GENERIC DELIMITATION OF ROTTBOELLIA AND RELATED GENERA (GRAMINEAE)

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SUMMARY

Generic delimitations within the Rottboelliastrae Stapf and Coelorachidastrae Clayton (formal name) are revised. *Coelorachis* Brongn., *Hackelochloa* O.Ktze, *Heteropholis* C.E. Hubb., *Ratzeburgia* Kunth, and *Rottboellia formosa* R.Br. are to be included in *Mnesithea* Kunth. *Heteropholis cochinchinensis* (Lour.) Clayton and its variety *chenii* (Hsu) Sosef & Koning are varieties of *Mnesithea laevis* (Retz.) Kunth. *Robynsiochloa* Jacq.-Félix is to be included in *Rottboellia* L.f. The necessary new combinations, a list of genera and representative species, and a key to the genera are given.

In the Appendix a new species of *Rottboellia*, *R. paradoxa* Koning & Sosef, is described from the Philippines. The enigmatic species *Rottboellia villosa* Poir. is transferred to *Schizachyrium villosum* (Poir.) Veldk., comb. nov.

INTRODUCTION

Historical background

The delimitation of the genera within the group of taxa represented by *Rottboellia* L. f. and its closest relatives, here taken in the sense of Clayton (1973), has always posed a considerable problem.

In former times Rottboellia contained many species. It was divided up in various ways, but the system of 5 subgenera as proposed by Hackel (1889) seemed most authoritative: Coelorachis (Brongn.) Hack., Hemarthria (R. Br.) Hack., Peltophorus (Desv.) Hack., Phacelurus (Griseb.) Hack., and Thyrsostachys Hack. When at the end of the last century and in the beginning of the present one many large grass genera were split up, e.g. Andropogon, Panicum, Stapf (1917) raised Hackel's subgenera to generic rank, reviving some old names formerly treated as synonyms, and created several new ones. Because of the pressure of other work he was unable to finish his investigations in this taxonomically complex group which was most unfortunate since this might have offered a more general agreement on the classification (Hubbard, 1956).

As far as the orthography of *Coelorachis* is concerned, it seems best to note immediately here that this, without an 'h' after the 'r' is the original spelling of Brongniart (1831), and not *Coelorhachis* (with an 'h') as it is commonly written. The original spelling has been retained here.

Since Stapf's time the number of genera involved has gradually increased. Pilger (1932) introduced Oxyrhachis, Thaumastochloa was separated from Ophiuros Gaertn.f. by Hubbard (1936), who later also distinguished Heteropholis (1956) from Manisuris L. Robynsiochloa Jacq.-Félix was created in 1960. Clayton (1981) reduced Manisuris to its type species and considered the rest as a new genus Glyphochloa. Thus a fair number of genera are present, the distinction of which has in many cases been subjected to serious criticism (e.g. Clayton, 1966; De Koning et al., 1983). Several attempts have been made to offer more clear and better defined generic limits, e.g. by Anton (1975), Camus (1919), and Clayton (1970; 1973; 1981), while other authors either on a smaller scale tried to point out the differences between two or three genera, or dealt with restricted areas thus lacking the general oversight, and then solved their problems (if they were even aware of them) in a traditional way. An exception is Jacq.-Félix's excellent treatment of the tropical African grasses (1962) which unfortunately did not cover all genera involved. Still, after all this work some questions have been left which are not easy to answer at all.

The aim and field of the present study

Since several of the genera involved occur in Malesia, a clarification of their status and delimitation through a thorough analysis of the characters used in the generic classification within the groups seemed highly desirable. To prevent a too restricted view of the subject, all available genera in and outside the area of the Coelorachidastrae and Rottboelliastrae (groups without a nomenclatural status) as circumscribed by Clayton (1973) have been included. They and their species have been listed at the end of this paper. Two have been omitted (*Eremochloa* Buse and *Jardinea* Steud.) from the discussion. The first appeared to be distinct enough and caused no problems. The second in our opinion does not belong in this group at all. The terminal panicle of *Jardinea* consisting of many, usually fascicled, sometimes branched, ebracteate racemes, sessile along a common axis is not found in any other genus here. Instead in the group under survey all racemes but the uppermost one(s) originate from the axil of a leaf, they are solitary or fascicled, but each always terminates a short shoot with leaves usually reduced to their sheaths.

The generic concept

As will be shown many of the boundaries between the genera treated in this paper break down under a rigidly critical examination, i.e. the characters on which they are based are of little value at the generic level when studied separately. However, the lumping of the genera as a result will no doubt lead to the creation of infrageneric taxa along the same unsatisfactory lines and the problem of their delimitation will thus persist. In essence we are confronted with the eternal question: 'What defines a 'good' genus?' We tend to share the views expressed by Clayton (1983) when he stated that the generic concept must be a compromise between biological reality and practical convenience. According to him this concept has developed gradually alongside classification in general. In recent times more information has become available to study a certain group in greater depth. A further division is then usually the result. New separate entities can be distinguished when new characters are introduced or given a greater 'weight'. These taxa are then usually given the rank of genus, and why not? If they are well-defined and have obvious boundaries there is at least some practical convenience. On the other hand, one should always consider as Clayton had remarked previously (1973) whether the gradual convergence of the concepts of genus and species is really desirable.

In the present case we find ourselves faced with a dilemma. From the view of practical convenience it would seem best to retain the many genera presently distinguished in this alliance, since uniting them will add to the confusion already sufficiently present. On the other hand, practical convenience should never dominate over scientific quality which here demands that at least some genera should be united. Still, one should be careful, for when one genus is added to another (whereby the value of the separating character(s) is reduced), other genera can hardly be maintained as they are separated by similar characters of little value. A botanical black hole results: the smaller and larger genera around the complex spiral down into it making its mass even greater and its circumference even more difficult to envisage. At the end it seems very likely that we will have just one large genus and perhaps a few smaller ones in the Rottboelliinae, and yet that would be most unsatisfactory. A way between Scylla and Charibdis must be sought and so, although often on admittedly weak grounds, we have opted to maintain a number of relatively small genera.

THE VARIOUS CASES

Heteropholis cochinchinensis versus Mnesithea laevis

We became involved in the present problem during our study of *Heteropholis* and *Thaumastochloa* (see De Koning et al., 1983). There we have shown that the generic differences between these two were open to questioning. We mentioned a curious collection of *Heteropholis cochinchinensis* (Lour.) Clayton var. *cochinchinensis* from Java, slightly aberrant in its spikelets and more so in its provenance, as it represented the only gathering known from that island and moreover rather isolated from the rest of the area of that taxon (see the map we gave). After the publication of our studies another specimen from Java (*Zollinger 3948*, W) came to our attention, which at first seemed to confirm the presence of the variety on that island, but which on closer inspection showed to our surprise that it represented a very depauperated form of *Mnesithea laevis* (Retz.) Kunth!

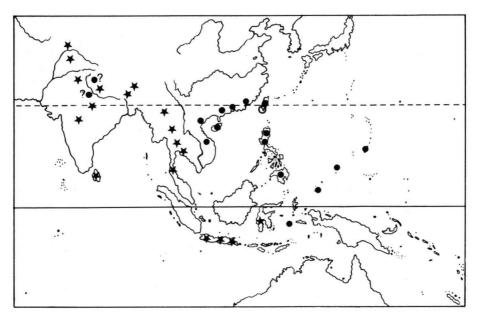
This species is common there and in the literature is always said to be distinguished easily from the related genera by the presence of two sessile and one pedicelled spikelet at each internode of the spike. Clayton (1981) already mentioned that the presence of such triplets is a plastic feature and that they afford no base for a generic split. Heidweiller & Van der Klaauw (in msc.) also had observed that this character is much more variable than is generally suggested. They reported that some collections even had a number of spikes with only a single triplet at their bases, or no triplets at all! On the other hand triplets may be present occasionally in several species of *Coelorachis* (Heidweiller & Van der Klaauw, msc.), while we (De Koning et al., 1983) have recorded them for a single specimen of *Thaumastochloa major* S.T. Blake. In the species of *Coelorachis* and *Thaumastochloa* spikes with paired spikelets only are the rule.

As Mnesithea laevis and Heteropholis cochinchinensis have always been regarded as distinct species of distinct genera, we did not pay particular attention to these observations until our noses were rubbed into them. To our vast surprise it then became evident that there are no morphologic characters to speak of, whereby *M. laevis* in its 'paired' state can be distinguished from *H. cochinchinensis* var. cochinchinensis! The first species (in the classical sense) is somewhat more robust (60-170 cm versus up to 60 cm), the spikes with paired spikelets only are somewhat narrower (0.9-1.5 versus 1.3-1.7 mm in diam.), the anthers are usually longer (1.7-3.5 versus 1.5-1.75 mm), and it seems to grow in places that have been less disturbed (one would have expected larger plants there with more developed spikes, i.e. with triplets). However, these are statistical differences, not hard and clear-cut ones, whereby each collection can be identified with 100% certainty.

Our first reaction after this discovery was that both taxa should be merged into M laevis, the oldest combination, without a further subdivision being possible, but then two odd observations were made.

Firstly, the distribution of the two show an almost vicariant pattern (map 1), especially within Malesia, where M. laevis occurs in Java, Bali, and Celebes, while H. cochinchinensis var. cochinchinensis is found in the Philippines, Moluccas, and on into Polynesia. Thus some collections in L previously thought by us to represent H. cochinchinensis var. cochinchinensis more likely are 'reduced' M. laevis: Kievits 1543 (the dubious record for Java), Murata et al. T-16580 and T-16988 (Thailand). Heteropholis cochinchinensis var. cochinchinensis has been mentioned for India (Bor, 1960; Babu, 1977; Raizada et al., 1957). At least the first reference (C. B. Clarke 33807-A, K) from Hazaribagh, Bihar, is most likely a depauperate form of *M. laevis*. Most of the spikes of the inflorescence have solitary sessile spikelets and no trace of pedicelled ones; a few joints had paired sessile spikelets. Furthermore, the leaf blades are pubescent, a feature never encountered in H. cochinchinensis var. cochinchinensis, but occasionally present in *M. laevis*. The other collections (Dehra Dun, Kansrao, Raizada & Puri s.n., and Nakronda Swamp, Raizada s.n.) we have not seen. If these would also represent such forms of M. laevis, the disjunction between the two would seem to be total.

Secondly, different chromosome numbers have been reported: 2n = 18 (Faruqi et al., 1979; Gould & Soderstrom, 1974; Mehra & Sharma, 1972; Murty, 1971; Sarkar et al., 1976) for specimens from Pakistan, India, and Ceylon and therefore as argued above most likely pertaining to *M. laevis*, and a single count of 2n = 36 (Chen & Hsu, 1962) for material from Taiwan which we have seen and which belonged to



Map 1. Distribution of the varieties of *Mnesithea laevis* (Retz.) Kunth. \star : var. *laevis*; \bullet : var. *cochinchinensis* (Lour.) Koning & Sosef; \circ : var. *chenii* (Hsu) Koning & Sosef. Note: the records of the second with the ? for India are based on literature records, not on specimens actually seen.

H. cochinchinensis var. *cochinchinensis*. We therefore have the impression that a taxonomic difference does exist, although it is hardly expressed in the morphology, and some nomenclatural recognition seems required. We have opted for the varietal level as we do not think a subspecific one should automatically follow from geographical and chromosomal difference not substantiated by any clear morphological one.

When H. cochinchinensis var. cochinchinensis is regarded as a variety of M. laevis, H. cochinchinensis var. chenii should follow, and new combinations are necessary.

Key to the varieties of Mnesithea laevis - Map 1

1a.	Sessile spikelets strictly solitary 2
	Sessile spikelets paired, at least somewhere in the spike and then usually at its
	base
2a.	Plant less than 60 cm tall. Racemes 1.3–1.7 mm diam 3
b.	Plant more than 60 cm tall. Racemes 0.9-1.5 mm diam. Depauperate forms of
	var. laevis
3a.	Sessile spikelets 2.7-4 mm long. Lower glume narrowly winged. Anthers 1.5-
	1.7 mm long var. cochinchinensis
b.	Sessile spikelets 4-4.5 mm long. Lower glume apically distinctly winged. An-
	thers c. 2.8 mm long var. chenii

- Mnesithea laevis (Retz.) Kunth var. cochinchinensis (Lour.) Koning & Sosef, comb. nov. – Phleum cochinchinensis Lour., Fl. Cochinch. (1790) 48. – Heteropholis cochinchinensis Clayton, Kew Bull. 35 (1981) 816. – Heteropholis cochinchinensis Clayton var. cochinchinensis: De Koning et al., Gard. Bull. Sing. 36 (1983) 147, f. 3a, map 1, for further synonymy. – Type: Hb. Loureiro s. n. (BM, holo; n.v.), Cochinchina.
- Mnesithea laevis (Retz.) Kunth var. chenii (Hsu) Koning & Sosef, comb. nov. Thaumastochloa chenii Hsu, Taiwania 16 (1971) 216, 335, f. 2. – Heteropholis cochinchinensis (Lour.) Clayton var. chenii Sosef & Koning, Gard. Bull. Sing. 36 (1983) 149, f. 3b, for further synonymy. – Type: Hsu 511 (TAI, holo, TI), Taiwan, Pingtung Co., O-luan-pi, ± at sea level, 21 Sept. 1959.

Heteropholis versus Mnesithea

As a consequence of the union of *Heteropholis cochinchinensis* with *Mnesithea laevis*, the obvious question arises whether the other species of *Heteropholis* are to be distinguished as a distinct genus. As we have shown before, the main difference between *H. cochinchinensis* and its former congeners was and is after its inclusion in *M. laevis* to be found in the rate of reduction of the pedicelled spikelet: it is a minute scale not articulating with its stipe against the presence of at least a (lower) glume articulating with the stipe. In its best developed form one male flower is present.

In most of the species and genera discussed in this paper the pedicelled spikelet is more or less reduced when compared with the sessile one(s). Many different states can be found and they form an almost perfect range in reductions. Pedicelled spikelets with one bisexual flower and an epaleate one can be found in *Coelorachis* and *Hemarthria* species, two male flowers are present in species of *Chasmopodium* and *Rottboellia*, only one male flower is developed in species of *Coelorachis*, *Glyphochloa*, and *Heteropholis sulcata* (Stapf) C.E. Hubb., only one or two articulating glumes (reduced or not) are present in species of *Coelorachis*, *Hackelochloa*, *Heteropholis*, and *Rhytachne*, a non-articulating scale is present in *M. laevis*, as already said, and in *Ratzeburgia pulcherrima* Kunth, while nothing at all is left in *Ophiuros* spp., *Oxyrhachis gracillima* (Baker) C.E. Hubb., and *Thaumastochloa* spp.

It is obvious that it is an arbitrary decision to draw a line between any two states and declare this a generic boundary. Different states occur within single genera or even within single species, e.g. in *Rottboellia cochinchinensis* (Lour.) Clayton (the former *R. exaltata* L. f.) and *Robynsiochloa purpurascens* (Robyns) Jacq.-Félix where one or two male florets may be present. Very peculiar is the situation in *Coelorachis parodiana* Henr., where on the same plant bisexual, male, and sterile pedicelled spikelets may be present, while the stipe varies from well-developed and \pm as long as the joint to virtually absent. Curiously enough the reduction of the stipe is accompanied not by a reduction of the spikelet, but on the contrary the spikelet is best developed when the stipe is smallest! Thus it seems unwarranted to regard the presence of a non-articulating scale against an articulating glume or spikelet as an acceptable generic limit between *Heteropholis* (without *H. cochinchinensis*) and *Mnesithea*. If this were to be considered there seems to be no reason not to divide *Heteropholis* into two or three genera based on the presence of one glume, two glumes, or the presence of a male floret. We therefore see no other solution than to merge *Heteropholis* as a whole into *Mnesithea* necessitating the following new combinations (for the recently described *Heteropholis annua* Lazarides, see the chapter 'The status of *Hackelochloa*' below):

- Mnesithea benoistii (Camus) Koning & Sosef, comb. nov. Heteropholis benoistii Camus, Bull. Soc. Bot. France 103 (1956) 476; De Koning et al., Gard. Bull. Sing. 36 (1983) 146, f. 2b, map 1, for further references. Ty pe: Benoist 1639 (P, , holo), Madagascar, Domaine Central, Manjakotompo, Ankatra, 1700 m alt., 20 Dec. 1951.
- Mnesithea nigrescens (Thw.) Koning & Sosef, comb. nov. Rottboellia nigrescens Thw., Enum. Pl. Zeyl. (1864) 364. - Heteropholis nigrescens C.E. Hubb. in Hook., Ic. Pl. 36 (1956) t. 3548, p. 4; De Koning et al., Gard. Bull. Sing. 36 (1983) 147, f. 2c, map 1, for further synonymy. - Type: Thwaites CP 867 (PDA, holo, K, n.v.; BM, BO, SING), Ceylon, Central Prov., Bagavantalawa, 1220 m alt.
- Mnesithea sulcata (Stapf) Koning & Sosef, comb. nov. Peltophorus sulcatus Stapf, Fl. Trop. Afr. 9 (1917) 59, comb. illeg. – Heteropholis sulcata C.E. Hubb. in Hook., Ic. Pl. 36 (1956) t. 3548, p. 2; De Koning et al., Gard. Bull. Sing. 36 (1983) 145, f. 2a, map 1, for further synonymy. – Ty pe: Homblé 56 (K, holo, BR), Zaire, Katanga, Lubumbashi (Elisabethville), Febr. 1912.

Rottboellia formosa

In order to solve the problem of the generic differentiation between *Heteropholis* and *Mnesithea* we had to broaden our scope and had to study the related genera more closely. Thus we happened upon *Rottboellia formosa* R. Br., an interesting species from the New Guinea and Northern Australian region. Probably because of its limited distribution no one seems to have questioned its inclusion in *Rottboellia*, a rather surprising thing since that genus has been the subject of such a severe fragmentation.

Clayton (1973) stated that although this species is very different in appearance from R. cochinchinensis, the structures of the spikelets would be the same. Van den Boogaart & Brinkman (msc.) have observed, however, that this is incorrect and we agree with their conclusions: the spikelets are quite different from those seen in Rottboellia proper (i.e., now consisting of R. cochinchinensis, R. coelorachis Forst. f.

and the new species *R. paradoxa* Koning & Sosef, described in the Appendix) and the species cannot be included in that genus. Instead, they are the same as seen in *Heteropholis* spp.: the sessile spikelet has an epaleate, sterile lower floret and a bisexual upper one. In *Rottboellia* the sessile spikelet has a paleate male lower floret. We therefore may regard it as closer to the species formerly included in *Heteropholis*, and thus more likely a member of *Mnesithea*.

Within the latter genus *Rottboellia formosa* still occupies a rather isolated position because of two features unique among the taxa studied. Firstly, there is the densely hirsute inflorescence, but at the generic level, however, we think pubescence should be disregarded. Secondly, the pedicelled spikelet is reduced to the two glumes, which have become slightly twisted, and interlock by structures which we have interpreted as vestigial wings or keels. This, however, we have not considered as a sufficient basis to create a new genus for this species. Several of the species in the various genera considered here have some peculiar features, but the distinction of a plethora of genera based on single, unique features usually does not seem to serve any great purpose. *Rottboellia formosa* is therefore best accommodated in *Mnesithea*:

Mnesithea formosa (R. Br.) Koning & Sosef, comb. nov. – Rottboellia formosa R. Br., Prod. 1 (1918) 206. – Type: R. Brown 6157 (BM, holo, n.v.), Australia, Bay of Carpentaria, Morgan's Island, 1 March 1803.

Coelorachis versus Mnesithea

As mentioned before Heidweiller and Van der Klaauw (msc.) had observed that there are a number of other species in this alliance, which more or less often have triplets of spikelets in their racemes. These have sometimes indeed been included in *Mnesithea* (Camus, 1919), while others have regarded them as belonging to *Coelo*rachis.

When *Heteropholis* and *Mnesithea* are united the differences with *Coelorachis* become very slight. Various authors have claimed that they consist of a fused (in *Mnesithea*) against a free stipe (in *Coelorachis*), and fasciculate against solitary racemes. The last character is indeed rather constant in most of the genera considered here, but unfortunately, or should we have said 'as was to be expected'?, it is a variable one in *Coelorachis* as a genus and also within *Mnesithea laevis* as a species. Both states can be observed, sometimes even within a single collection leaving us with the relation between the joint and the stipe as a final criterion.

Now we really start to thread on dangerous grounds. We have remarked on this character before (De Koning et al., 1983) and then said that closer scrutiny might show the unreliability of it, although it has always been treated as a prime one when subdividing the complex (see also Clayton, 1973; Jacques-Félix, 1962; Stapf, 1917). Clayton has regarded it as the decisive feature whereby his Coelorachidastrae and Rottboelliastrae can be distinguished, but in some species it is difficult to decide where to go.

Thus we have *Heteropholis sulcata*, where in some specimens the stipe is fused for only halfway with the joint and completely so in others.

Rottboellia paradoxa has stipes which are adnate in their lower half.

In Robynsiochloa purpurascens it usually is adnate for halfway as well, but a range from completely free to completely fused is present.

In some specimens of *Rottboellia cochinchinensis*, especially those from the Philippines (e.g. *Santos 6132*, L), there is a small foramen at the base of the stipe, whereby the latter is not fused for a very small distance. It is possible that fusion is here also only partial, but the extremely indurated stipe and lower glume of the sessile spikelet make it very difficult to ascertain this. In attempts to dissect the structures so much force has to be applied that the tissues rupture before giving way, and the original state is then difficult to reconstruct.

In Rottboellia laevispica Keng, according to the type specimen (Griffith & Steward 996, US), the racemes have both completely to partly fused to completely free pedicels.

Many specimens of *Mnesithea laevis* have the spikelets in triplets and then the stipe is fused to the joint only at its tip. This is the only part which could possibly be fused, anyway, because of the configuration caused by the sessile spikelets which are adjacent through the foramen between stipe and joint.

Specimens of *Rottboellia coelorachis* from New Caledonia (e.g. *Balansa 712, Morat 6199, Schmid 3768*) also demonstrate the presence of the complete range between fused and free stipes. It must be noted that completely free stipes only occur in the lowermost pedicelled spikelet. The fusion of the stipe and the joint is in this species rather weak and one might regard them more as cohering than actually fused. This variability was so surprising to Henrard (1941) that he thought that perhaps two taxa might be present in New Caledonia.

Two collections of *Coelorachis striata* (Steud.) Camus (van Beusekom et al. 3597, Iwatsuki et al. T-10929, L) have the stipe fused in the lower part to completely so to the joint, while in other specimens seen they are always completely free.

Anton (1975) mentioned the occasional presence of free stipes in *Hemarthria al*tissima (Poir.) Stapf & Hubb.

There are therefore a number of exceptions to the rule which would divide the Coelorachidastrae from the Rottboelliastrae, which makes the character suspect. On the other hand, when one would reject its value at the generic level, the differences between several genera would be hard to maintain (the black hole effect!). *Coelorachis* and *Rottboellia* s.s. then only seem to differ by the presence of a sterile lower floret in the sessile spikelet of the first genus against a male floret in the second one.

It will have become clear that the only character which apparently remained to distinguish *Coelorachis* and *Mnesithea* is both an inter- and infrageneric variable. By the absence of any other unassailable feature it is therefore impossible to maintain the two.

This decision is supported by the presence of the peculiar, monotypic genus *Ratzeburgia* Kunth. Its only species, *R. pulcherrima* Kunth, collected only three times in Burma (*Wallich 8868, Collett s.n., U Thein Lwin 354, K*), is the 'missing link' between *Coelorachis* and *Mnesithea*. Its inflorescence is solitary, the spikelets as

a rule are also in triplets, the stipe is free, and the pedicelled spikelet is reduced to a non-articulating scale. It therefore also has to be included in *Mnesithea*, which is expanding wider and wider. A fair number of new combinations are then necessary.

- Mnesithea afraurita (Stapf) Koning & Sosef, comb. nov. Rottboellia afraurita Stapf, Bull. Soc. Bot. France 55 (1908) Mém. 8, 98. – Coelorachis afraurita Stapf, Fl. Trop. Afr. 9 (1917) 80. – Type: Chevalier 232 (K, holo; P, n.v.), Mali, Bammako, Soknati-falls, 20 Jan. 1899.
- Mnesithea aurita (Steud.) Koning & Sosef, comb. nov. Rottboellia aurita Steud., Syn. 1 (1854) 361. – Coelorachis aurita Camus, Ann. Soc. Linn. Lyon, n.s. 68 (1921) 197. – Type: Anon. s.n. s.d. in Hb. Steudel?, then P, holo, n.v., Brazil.
- Mnesithea balansae (Hack.) Koning & Sosef, comb. nov. Rottboellia balansae Hack. in Mart., Fl. Bras. 2, 3 (1883) 312. – Coelorachis balansae Camus, Ann. Soc. Linn. Lyon, n.s. 68 (1921) 197. – Type: Balansa 291 (W, holo, n.v.; L), Paraguay, Villa Bica, 12 Dec. 1874.
- Mnesithea capensis (Stapf) Koning & Sosef, comb. nov. Coelorachis capensis Stapf, Kew Bull. (1916) 234. – Type: Sim 2733 (BM, holo, n.v.), South Africa, Coast Region, Stutterheim Div., Fort Cunninghame.
- Mnesithea clarkei (Hack.) Koning & Sosef, comb. nov. Rottboellia clarkei Hack., Oesterr. Bot. Zeitschr. 41 (1891) 8. – Coelorachis clarkei Blatter & McCann, J. Bomb. Nat. Hist. Soc. 82 (1927) 33. – Manisuris clarkei Bor ex Santapau, Fl. Khandala (1953) 357. – Type: C.B. Clarke 21075 (W, holo, K, n.v.), India, Chota Nagpur, Parasnath, 610 m alt.

Bor (1961) remarked that this was a 'strange' species, certainly not belonging to either *Coelorachis* or *Rottboellia*. It is indeed somewhat aberrant because of the swollen joints, and the apparently different habit with often branched culms and short racemes. To us, however, these characters seem insufficient to assign a distinct separate generic rank to this species.

- Mnesithea cylindrica (Michx.) Koning & Sosef, comb. nov. Tripsacum cylindricum Michx., Fl. Bor. Am. 1 (1803) 60. Manisuris cylindrica O.Ktze, Rev. Gen. Pl. 2 (1891) 779. Coelorachis cylindrica Nash, N. Amer. Fl. 17 (1909) 85. Type: Michaux s.n. (P, holo, n.v.), Florida.
- Mnesithea glandulosa (Trin.) Koning & Sosef, comb. nov. Rottboellia glandulosa Trin., Mém. Ac. Sc. St. Pétersb. VI, 2 (1833) 250. – Manisuris glandulosa O. Ktze, Rev. Gen. Pl. 2 (1891) 780. – Coelorachis glandulosa Stapf ex Ridley, Fl. Mal. Pen. 5 (1925) 204. – Type: Hb. Trinius (LE, holo, n.v.), Java.

- Mnesithea helferi (Hook. f.) Koning & Sosef, comb. nov. Rottboellia helferi Hook. f., Fl. Br. India 7 (1896) 158. – Coelorachis helferi Henr., Blumea 4 (1941) 518. – T y p e: Helfer s. n. (K, holo, n.v.), Burma, Tenasserim.
- Mnesithea impressa (Griseb.) Koning & Sosef, comb. nov. Rottboellia impressa Griseb., Cat. Pl. Cub. (1866) 235. – Coelorachis impressa Nash, N. Amer. Fl. 17 (1909) 85. – Type: Wright 3904 (GOET?, n.v.), W. Cuba, 1865.
- Mnesithea khasiana (Hack.) Koning & Sosef, comb. nov. Rottboellia striata Steud. subsp. khasiana Hack., Mon. Androp. (1889) 302. Coelorachis khasiana Bor, Ind. For. Rec. Bot. 1, 3 (1938) 101. Lectotype (here appointed): Hooker f. & Thomson s. n. (B, holo, K, n.v.; L), tropical parts of Khasia, 305-610 m.
- Mnesithea laevispica (Keng) Koning & Sosef, comb. nov. Rottboellia laevispica Keng, J. Wash. Ac. Sc. 21 (1931) 157, f. 2. – Type: Griffing & Steward 996 (US, holo), China, Anhwei, W. of Chu Chow, 24 Sept. 1921.
- Mnesithea lepidura (Stapf) Koning & Sosef, comb. nov. Coelorachis lepidura Stapf, Fl. Trop. Afr. 9 (1917) 79. – Type: Kirk s.n. (K, holo, n.v.), Mozambique, Zambesi Delta, Kongone River.
- Mnesithea parodiana (Henr.) Koning & Sosef, comb. nov. Coelorachis parodiana Henr., Blumea 4 (1941) 515. – Type: Parodi 8410 (L, holo), Argentina, Prov. Formosa, Las Lomitas, 1928.
- Mnesithea pulcherrima (Kunth) Koning & Sosef, comb. nov. Ratzeburgia pulcherrima Kunth, Rév. Gram. 2 (1831) 487, t. 158. – Type: Wallich 8868 (K, holo), Burma, banks of Irrawaddy River, Sept. 1826.
- Mnesithea ramosa (Fourn.) Koning & Sosef, comb. nov. Apogonia ramosa Fourn., Mex. Pl. Gram. 2 (1886) 63. – Coelorachis ramosa Nash, N. Amer. Fl. 17 (1909) 86. – Lectotype: Bourgeau 2647 (P, holo, L), Mexico, Rio Blanco near Orizaba, 1865–1866.
- Mnesithea rottboellioides (R. Br.) Koning & Sosef, comb. nov. Ischaemum rottboellioides R. Br., Prod. 1 (1810) 205. – Coelorachis rottboellioides Camus, Ann. Soc. Linn. Lyon, n.s. 68 (1921) 197. – Type: R. Brown 6156 (BM, holo, CANB, n.v.), Australia, Bay of Carpentaria, April 1803.
- Mnesithea rugosa (Nutt.) Koning & Sosef, comb. nov. Rottboellia rugosa Nutt., Gen. N. Amer. Pl. 1 (1818) 84. - Manisuris rugosa O. Ktze, Rev. Gen. Pl. 2 (1891) 780. - Coelorachis rugosa Nash, N. Amer. Fl. (1909) 86. - Type: (A.A.?) Baldwin s. n. (ubi?), Florida, 1818.

- Mnesithea selloana (Hack.) Koning & Sosef, comb. nov. Rottboellia selloana Hack. in Mart., Fl. Bras. 2, 3 (1883) 312. – Coelorachis selloana Camus, Ann. Soc. Linn. Lyon, n.s. 68 (1921) 197. – Type: Sellow s.n. (W, holo, n.v.), Uruguay, Montevideo.
- Mnesithea striata (Steud.) Koning & Sosef, comb. nov. Rottboellia striata Nees ex Steud., Syn. 1 (1854) 361. – Coelorachis striata Camus, Ann. Soc. Linn. Lyon, n.s. 68 (1921) 197. – Lectotype (here appointed): Wallich 8877C (Gomez) (P, holo, K, W, n.v.), Burma, Tavoy, Oct. 1827.

Steudel (1854) cited *Wallich 8876* and 8877 as the syntypes. The first number was stated by Wallich to have been collected in Singapore, but the species has never been found there again (see also Ridley, Mat. Fl. Mal. Pen. 3, 1907, 162). In fact it is unknown from the whole of Malesia. Sikdar et al. (Bull. Jard. Bot. Nat. Belg. 50, 1980, 96) stated that the duplicate in CAL would be *Coelorachis (= Mnesithea) glandulosa*, which is quite common in Singapore. The second number consists of three different collections, 8877A, B and C. The first came from Tong Dong and is most likely the type of *Coelorachis striata* var. *laevis* Stapf ex Bor, although Bor citing this locality gave as the number *Wallich 8877D*.

Wallich 8877B has been mentioned as belonging to M. glandulosa by Hackel (1889) and Ridley (1907: '8887').

Wallich 8877C was collected by Gomez in Tavoy, a locality that probably was misquoted by Hackel (1889) as 'Tappy'. This collection seems the best choice as the lectotype.

Hackel (1889) proposed a number of varieties based on the presence of an indument or on the sculpture of the lower glume of the sessile spikelet. He was followed in this by later authors. However, it seems to us that these so-called taxa (with the exception of var. *khasiana* = M. *khasiana* (Hack.) Bor) are merely variations upon a theme and that they cannot be maintained.

Mnesithea subgibbosa (Hack.) Koning & Sosef, comb. nov. – Rottboellia loricata Trin. subsp./var. subgibbosa Winkl. ex Hack. in Mart., Fl. Bras. 2, 3 (1883) 311 (pro subsp.), t. 71 (pro var.), nom. alt. – Rhytachne subgibbosa Clayton, Kew Bull. 20 (1966) 261. – Type: Riedel s.n. (LE, holo, n.v.), Brazil, prov. Sao Paulo, Mugy.

Hackel (1883) distinguished three infra-specific taxa under Rottboellia loricata Trin.: 'genuina' (must now be 'loricata'), 'glaberrima', and 'subgibbosa'. In the text he called these subspecies, under the plate they are regarded as varieties. In both cases the names are valid and to be regarded as nomina alternativa. Clayton (1966) regarded R. loricata genuina as a synonym of Rhytachne rottboellioides Desv. and united the latter two in Rhytachne subgibbosa. We agree that the first taxon is a Rhytachne, the other one, however, lacks the awned glumes and the lower floret of the sessile spikelet is sterile, not male. This species is therefore to be included in Mnesithea (see the chapter 'Rhytachne versus Mnesithea s.1.' below).

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- Mnesithea tessellata (Steud.) Koning & Sosef, comb. nov. Rottboellia tessellata Steud., Syn. 1 (1854) 362. – Manisuris tessellata Scribn., Bull. U.S. Dept. Agric., Div. Agrost. 20 (1900) 20, f. 9. – Coelorachis tessellata Nash, N. Amer. Fl. 17 (1909) 86. – Type: Riehl 60 (P, holo, n.v.), U.S.A., Louisiana.
- Mnesithea tuberculosa (Nash) Koning & Sosef, comb. nov. Manisuris tuberculosa Nash, Bull. N.Y. Bot. Gard. 1 (1900) 430. – Coelorachis tuberculosa Nash, N. Amer. Fl. 17 (1909) 86. – Rottboellia tuberculosa Hitchc., Proc. Biol. Soc. Wash. 41 (1928) 163. – Type: Nash 1074 (NY, holo, n.v.), U.S.A., Florida, Lake Co., 16–30 June 1894.

A note on the name Coelorachis

We realize that the expansion of *Mnesithea* proposed above will not be agreeable to everyone and that some will want to maintain *Coelorachis* as distinct. For them a note on the typification and application of this name seems in order.

Brongniart (1831) when he described *Coelorachis* as a 'new' genus (note the orthography!), identified the only species with *Aegilops muricata* Retz., now *Eremochloa muricata* (Retz.) Hack. His description and plate, however, were based on two specimens from Malesia, and from these it is clear that he misidentified them. So, what is the type of *Coelorachis*? Some will argue that since the combination *C. muricata* was based on *Aegilops muricata*, the type specimen of that name is also the type of the generic name *Coelorachis*. The result of this is then that *Coelorachis* must replace the name *Eremochloa* Buse, as the latter dates from 1854. This is obviously a most undesirable consequence as *Coelorachis* will then be used in a sense different from general and ancient custom. Supporters of this line of reasoning will surely favour a proposal for conservation of *Coelorachis*. Logically, they then should regard Brongniart's original material, the base for his description and plate, as the preferred lectotype.

Others, taking a different line, will regard the protologue to consist of two discordant elements: the material on which the description and plate were based, and the reference to the basionym. The combination *Coelorachis muricata* will then still remain a synonym of *Eremochloa muricata*, of course, but the description and plate can be referred to as *Coelorachis muricata* auct. non Brongn., and *this* will be considered to be the type of the generic name.

The result of both actions is the same, but the last option is the least involved and therefore to be preferred: the type of the name *Coelorachis* must be sought among the two collections seen and described by Brongniart and we appoint here *Ventenat* s. n., collected in Ambon (P), as the lectotype, as Brongniart used that one for his plate. The correct name of the species (in their, not our concept) would then be *Coelorachis glandulosa* (Trin.) Stapf ex Ridley. It will be noted that the type of the type species is different from that of the genus. This is not an unusual case; such different types also occur when the name of the original type species of a genus had to be replaced because of the existence of an older, heterotypic epithet that had to be used.

The status of Hackelochloa

Hackelochloa O.Ktze, a genus of the Old World tropics, reportedly has two species: H. granularis (L.) O. Ktze and H. porifera (Hack.) Rhind. Bor (1960) stated that the last one would differ from the first by its larger spikelets and a more pronounced sculpture on the lower glume of the sessile spikelet. Although he mentioned that 'little is known of this species', he nevertheless reported a rather wide distribution for it and labeled the following specimens in K: India: C.B. Clarke 9752-A (Sikkim, Darjeeling, isotype?), Burma: Belcher KC 819 (Tang H'pre area), Griffith KD 446, Helfer s.n. (Tenasserim, Mergui), Keena, U Tun Aung & Rule 1824 (Tenasserim, Tavoy), and Balansa 4940 (Tonkin). There is also a Wight collection without provenance. It is not clear what was Bor's base for his reference to China (R. Schouten, oral comm.). Notwithstanding this extensive area, we have failed to find any representative specimen in the holdings of the Rijksherbarium. Inspection of the holotype (C.B. Clarke 9752-B) received from W showed that this consists of an apparently fairly robust plant with indeed large sessile spikelets with pronouncedly sculptured lower glumes. We have seen similar specimens from Sumatra in L (Rahmat si Boeea 6284, Aceh; de Voogd 1517, Palembang) which also have fairly large (1.5-1.7 mm long, thus not as large as in the type) and similar well-decorated glumes, but except for these rather extreme states no other differentiating characters could be found. We therefore consider H. porifera to represent merely a robust, large-spikeled form of H. granularis, not worthy of any status.

Recently Lazarides (1985) has described a new species of *Heteropholis, H. annua* Lazarides, from W. Australia. Inspection of type material showed that this is not a *Heteropholis* at all, but that it is very close to *Hackelochloa granularis*. The racemes of both species are very similar in appearance because of the contrast between the pale coloured sessile spikelets and the relatively larger, darker pedicelled ones. The sessile spikelet has a wingless, slightly globose lower glume with some faint sculpture which brings that of *H. granularis* to mind. A transfer of *Heteropholis annua* to *Hackelochloa* would therefore seem in order.

Hackelochloa has never been subjected to a critical analysis as to its generic status. It now appears to us to be identical with *Mnesithea*. Hackelochloa granularis differs mainly by its globose sessile spikelets with wingless lower glumes. The annual habit offers no distinction as that is present also in *Mnesithea formosa*. The structure of the raceme looks different because of the slightly oblique articulation and the absence of a well-developed cavity for the sessile spikelet. This gives the raceme an irregular, non-cylindric shape. This, however, is only appearance, artificially so, because of the oversized sessile spikelet which demands room. Heteropholis annua, however, turns out to be more or less intermediary, as it has a straight articulation and only a slightly globose lower glume.

Chromosome counts, e.g. by Pohl & Davidse (1971) all record 2n = 14 for *Hackelochloa granularis* (L.) O.Ktze, implying a basic number of x = 7, which is different from that of *Mnesithea* for which only x = 9 has been reported. Unfortunately the number of *Heteropholis annua* is presently unknown.

Mainly because of this aberrant basic number we at first have hesitated to unite *Hackelochloa* with *Mnesithea* although the morphological differences are in essence not very impressive. Now that we have seen *Heteropholis annua*, we felt forced to add yet another generic synonym to *Mnesithea* and to make the following new combinations:

- Mnesithea annua (Lazarides) Koning & Sosef, comb. nov. Heteropholis annua Lazarides, Nuytsia 5 (1985) 288, f. 1c, d, 7f. Type: Kenneally 8219 (CANB, holo, BRI, DNA, K, L, PERTH, US), W. Australia, Mitchell Plateau, 12 km SW of mining camp, Camp Creek, Gauging Station, 14°53'10"S, 125°45'5" E, 3 May 1982.
- Mnesithea granularis (L.) Koning & Sosef, comb. nov. Cenchrus granularis L., Mant. 2, App. (1771) 575. – Hackelochloa granularis (L.) O. Ktze, Rev. Gen. Pl. 2 (1891) 776. – Type: Hb. Linné 1217-12 (LINN), India orientalis.
- Manisuris porifera Hack., Oesterr. Bot. Zeitschr. 41 (1891) 48. Hackelochloa porifera (Hack.) Rhind, Grasses of Burma (1945) 77. – Type: C.B. Clarke 9752-B (W, holo, K), Sikkim, Darjeeling, 22 Oct. 1869.

CHARACTER ANALYSES

It will be clear that the black hole effect mentioned in the introduction now becomes a threat. As it has become apparent that a number of characters frequently used in the delimitation of genera in the *Rottboellia*-complex are so weak, the question arose whether or not this effect can be prevented. Therefore it seemed best to make a critical analysis of other so-called differentiating characters not mentioned in the preceding chapters.

The elaiosome

The elaiosome (or 'callus knob') is a peculiar and unique character present in most members of this group. It is a knob-like structure at the base of the joints of the rachis visible after articulation which fits into the cavity in the top of the preceding joint as a key in a lock. It is derived from the vascular bundles running through the rachis, but apparently in at least *Mnesithea laevis, Ophiuros exaltatus, Rhytachne* gonzalezii Davidse, and Rottboellia cochinchinensis it contains oily substances, which attract ants, who then carry away the diaspore (Beumée, 1927; Davidse, 1984). The absence or presence of this structure seems to be correlated with the rate of fragility of the rachis and the angle of the disarticulation of the joints: it is usually best developed when the rachis is very fragile with straight planes, and absent when the rachis is tenacious and the joints have oblique planes, as in Hemarthria and Oxyrhachis.

These three anatomical characters (mode of connection, oblique planes, and elaiosome) obviously also play a role in keeping the raceme intact during the maturation process. In Oxyrhachis and all but one species of Hemarthria, where the elaiosomes are absent, fragmentation takes place late. The joints are joined together sufficiently strong to achieve this, the rate of cohesion is increased moreover by the large adjacent surfaces of the oblique planes of disarticulation. Possible 'proofs' of this supposition are offered by a) *Hemarthria sibirica* (Gand.) Ohwi, the only species of that genus where the raceme is fragile and, remarkably, has straight planes of articulation and a small elaiosome; b) *Thaumastochloa major* S.T. Blake, where the elaiosome of the large spikes (this species has heteromorphous spikes!) are only weakly developed, while it is the only species of the genus with oblique articulations. In the other genera the key/lock structure of the elaiosome ensures that fragmentation does not take place prematurely.

Both an elaiosome and a slightly oblique articulation are present in *Hackelochloa* granularis (L.) O. Ktze and Robynsiochloa purpurasens (Robyns) Jacq.-Félix. We think this effect is caused by the sessile spikelet which is relatively large compared to the joint. The joints are bent and the articulation must enlarge in an oblique way to make room for the spikelet. The same sort of 'artificial obliqueness' occurs in *Thaumastochloa monilifera* Sosef & Koning, where the joints themselves are extremely inflated and of an irregular shape, which results in slightly oblique planes.

Unfortunately, both an elaiosome and a tough rachis are present in *Chasmopo*dium and *Robynsiochloa purpurascens*, where the joints themselves seem to be more fragile than the sutures, at least in the herbarium. Field observations are necessary here to see if this is artificial or not.

The mode of disarticulation and hence that of dispersal has here been considered as an important feature to distinguish genera by. It may well be argued that in many other instances dispersal has no taxonomic effect at the generic level but, as in our distinction between *Heteropholis* and *Thaumastochloa* a satisfactory 'natural' grouping seems to result, in the present instance a heavier weight to this character seems to be admissible. The presence of an elaiosome can therefore be considered as a rather important feature.

The structure of the rachis joint

In most of the genera studied here the joint has become enlarged or inflated and contains a cavity in which the sessile spikelet is embedded. The stipe of the pedicelled spikelet usually is appressed to the joint and may eventually fuse with it, which in both cases leads to a more complete enclosure of the sessile spikelet. The raceme thus has obtained the cylindric shape so typical for most members of the *Rottboellia* complex.

The rate of enlargement of the joint appears to be fairly fixed within the genera, but it is quite difficult to express this in some kind of character state. The difference in joint morphology between most genera is a gradual (a purely quantitative) one and therefore it is virtually impossible to distinguish in this respect between genera with free and appressed against fused stipes (the majority of the cases).

In our opinion the character may be of some significance in two obvious cases only. *Chasmopodium* and *Eremochloa* provide the most plesiomorphic state. In these genera the joints are not inflated, while the stipes are free from them. In *Chasmopodium* there is a window or foramen between joint and stipe, through which the back of the sessile spikelet can be seen. The delimitation of *Eremochloa* causes no real difficulty because of other aspects, that of *Chasmopodium* will be discussed more extensively below.

States of relative position of the sessile spikelet

The sessile spikelets more or less alternate in a left and right row, which is obviously derived from the right/left positions seen in most other Andropogoneae with flattened rachises. In *Ophiuros* and *Oxyrhachis* there has been an even greater shift and the two rows are opposed. That this is only a further derivation can be seen from the pedicelled spikelets, which still alternate to the left and right hand, on the outer side of the sessile ones. It might be wondered what genetic cause underlies this arrangement, which at first sight is quite striking. It could be assumed that a larger or smaller shift is not very significant: after all the important thing is that a shift has taken place (a qualitative character), and not so much how far it went (a quantitative feature). This thought would bring *Ophiuros* closer to *Thaumastochloa*, but a union of the two seems unreasonable because of the scabrous peduncle and its curious basal dehiscence with a persistent lowermost spikelet in the latter genus, a unique syndrome.

Ophiuros then also becomes close to *Mnesithea*, but the complete absence of the pedicelled spikelets distinguishes it from that genus, a reason sufficient to keep the two separated.

Oxyrhachis is obviously distinct from the other genera by the combination of an absent elaiosome, an exceptionally oblique base of the joint, and the completely reduced pedicelled spikelet.

From these correlations we have the idea that the opposite rows of sessile spikelets are more than just a phase of the general tendency to have their positions shifted, but that on the contrary this character does give a good argument in the distinction of genera here.

Development of the lower floret of the sessile spikelet

The greater number of genera have sterile, epaleate lower florets. (The upper floret is always bisexual.) Exceptions are *Chasmopodium*, *Rottboellia*, and *Robynsiochloa*, which have male lower florets. *Rhytachne* generally has a male one as well, but in two species, *R. gonzalezii* and *R. triaristata* (Steud.) Stapf, it is sterile and paleate in the first, epaleate in the second. These species, however, can hardly be placed in another genus because of the presence of at least an awned upper glume. Finally there is *Ophiuros exaltatus* (L.) O.Ktze, where the florets may be male or sterile within the same inflorescence, the first in its lower part, the second in the upper one. There was insufficient material of the other species of *Ophiuros* to check whether this variation occurs there as well. As reduction of parts usually takes place upward in an inflorescence, the logical assumption that sterile florets are derived from paleate and sexual, in this case male ones (and these of bisexual ones), is corroborated.

Within *Mnesithea* s.l. the floret is usually sterile and epaleate, but in some species a palea is present, obviously an intermediary stage. Male flowers never have been mentioned in literature, nor observed by us.

The character states seem to be reasonably stable in groups of species otherwise also more or less similar, so, despite the exceptions, they seem of some use by extrapolation in the attempt to define generic limits.

SOME PROBLEMS THAT REMAINED

In the preceding discussion the most important and troublesome characters for generic delimitation have been treated. Some minor problems have not been mentioned, however, and these will be discussed below.

Rhytachne versus Mnesithea s.l.

The differences between *Rhytachne* and the former species of *Coelorachis* have been the subject for an extensive discussion by Clayton (1966). Even after an extensive numerical study (Clayton, 1970) the problems concerning their differentiation were not solved satisfactorily. The genera were distinguished by him as shown below.

	Coelorachis	Rhytachne
basal sheaths	compressed	terete
racemes	nearly always fasciculate	solitary
spikelet	often longer than joint	always shorter than joint
lower glume	winged	not winged
glumes	muticous	awned

As far as the sheaths are concerned we observed that in many species of *Coelorachis* the expression of this character is rather variable. The same goes for the fasciculate racemes as has been mentioned previously and these characters have therefore to be deleted. In *Mnesithea subgibbosa* the lower glume is not winged. In *Rhytachne furtiva* Clayton the awns of the glumes are completely absent and in *R. rottboellioides* very variable in length. A character not mentioned by Clayton may be added: in *Rhytachne* the lower floret of the sessile spikelet is usually male, but sometimes sterile as in *R. gonzalezii* (only the upper glume awned) and in *R. triaristata* (both glumes awned). In *Coelorachis* this floret is always sterile. In the present sense of *Mnesithea* this situation is not altered. The two genera are therefore polythetically defined, i.e. not all differentiating characters are shared by the members of either genus. The differences are slight but probably sufficient to maintain the genera as distinct.

Robynsiochloa versus Rottboellia

There are a number of differences between *Rottboellia* and *Robynsiochloa*, but most of these seem to be not very 'heavy' at the generic level and are used as specific ones in the other genera. The main character by which the two genera can be distin-

guished is the rate of inflation of the joints, which in the first genus completely encloses the sessile spikelet in an excavation formed jointly with the fused stipe, while in the second genus the joint is much less inflated and the excavation hence much shallower. The rate of inflation of the joints is, as said before, a gradual one in this alliance. When no correlating characters can be found, this difference between the taxa can therefore hardly be used as 'proof' for the existence of two distinct genera.

Especially after the discovery of *Rottboellia paradoxa*, which has a sterile pedicelled spikelet and a stipe which is partly adnate to the joint, the two genera have come so close that we do not hesitate to unite them. In favour of this decision are also the counts made by Dujardin (1978). He reported that both *Rottboellia cochinchinensis* and *Robynsiochloa purpurascens* have 2n = 20, while their karyograms seem almost identical. Gould & Soderstrom (1974) published 2n = 40 and once 2n = 36for the first species, so apparently the common basic number of x = 9 also occurs in the first species. On the other hand the basic number of x = 5 has only been reported once in this group by Chen & Hsu (1962) for *Hemarthria altissima*.

A rather peculiar species is Robynsiochloa goalparensis (Bor) Clayton, originally described as a Rottboellia by Bor. Clayton (1981) stated that 'the flattened dorsiventral raceme falls within the circumscription of Robynsiochloa'. This character, as stated above, we regard as a clinal one, not to be used at the generic level. The species clearly is closely related to either two of the genera. As this species and R. paradoxa may be regarded as intermediate between the two species of Rottboellia (s.s.) and the only one of Robynsiochloa (s.s.), not even an infrageneric distinction seems sensible.

Chasmopodium

The genus Chasmopodium is obviously closely related to Rottboellia (now including Robynsiochloa). Its sessile spikelet has the V-shaped upper glume as in R. cochinchinensis and R. coelorachis, and the male lower floret, while the pedicelled spikelet has two male florets. The cause of its generic distinction is found in the quite aberrant structure of the joints. The joints are not inflated, hence a cavity within the joint for the sessile spikelet is absent. The stipe is free and between stipe and joint there is a window or foramen through which the upper glume of the sessile spikelet may be seen (see above under the character analyses). In view of what we have found about the value of free versus fused stipes and development of excavations in the joint, these differences seem minor and one might be excused if one would regard Chasmopodium as yet another aspect of Rottboellia. Dujardin (1978), however, has observed considerable caryological differences between Chasmopodium on one side and Robynsiochloa and Rottboellia on the other. As said above, Rottboellia has x = (9 or) 10, but *Chasmopodium* has 2n = 16, with a base of x = 8. Moreover, the karyotypes which are so similar within Rottboellia s.l. are substantially different from that of Chasmopodium. We therefore think that at least for the present the generic status of Chasmopodium should be maintained.

Manisuris

Manisuris has had a chequered history: at one time it included numerous species, recently it has been reduced to its type, *M. myuros* L., by Clayton (1981), who placed the other taxa in his new genus *Glyphochloa*, a step with which we fully agree. This decision is based on the structure of the raceme of *Manisuris*, which has the pedicelled spikelet fused to and dropping off with the next joint above. Thus each joint (except the lowermost) seems to have two sessile spikelets and no pedicelled ones. This unique character in the group together with the exceptionally broad apical wing and the two curious lateral ones along the margins of the corrugated lower glumes seems to offer a sufficient base to retain the genus.

Glyphochloa

This genus is characterized by the weird, beautiful lower glumes. These are one- or two-caudate, conspicuously winged and covered with ridges, tubercles, and/or hairs. Taken together the species seem to form a natural group, supported by the fact that they are all annual. (What we think, however, of that as a generic character we have discussed before: De Koning et al., 1983; our doubts as to its value has been enhanced by the discovery that *Rottboellia coelorachis* is a perennial, while *R. cochinchinensis* is an annual, and *R. goalparensis* and *R. purpurascens* seem to be so as well.) The species have recently been revised in an excellent way by Jain (1970, under *Manisuris*).

Thaumastochioa

We have recently revised this genus (De Koning et al., 1983) and have not changed our mind about its distinctness. The delimitation as then used against the former genus *Heteropholis*, now joined with *Mnesithea*, and the other genera now studied more closely remained, except for the annual habit, which we then thought to be doubtful at best.

Dr. M. Zandee, Leiden, kindly placed at our disposal the results of a cladistical analysis, using the data of De Koning et al. (1983) for a comprehensive computer program. Many more possible cladograms could therefore be checked. The 'best' one found, with as few apomorphies as possible, divided the species of *Heteropholis* and *Thaumastochloa* into two groups, which coincide with the present genera. It differed in some minor details only from the fig. 1A given there. Since the same data were used, the result may be regarded as biased; on the other hand we were rather pleased to note that our conclusions were supported by a sophisticated program and mainframe.

EPILOGUE

This review has been based primarily on morphological characters with some chromosome counts thrown in. We think that the views expounded here will serve as an aid towards the disentanglement of the *Rottboellia*-complex, but clearly the last word has not been said. A really stable situation will only be reached when far more data are available, e.g. from anatomy, cytology, and, if possible, hybridization experiments, which, as far as we know, have not been attempted, or if so, have not been reported because of lack of success, which in itself would still have been interesting to know.

KEY TO THE GENERA

1 a.	Sessile spikelets in two opposite rows Pedicelled spikelets reduced to a micro-
	scopic scale to absent
b.	Sessile spikelets in two alternating rows on \pm one side of the rachis $\ldots 3$
2a.	Rachis fragile, disarticulating easily. Articulations with a straight transverse
	plane. Elaiosome present Ophiuros
b.	Rachis tough, not readily disarticulating. Articulations with a very oblique plane.
	Elaiosome absent Oxyrhachis
3a.	Plane of the articulation straight to slightly oblique. Elaiosome present. Sessile
	and pedicelled spikelets dissimilar. Pedicelled spikelet usually male or sterile. 4
b.	Plane of the articulation usually oblique. Elaiosome usually absent. Sessile and
	pedicelled spikelets similar, both with 1 bisexual floret
4a.	Lower floret of the sessile spikelet usually male, when sterile at least the upper
	glume awned (Rhytachne spp.) 5
b.	Lower floret of the sessile spikelet sterile Glumes muticous
5a.	Glumes of the sessile spikelet muticous, smooth. Upper glume usually V-shaped.
	Pedicelled spikelet usually with 1 or 2 male florets
b.	Glumes of the sessile spikelet usually awned, if not lower glume rugose. Upper
	glume dorsally rounded. Pedicelled spikelet sterile Rhytachne
6a.	Stipe free from the only slightly thickened joint, both forming a foramen through
	which the sessile spikelet can be seen. Joint and pedicel ciliolate on the adjacent
	margins
b.	Stipe at least basally to completely fused with the much inflated joint, rarely the
	lowermost stipe completely free. Joint and pedicel glabrous or at most ciliolate
	at base
7a.	Peduncle smooth, not falling with the lowermost joint. Pedicelled spikelet more
	or less well-developed or apparently with 2 sessile spikelets on each joint, then
	only the lowermost joint with a single sessile spikelet
b.	Peduncle scabrous, falling with the lowermost (or only) joint. Pedicelled spikelet
	absent Thaumastochioa
8a.	Lower glume of the sessile and pedicelled spikelets either 1- or 2-caudate, or
	margins pectinate
b.	Lower glume of the sessile and pedicelled spikelets not 2-caudate and margin not
	pectinate

9a. Rachis tough. Joints not inflated. Pedicelled spikelets virtually absent

Eremochloa

- b. Rachis fragile. Joints inflated. Pedicelled spikelets more or less developed Glyphochloa
- 10 a. Pedicelled spikelets not fused with the internode above it: each joint with 1 (or 2) sessile and 1 more or less developed pedicelled ones Mnesithea
 - b. Pedicelled spikelets fused with the internode above it: each joint apparently with 2 sessile spikelets, only the lowermost one with 1 sessile spikelet

Manisuris

LIST OF SPECIES

The inclusion of a specific name in this enumeration does not indicate that we have any opinion on its taxonomic status or nomenclatural correctness. All have been taken from the most recent literature available, but their revision was not the scope of the present study on generic delimitations.

Chasmopodium	(Hemarthria)		
afzelii Stapf	uncinata R. Br.		
caudatum (Hack.) Stapf	vaginata Buse		
Eremochloa	Manisuris		
bimaculata Hack.	myuros L.		
ciliaris (L.) Merr.	Mnesithea		
ciliatifolia (Munro) Hack.	afraurita (Stapf) Koning & Sosef		
eriopoda C.E. Hubb.	annua (Lazarides) Koning & Sosef		
muricata (Retz.) Hack.	aurita (Steud.) Koning & Sosef		
ophiuroides (Munro) Hack.	balansae (Hack.) Koning & Sosef		
petelotii Merr.	benoistii (Camus) Koning & Sosef		
zeylanica (Thw.) Hack.	cancellata (Ridley) Ridley		
Glyphochloa	capensis (Stapf) Koning & Sosef		
acuminata (Hack.) Clayton	clarkei (Hack.) Koning & Sosef		
divergens (Hack.) Clayton	cylindrica (Michx.) Nash		
forficulata (Fischer) Clayton	formosa (R. Br.) Koning & Sosef		
goaensis (Rao & Hemadri) Clayton	geminata (Hack.) Ridley		
mysorensis (Jain & Hemadri) Clayton	glandulosa (Trin.) Koning & Sosef		
ratnagirica (Kulk. & Hemadri) Clayton	granularis (L.) Koning & Sosef		
santapaui (Jain & Desh.) Clayton	helferi (Hook. f.) Koning & Sosef		
talbotii (Hook. f.) Clayton	impressa (Griseb.) Koning & Sosef		
Hemarthria	khasiana (Hack.) Bor		
altissima (Poir.) Stapf & Hubb.	laevis (Retz.) Kunth (incl. Heteropholis		
compressa (L.) R. Br.	cochinchinensis (Lour.) Clayton = var.		
debilis Bor	cochinchinensis (Lour.) Koning & Sosef;		
humilis Keng	Thaumastochloa chenii Hsu = var.		
longiflora (Hook. f.) Camus	chenii (Hsu) Koning & Sosef)		
natans Stapf	laevispica (Keng) Koning & Sosef		
pratensis (Balansa) Clayton	lepidura (Stapf) Koning & Sosef		
protensa Steud.	mollicoma (Hance) Camus		
sibirica (Gard.) Ohwi	nigrescens (Thw.) Koning & Sosef		
stolonifera Bor	parodiana (Henr.) Koning & Sosef		

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(Mncsithea)

pulcherrima (Kunth) Koning & Sosef ramosa (Fourn.) Koning & Sosef rottboellioides (R. Br.) Koning & Sosef rugosa (Nutt.) Koning & Sosef selioana (Hack.) Koning & Sosef striata (Steud.) Koning & Sosef subgibbosa (Hack.) Koning & Sosef sulcata (Stapf) Koning & Sosef tessellata (Steud.) Koning & Sosef tuberculosa (Nash) Koning & Sosef **Ophiuros** bombaiensis Bor exaltatus (L.) O. Ktze papillosus Hochst. Oxyrhachis gracillima (Baker) C.E. Hubb. Rhytachne furtiva Clayton glabra (Gledhill) Clayton gonzalezii Davidse gracilis Stapf guianensis (Hitchc.) Clayton

(Rhytachne) latifolia Clayton megastachya Jacq.-Félix perfecta Jacq.-Félix robusta Stapf rottboellioides Desv. triaristata (Steud.) Stapf Rottboellia cochinchinensis (Lour.) Clayton (= R. exaltata L. f.) coelorachis Forst. f. goalparensis Bor paradoxa Koning & Sosef (see Appendix) purpurascens Robyns Thaumastochloa brassii C.E. Hubb. major S.T. Blake monilifera Sosef & Koning pubescens (Benth.) C.E. Hubb. rariflora (F.M. Bailey) C.E. Hubb. rubra Sosef & Koning striata Sosef & Koning

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APPENDIX

1. A new species of Rottboellia

A curious specimen, Santos 8019, was received from Dr. J. V. Santos, Manila, that showed a remarkable blend of character states distinguishing it clearly from any other species here studied. As can be seen from the table below, the species shares characters with both *Mnesithea* and *Rottboellia*. Habitually it is most like *Mnesithea* spp., but the sessile spikelet with a male lower floret places it in *Rottboellia* as we have tried to define it. The 'black hole effect' strikes again!

The curious plant might be shrugged off as an intergeneric hybrid between Rottboellia cochinchinensis and a Philippine Mnesithea species, either M. glandulosa or M. rottboellioides. It is then curious that such a hybrid has never been mentioned before, although the species are sympatric over a large area of their distribution. It must be remembered also that the Philippine grass flora is rather well known because of the works by Merrill, who started out by being an agrostologist, and by Santos, another keen and dedicated student of the grasses. Furthermore no hybrids between any of the species of the group have apparently been reported (with a possible exception in Thaumastochloa, see De Koning et al., 1983), which suggests that the species are fairly well isolated genetically speaking in contrast to the vague generic delimitations.

	Rottboellia cochinchinensis	Santos 8019	Mnesithea glandulosa M. rottboellioides
sheaths	b.b. hairy*	b.b. hairy*	glabrous
rachis	strongly inflated	slightly inflated	slightly inflated
sessile spikelet: upper glume	V-shaped	convex	convex
lower glume	not winged	not winged	winged
lower floret pedicelled spikelet:	male	male	neuter
pedicel	fused	partly fused	free
	glabrous	margins ciliolate	margins ciliolate
callus	glabrous	sometimes ciliolate	sometimes ciliolate
glumes	glabrous	sometimes ciliolate	sometimes ciliolate
floret	male	neuter	neuter

* b.b. hairy = with bulbous based bristles.

Because of the generic definitions ensuing from our research we deemed it best to describe it as a new species in *Rottboellia*, although it might just as well be regarded as a member of *Mnesithea* in which the plesiomorphic state of a male lower floret in the sessile spikelet has been retained.

Rottboellia paradoxa Koning & Sosef, spec. nov. - Fig. 1.

Species a Rottboellia cochinchinensi habitu graciliore, rachis internodiis tenuioribus, spiculae sessilis gluma superiore dorso rotundata, spiculae pedicellatae neutrae pedicello libro in dimidio superiore differt. - Typus: J. V. Santos 8019 (L, holo; PNH, n.v.), Philippines, Luzon, lower slope of Mt Sto Tomas, 23 Nov. 1976.

Perennial. Culms erect, c. 170 cm tall. Sheaths appressed, covered with stiff b.b. hairs. Ligule collar-shaped, c. 2.5 mm long, membranous, margin strongly ciliolate. Blades flat, linear, up to 50 cm by 16 mm, narrowed at base, margins scabrous, both surfaces with scattered b.b. hairs that fall off easily, persisting longest on the upper surface. Peduncle enclosed by the uppermost sheath, c. 0.7 mm diam., glabrous, smooth, not articulating at base. Racemes solitary, simple, terete. Joints slightly inflated, base slightly oblique, with a distinct elaiosome. Spikelets paired, one sessile, one pedicelled, unilateral in 2 alternating rows, muticous. Sessile spikelet sunken into the joint, 2-flowered, the lower floret male, the upper bisexual. Lower glume convex, oblong, 7-7.5 by c. 0.2 mm, margins narrowly infolded, apex acutish, not winged, 13-nerved, coriaceous, smooth. Upper glume strongly convex, c. 7.5 by 2.3 mm, 9- or 11-nerved, pergamenta-

ceous, otherwise as the lower one. Lemmas and paleas with involute margins. Lower lemma 1-nerved, pergamentaceous. lets (Santos 8019, type). Upper lemma 3-nerved, membranous. Paleas not nerved,

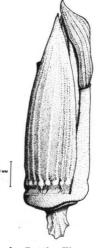


Fig. 1. Rottboellia paradoxa Koning & Sosef. Joint with pair of spike-

otherwise as their lemmas. Lodicules cuneate, glabrous. Anthers slender, 3-4 mm long. Stipe of the pedicelled spikelet at least for its lower half adnate to the joint, 4-5.2 mm long, margins ciliolate. Pedicelled spikelet much reduced, slightly asymmetrical, neuter, with 2 glumes and 2 lemmas, articulating at base. Callus sometimes with a few cilia. Lower glume c. 5 by 1.2 mm, 10-nerved, herbaceous, sometimes ciliolate at base and along the margins. Upper glume c. 5 by 1.2 mm, 6-nerved, pergamentaceous, midrib scabrous. Lemmas much reduced, scarious. Lodicules absent.

Distribution. Philippines, Luzon, lower slope of Mt Sto Tomas.

Ecology. Unknown.

Eponymy. Named for its problematic generic disposition.

2. Rottboellia villosa Poir.

Rottboellia villosa Poir. in Lamk., Encycl. 6 (1804) 313 ('Rottbolla'); Hack., Mon. Androp. (1889) 313. - Type: Commerson s.n. (P-JU, holo, n.v.; P, herb. gén., iso!), 'Indes'.

= Schizachyrium villosum (Poir.) Veldk., comb. nov.

Because it was filed under Rottboellia an isotype of Poiret's combination was received on loan from Paris. Not much attention was ever paid to the correct application of the name except that Hackel suggested that it might be a *Schizachyrium* or an *Ischaemum*. Although it was described as an Indian species, it was not mentioned by Bor (1960).

It is a rather remarkable specimen because of the presence of a solitary, terminal, long-exserted spike and the absence of a spatheole; instead there is a normally developed non-inflated sheath and a linear 6 cm long leaf blade. This may be an individual aberration, but discounting these features did not result in the discovery of matching material or descriptions. It certainly does not seem to be an Asian species. To draw attention to it the above combination is here proposed and a brief description is given below.

Base absent, lower internodes without sheaths, therefore probably a perennial plant. *Culms* slender, c. 50 cm long, internodes (with sheaths) 1.5 mm diam. Sheaths glabrous, smooth. Auricles and ligule c. 1 mm high. *Leaf blades* flat, linear, 8–9.5 cm by c. 1.9 mm, glabrous, scaberulous, acute. Peduncle 9 cm long. *Raceme* c. 5.5 cm long. Joints slender, inflated upwards, c. 3.5 mm long, pilose along the edges and around the callus, hairs c. 1.5 mm long. *Spikelets* imbricate, 4–5.75 mm long. Sessile spikelets 1-, not 2-flowered, dorso-ventrally compressed. *Lower glume* with a longitudinal groove, distinctly nerved in the upper part, glabrous, upwards scabrous. *Upper lemma* c. 4 mm long, apical lobes c. 1.5 mm long. *Awn* geniculate; column c. 3.25 mm long, arista c. 5.5 mm long. Anthers 3, c. 1.75 mm long. No caryopses seen. *Stipes* slender, c. 4.25 mm long, pilose along the edges and below the callus. Pedicelled spikelet c. 4 mm long, excl. the c. 0.5 mm long terminal bristle of the lower glume.