, already criticized Kükenthal's subdivision of the genus as being mainly based on the types of dispersal worked out in Benl's paper of 1937, which were not intended to reflect taxonomical affinities (see BENL, 1950).

From the foregoing it will be clear that the natural place of the two species under discussion cannot be in *Gahnia*, but must rather be in *Cladium* on account of the trigonous stems, the revolute leaves, the distichous glumes, the presence of an imperfect secondary flower, the three stamens, and the greatly thickened style-base which remains fused to the nut proper. Especially the distichy of the glumes and the persistence of the corky style-base should be decisive, not the occurrence of fixing mechanism in the fruits.

If I have so far opposed the generic characters of *Gahnia* and *Cladium*, the latter name must be taken in its wide sense adopted by Kükenthal and others. With good reason KOYAMA (1956) restricted *Cladium* to *C. jamaicense* Crantz and its few immediate allies. The other species he referred to *Machaerina* Vahl. Unfortunately there are some reasons why transfer of *Morelotia gahniaeformis* and *Lampocarya affinis* to *Machaerina* appears to be less desirable. Their leaves are dorsoventrally flattened and probably three-ranked, the ultimate internode of the rhachilla (Fig. I, 2) is elongated though not so pronouncedly as in *Schoenus* L., and a certain resemblance in habit to species such as *Schoenus falcatus* R. Br. cannot be denied. However, as in *Schoenus* no corky style-base is found and the type of the nut is more or less different, transfer to *Machaerina* seems more justified and is in any case preferable to retention in *Gahnia*.

In the group often referred to as subfamily *Rhynchosporoideae* interrelationships are very intricate. KÜKENTHAL's attempts (1938) to elucidate the difficult morphological and taxonomical problems were not very successful. As it is my present purpose to clear up the circumscription of the genus *Gahnia*, I will leave the delimitation of the related genera, and especially the eventual splitting up of *Machaerina*, to future research.

I have seen only two rather poor specimens of another species which in my opinion is certainly misplaced in *Gahnia*, but the actual affinity of which I still do not know. I am alluding to *Gahnia hystrix* J. M. Black (Fig. II, 12-15), in which peculiar dwarf species from

Kangaroo Island, S. Australia, the glumes are distichously arranged and there is an imperfect flower subordinate to the perfect one, as in *Gahnia gahniaeformis* and *G. affinis*. On the other hand the flowers are hexandrous, all the internodes of the rhachilla are very short, and the habit is quite different. S. T. BLAKE (1943) observed some two-flowered spikelets, but it is not clear whether both flowers were perfect. I wonder whether *Gahnia hystrix* could be related to *Tetraria octandra* (Nees) Kük. The latter was segregated from *Tetraria* by CLARKE (1908) and made the type of a new genus, *Tetrariopsis*, which since has fallen into oblivion. I have seen only a flowering specimen of this *Tetrariopsis*, in which the structure of the spikelet is apparently very similar to that in *Gahnia hystrix*.

The great diversity of opinion as to the generic assignment of *Gahnia filum* (Labill.) F. v. M. already points to the difficulties met with in this species. Originally it was described in *Schoenus*, R. Brown transferred it to *Cladium*, Boeckeler to *Baumea*, and F. von Müller to *Gahnia*. It is difficult to understand why BENL (1940, p. 232; 1950, p. 89) regarded it as conspecific with *Gahnia trifida* (Fig. II, 8), as already BENTHAM (1878) had shown the essential differences with the latter species and had referred them respectively to *Cladium* and *Gahnia*. Because in *Gahnia filum* there are only two glumes to each spikelet, it is difficult to decide whether they are distichously arranged, and the narrow nut with rather small style-base is very peculiar (Fig. II, 16–18). I am inclined to agree with Bentham's opinion that the two species are not congeneric and to refer *Schoenus filum* Labill. to *Machaerina*, but also in this case I must defer my conclusion until more materials will be available to me.

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Machaerina affinis (Brongn.) Kern, comb. nov.—*Lampocarya affinis* Brongn. in Duperrey, Voy. Bot., Atl. Phan. (1829) t. 29; text, Phan. (1834) 166.

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