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## CLARIFYING THE GENERIC LIMITS OF *TALBOTIELLA* AND *HYMENOSTEGIA* (DETARIEAE, CAESALPINIOIDEAE, LEGUMINOSAE)

BARBARA A. MACKINDER<sup>1</sup>, JAN J. WIERINGA<sup>2</sup>, ILONA LUNENBURG<sup>2</sup>  
& HANNAH BANKS<sup>1</sup>

<sup>1</sup>Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK;  
b.mackinder@kew.org

<sup>2</sup>Wageningen University, Biosystematics Group, National Herbarium of the  
Netherlands, Wageningen University Branch, Generaal Foulkesweg 37,  
6703 BL Wageningen, the Netherlands

### Abstract

The formal description of four species of Cameroonian forest legume trees new to science has been hampered by uncertainty as to whether their correct generic placement is within *Hymenostegia* Harms or *Talbotiella* Baker f. As there has been doubt as to whether these two genera differ from one another, an investigation was undertaken so that the new species could be correctly assigned to genus. Using morphological, molecular and pollen data, our study supports the recognition of *Hymenostegia* and *Talbotiella* as distinct genera, consequently the new species are correctly placed in *Talbotiella*. In addition, our data reveal the extensive heterogeneous nature of *Hymenostegia* as currently circumscribed and the need to transfer *H. breteleri* to *Talbotiella*.

### Résumé

**Clarification des limites génériques de *Talbotiella* et *Hymenostegia* (Detarieae, Caesalpinioideae, Leguminosae).** La description formelle de quatre espèces nouvelles à la science des arbres camerounais des Légumineuses de forêt a été entravée par l'incertitude de savoir si leur placement générique correct est chez *Hymenostegia* Harms ou *Talbotiella* Baker f. Car ayant douté de savoir si ces deux genres sont différents l'un de l'autre, une recherche a été entreprise de sorte que les nouvelles espèces aient pu être correctement assignées au genre correspondant. Utilisant les données morphologiques, moléculaires et de pollen, notre étude confirme que *Hymenostegia* et *Talbotiella* sont distincts et que les nouvelles espèces sont correctement placées dans *Talbotiella*. En outre, nos données indiquent la nature hétérogène étendue de *Hymenostegia* comme actuellement circonscrit et la nécessité de transférer *H. breteleri* à *Talbotiella*.

**Key words:** Africa, Fabaceae, Leguminosae, morphology, palynology, phylogeny, pollen.

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**1 Introduction**

This study was prompted by the need to describe four Cameroonian endemic legume tree species as new to science. Prior to this study, a major impediment to their description was uncertainty as to their correct generic placement. All the undescribed species have paripinnate, multijugate leaves, apetalous flowers and belong to tribe Detarieae. Their correct generic assignment could be determined either to *Hymenostegia* Harms or to *Talbotiella* Baker f. but the boundary between the two genera was unclear. Morphological, nucleotide sequence and pollen surface characters were appraised in an attempt to resolve one fundamental question: Is *Talbotiella* distinct from *Hymenostegia* or are they congeneric?

In 1897, Harms established the genus *Hymenostegia* to accommodate three species which he transferred from *Cynometra*. During the next 70 or so years a further 24 species of *Hymenostegia* were described, although many were subsequently transferred to other genera. Currently, *Hymenostegia* is a poorly understood genus of 16 forest tree species from West and West-Central Africa (Mackinder, 2005).

In 1914 E. G. Baker described the monotypic genus *Talbotiella* to accommodate a species of caesalpinoid legume new to science, *T. eketensis*, from SE Nigeria (Baker, 1914). In 1928 Hutchinson and Greenway added a second species, *T. gentii* from Ghana (Hutchinson & Dalziel, 1928) and in the following year, Baker made a third addition to the genus with the publication of *T. batesii* from Cameroon (Baker, 1929). No further species have been described since then but there have been persistent doubts about the generic status of *Talbotiella* with respect to *Hymenostegia* (Léonard, 1951, 1957; Cowan & Polhill, 1981).

**2 Léonard's postulate of a single evolutionary series**

*Talbotiella* is characterised by the combination of persistent imbricate bud scales, persistent narrow petaloid bracteoles and the absence of petals, but many *Hymenostegia* species possess one or both of the first two characters (Table 1).

TABLE 1. Character combination on which the genus *Talbotiella* was based and the comparative character states found in *Hymenostegia*.

| Character                             | <i>Talbotiella</i> | <i>Hymenostegia</i> |
|---------------------------------------|--------------------|---------------------|
| Persistent imbricate bud scales       | always present     | often present       |
| Persistent narrow petaloid bracteoles | always present     | sometimes present   |
| Petals                                | 0                  | (1) 2 – 5           |

In 1951 on consecutive pages, Léonard published accounts of *Hymenostegia* (Léonard, 1951a) and *Talbotiella* (Léonard, 1951b). He noted that the species of *Hymenostegia* presented a progressive reduction of petals from 5 to 2(1) and postulated that the apetalous *Talbotiella* may merely be the end of an evolutionary series that began in *Hymenostegia*. Léonard suggested that *Talbotiella* might be better treated as a section of *Hymenostegia*, but he stopped short of formalising the transfer until more material of *Talbotiella* became available for study.

## Clarifying the generic limits of *Talbotiella* and *Hymenostegia*

In this paper we considered Léonard's postulate in the light of new data, specifically vegetative characters, nucleotide sequence data and pollen surface characters, and we re-examined floral characters. If new data confirm Léonard's postulate, then *Talbotiella* must be considered congeneric with *Hymenostegia*. In order not to render *Hymenostegia* paraphyletic the three described species of *Talbotiella* should be transferred there and the four species new to science must be described in *Hymenostegia*, resulting in its expansion to 23 species.

If, however, new data refute Léonard's postulate, then *Talbotiella* should be upheld as a distinct genus within which the four species new to science will be described bringing the total to seven species. *Hymenostegia* would thus remain a genus of 16 species.

### 3 Evidence from vegetative morphology

Vegetative characters examined in the study were those which had previously shown utility, either singly, or more frequently, in combination, in the recognition of either generic or species limits in other members of Detarieae. The 23 vegetative morphological characters surveyed are listed in Table 2. Characters were scored from selected herbarium specimens on loan from the following herbaria: BM, BR, FHO, K, MO and P, and from WAG where the study was undertaken (species investigated and voucher details available on request from B. Mackinder). In addition to the described species of *Talbotiella*, *Hymenostegia*, and the four species awaiting description, species from five other Detarioid genera (*Cynometra*, *Leonardoxa*, *Loesenera*, *Plagiosiphon* and *Scorodophloeus*) were also surveyed. These five additional genera are considered to have generic affinities with *Hymenostegia* and *Talbotiella* based on morphological similarities and/or as indicated by a maximum parsimony phylogenetic analysis based on *trnL* data (Bruneau *et al.*, 2001).

Most of the vegetative characters surveyed were not informative in the study group, their ranges of variation being continuous with, overlapping with, or contained within, the ranges of other taxa in the study. However, six characters (in combination) showed considerable utility in recognising taxa within the group (Table 2). The pattern of variation of these six characters among the taxa studied is presented in Table 3.

*Talbotiella* species share a unique combination of vegetative characters with a core group of eight *Hymenostegia* species which includes *H. floribunda*, the type species of the genus. From hereon we shall refer to this core group as *Hymenostegia sensu stricto* (Table 4).

Variation in the stipule base was only seen in *Talbotiella gentii*, some of which presented auriculate bases, some lacked these and occasionally both states were seen in the same collection. Nonetheless, the plasticity of stipules observed in this species does not preclude a hypothesis that, based on a shared combination of vegetative characters, *Hymenostegia sensu stricto* and *Talbotiella* form a clade, but stipule morphology does not provide evidence as to whether the genera are congeneric or sister to each other. In either case the hypothesis is based on the assumption that the shared characters are synapomorphies. However, were we to sample even more widely, it is possible that the unique character combination would be discovered in other, more distant taxa. If the shared characters were synplesiomorphies, they would not support a *Hymenostegia sensu stricto* / *Talbotiella* clade.

The unique combination of characters shared by *Hymenostegia sensu stricto* and *Talbotiella* is not found in the other taxa thus far included which collectively present seven different character combinations and are collectively hereafter referred to as "ex *Hymenostegia*" (Table 4). The considerable diversity of character combinations present

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TABLE 2. Vegetative characters used for assessing generic limits in *Talbotiella*, *Hymenostegia*, *Cynometra*, *Leonardoxa*, *Loesenera*, *Plagiosiphon* and *Scorodophloeus*. The six characters which, in combination, were most taxonomically useful in this study are emboldened.

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|  |
|--|
| <b>stipule fusion</b> ; free or fused basally  |
| stipule insertion; lateral or interpetiolar  |
| <b>stipule auricle</b> ; present or absent   |
| gland like appendages; present or absent on stipules or on bud scales  |
| leaflet number; minimum number of leaflets per leaf  |
| leaflet number; maximum number of leaflets per leaf  |
| <b>leaflet glands on underside of distal half of leaflets</b> ; number   |
| <b>leaflet glands on underside of proximal half of leaflets</b> ; number   |
| hydathodes; present or absent  |
| leaflet indumentum upper; absent or present (describe if present)  |
| <b>lower leaflet surface indumentum</b> ; absent or present (describe if present)  |
| leaflet indumentum margin; absent or present (describe if present)   |
| leaflet apex shape; acute, rounded or emarginate   |
| leaflet base proximal shape; rounded or angular  |
| midvein; symmetrical or oblique  |
| midvein ending; becoming obscure towards apex, clearly reaching the apex.  |
| <b>leaf rachis</b> ; terete, striate, canaliculate or winged   |
| leaf rachis top indumentum; absent or present (describe if present)  |
| leaf rachis lower surface indumentum; absent or present (describe if present)  |
| leaflets sub-opposite (at least some pairs); present or absent   |
| position along the leaf rachis of the largest pair of leaflets; calculated as percentage of the total number of leaflet pairs per leaf ( $\text{juga}/\text{total jugae} \times 100$ ) |
| leaflet length to width ratio; ratio in longest leaflet  |
| leaflet length to width ratio; ratio in shortest leaflets  |

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in these taxa lead us to conclude that *Hymenostegia*, as currently circumscribed, is a heterogeneous assemblage. The heterogeneity of *Hymenostegia* as traditionally circumscribed had been previously been noted by Bruneau *et al.* (2001), who sampled eight species (five *Hymenostegia sensu stricto* species and three ex *Hymenostegia* species) but only now after wider sampling, is the extent of the full heterogeneity apparent.

TABLE 4. Species assigned to *Hymenostegia sensu stricto* species and those excluded from the genus (ex *Hymenostegia* species) based on vegetative characters.

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| <b><i>Hymenostegia sensu stricto</i> species</b> | <b>ex <i>Hymenostegia</i> species</b> |
|--|---------------------------------------|
| <i>H. breteleri</i>                              | <i>H. afzelii</i>                     |
| <i>H. felicitis</i>                              | <i>H. aubrevillei</i>                 |
| <i>H. floribunda</i>                             | <i>H. bakeriana</i>                   |
| <i>H. klainei</i>                                | <i>H. brachyura</i>                   |
| <i>H. mundungu</i>                               | <i>H. gracilipes</i>                  |
| <i>H. neoaubrevillei</i>                         | <i>H. laxiflora</i>                   |
| <i>H. normandii</i>                              | <i>H. ngounyensis</i>                 |
| <i>H. pellegrinii</i>                            | <i>H. talbotii</i>                    |

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TABLE 3. Selected vegetative characters as observed in *Talbotiella*, *Hymenostegia* and putatively related taxa. The first three rows share a character combination which is not found in other taxa in the study. Each of the other rows contains a unique combination of characters. Dist. = number of distal leaflet glands; Prox. = number of proximal leaflet glands.

| Taxa  | Stipule fusion | Stipule base                  | Dist. | Prox.  | Lower leaflet surface indumentum | Leaf rachis shape               |
|---|----------------|-------------------------------|-------|--------|----------------------------------|---------------------------------|
| <i>Talbotiella batesii</i> Baker f. and <i>T. ekatensis</i> Baker f.                                | free           | auriculate                    | 1-3   | 0      | appressed puberulous             | canaliculate                    |
| <i>Talbotiella gentii</i> Hutch. & Greenway   | free           | auriculate and not auriculate | 1-3   | 0      | appressed puberulous             | canaliculate                    |
| <i>Hymenostegia</i> spp. including type ( <i>H. floribunda</i> ) but excluding species listed below | free           | auriculate                    | 1-7   | 0 (-2) | appressed puberulous             | canaliculate                    |
| <i>Hymenostegia aubrevillei</i> Pellegr.  | free           | not auriculate                | 2-3   | 1      | appressed puberulous             | terete to narrowly canaliculate |
| <i>Hymenostegia afzelii</i> Harms   | fused          | not auriculate                | 4-7   | 1-4    | glabrous                         | winged                          |
| <i>Hymenostegia laxiflora</i> Harms   | fused          | not auriculate                | 0-5   | 1-2    | glabrous                         | canaliculate                    |
| <i>Hymenostegia bakeriana</i> Hutch. & Dalziel and <i>Hymenostegia talbotii</i> Baker. f.           | fused          | not auriculate                | 0-19  | 0-3    | glabrous                         | terete                          |
| <i>Hymenostegia brachyura</i> (Harms) J. Léonard  | free           | not auriculate                | 2-6   | 0      | pubescent                        | canaliculate                    |
| <i>Hymenostegia gracilipes</i> Hutch. & Dalziel   | fused          | not auriculate                | 4-12  | 1      | appressed puberulous             | canaliculate                    |
| <i>Hymenostegia ngounyensis</i> Pellegr.  | free           | not auriculate                | 0     | 0      | glabrous                         | striate                         |
| <i>Cynometra sensu stricto</i> ( <i>C. cauliflora</i> L.)   | fused          | not auriculate                | 0     | 0      | scattered pubescent              | not applicable                  |
| <i>Cynometra sens. lat.</i> ( <i>C. hankii</i> Harms)   | free           | not auriculate                | 1-3   | 0      | scattered pubescent              | sub-winged                      |
| <i>Leonardoxa africana</i> (Baill.) Aubrév.   | fused          | not auriculate                | 0     | 0      | scattered puberulous             | terete                          |
| <i>Loesenera</i> spp.   | free           | not auriculate                | 1-3   | 1      | appressed puberulous             | terete                          |
| <i>Plagiosiphon</i> spp.  | free           | not auriculate                | 0-2   | 0 (-1) | glabrous                         | canaliculate                    |
| <i>Sarodophloeus zenkeri</i> (Taub.) J. Léonard   | free           | not auriculate                | 1-4   | 0      | appressed puberulous             | canaliculate                    |

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#### 4 Evidence from nucleotide sequence data

Two datasets are available, *rbcL* and *trnL* which may be relevant to resolving the generic limits of *Talbotiella* and *Hymenostegia*.

##### ***RbcL***

A model-based (Mr Bayes) phylogenetic analysis using *rbcL* sequences (Lunenburg, 2006) included a wide sampling from within *Hymenostegia* and *Talbotiella* as well as from many other detarioid genera (Fig. 1).

The final alignment of 62 accessions (for voucher details see Appendix 1) and 734 characters (available from Lunenburg) yielded 77 parsimony informative characters. Alignment was straightforward with no insertions or deletions, but a lack of variation resulted in few informative characters and concomitantly produced a relatively unresolved and weakly supported phylogeny. Nonetheless, Lunenburg's (2006) analyses recovered a clade comprising all six *Hymenostegia sensu stricto* species sampled (Clade 1). Two of the three accessions of *H. felicitis* were in this clade but a third accession was anomalously placed with *Plagiosiphon multijugus* and *Scorodophloeus zenkeri*, possibly due to lab error or contamination. A second clade (Clade 2) was recovered that included *T. gentii*, (the only described *Talbotiella* successfully amplified) and three of the species awaiting description (the fourth failed to amplify) suggesting their affinity with *Talbotiella*, along with two ex *Hymenostegia* species (Clade 2).

Lunenburg's analysis was congruent with the findings of the study based on vegetative morphology as to which species belong in *Hymenostegia sensu stricto* and which do not. Six accessions representing four other ex *Hymenostegia* species were placed outside Clades 1 and 2. The two accessions of *Hymenostegia ngounyensis* were placed together in a clade that also contained *Anthonotha macrophylla* P. Beauv. and *Berlinia occidentalis* Keay; the positions of *Hymenostegia afzelii*, *H. brachyura* and *H. aubrevillea* were unresolved.

The relationship of the two weakly supported Clades 1 and 2 were unresolved. However, Lunenburg (2006) generated a consensus network (not shown) using the software Splittree3 that indicated that, in at least a third of the equally likely Bayesian tree topologies obtained, Clade 1 was not sister to Clade 2.

##### ***TrnL***

The maximum parsimony phylogenetic analyses of Bruneau *et al.* (2001) based on *trnL* nucleotide sequence data, were designed to investigate higher level relationships across subfamily Caesalpinioideae. One supplementary finding of these analyses was that *Hymenostegia*, as currently circumscribed, was not recovered as monophyletic. Of the eight *Hymenostegia* species sampled by Bruneau *et al.* (2001), the five *Hymenostegia sensu stricto* species, including the type species *H. floribunda*, were resolved in a clade with *T. gentii* (the only *Talbotiella* available for sampling), *Leonardoxa africana* and *H. talbotii* (ex *Hymenostegia*) placed as closest relatives although their individual positions were not resolved. The two further ex *Hymenostegia* species sampled, *H. afzelii* and *H. ngounyensis* were placed outside this grouping and not together.

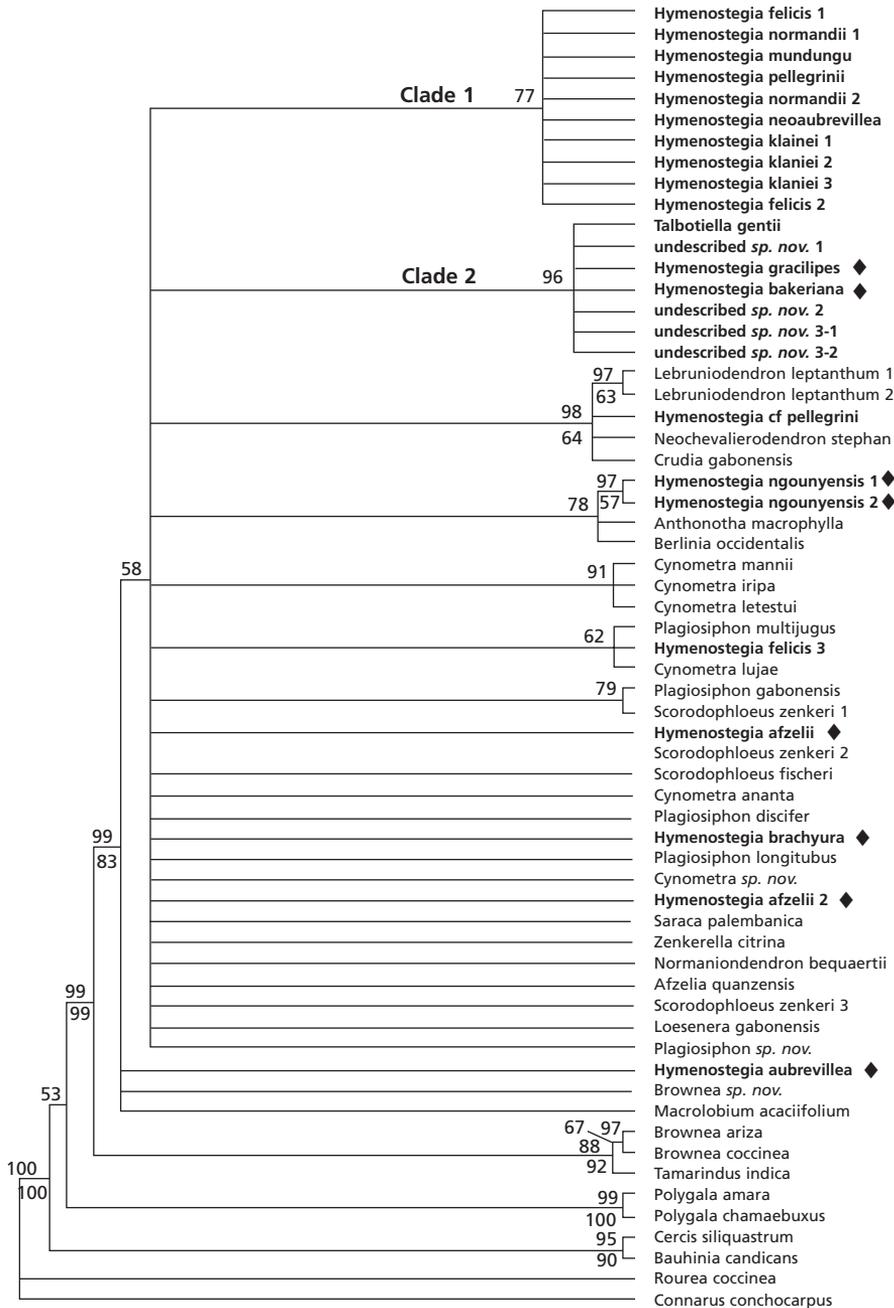
Clarifying the generic limits of *Talbotiella* and *Hymenostegia*

FIG. 1. Bayesian consensus tree from the *rbdL* analyses reproduced from Lunenburg, 2006. Bayesian posterior probabilities above 50 are shown above the line and Jackknife support values above 50% are shown below. Multiple accessions of the same taxon are distinguished by numbers e.g. 1, 2 etc. following the specific epithet. Taxa considered in this study are emboldened. Ex *Hymenostegia* species are marked with black diamonds.

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**5 Evidence from floral morphology**

Léonard's postulate (1951) that *Talbotiella* and *Hymenostegia* are parts of the same evolutionary series was founded on observations of petal number. In *Hymenostegia* (as understood in 1951) he recorded a range of (1) 2–5 petals for the genus. After undertaking numerous dissections of the described species of *Hymenostegia* we conclude that the number of well developed, showy petals is a reliable character for distinguishing species. Furthermore, with one exception (discussed below), *Hymenostegia sensu stricto* species produce either two or three well-developed spatulate petals.

Of the species of *Hymenostegia* in which Léonard observed a sequential reduction in petal number, all but *H. gracilipes* (ex *Hymenostegia*) possess two or three well-developed spatulate petals, 7–10 × c. 3 mm. Nevertheless, during floral dissections it was not unusual for the authors to encounter one or two rudimentary petals which never exceeded 6 × 0.5 mm and were usually shorter and narrower. The presence or absence of these rudimentary petals (which Léonard included to derive petal numbers of four and five, including five for the type species *H. floribunda*) varied among collections of the same species and even within the same accession. We therefore suggest the erratic presence of these structures renders them unsuitable for inclusion in a quantitative evolutionary series. Thus we consider the species of *Hymenostegia sensu stricto* to be characterised by the presence of two or three well-developed spatulate petals providing a clear distinction from *Talbotiella* species which lack petals.

An exception to the pattern of producing two to three well-developed petals is *Hymenostegia breteleri* Aubrév., the only member of the genus to be described since Léonard published his observations in 1951. This rare species was not included in the *trnL* analysis (Bruneau *et al.*, 2001), nor was it successfully amplified for the *rbcL* study, so there is no molecular data available to test its placement in *Hymenostegia sensu stricto*. During the Inselberg excursion held during the AETFAT congress this species endemic to the Yaoundé area was recollected, enabling its incorporation in future studies. *Hymenostegia breteleri* possesses the combination of vegetative characters that are common to the species of *Hymenostegia sensu stricto* and *Talbotiella* but apetalous and pollen characters (see below) suggest that it is misplaced in *Hymenostegia* and should be transferred to *Talbotiella*.

**6 Evidence from pollen morphology**

Pollen of *Hymenostegia afzelii* and *H. floribunda* has been previously illustrated as part of a survey of Detarieae pollen (Banks & Klitgaard, 2000). For the present study, we examined pollen from two species of *Talbotiella* (the type *T. eketensis* and *T. gentii*), four species of *Hymenostegia sensu stricto* (the type *H. floribunda* as well as *H. klainei*, *H. mundungu* and *H. breteleri*), and two of the undescribed species, using a scanning electron microscope (SEM).

The pollen of both *Talbotiella* species had narrow apertures and was fully tectate. In contrast, the species of *Hymenostegia sensu stricto* (not including *H. breteleri*) had pollen with broader apertures and was only semi-TECTATE. Pollen from the type species of the two genera is shown for comparison in Figs 2A and 2B. Pollen of two of the undescribed species (Figs 2C and 2D) resembles the pollen of *T. eketensis* (the type species of *Talbotiella*) as does that of *Hymenostegia breteleri* supporting the hypothesis that *H. breteleri* is more closely related to the species currently placed in *Talbotiella*.

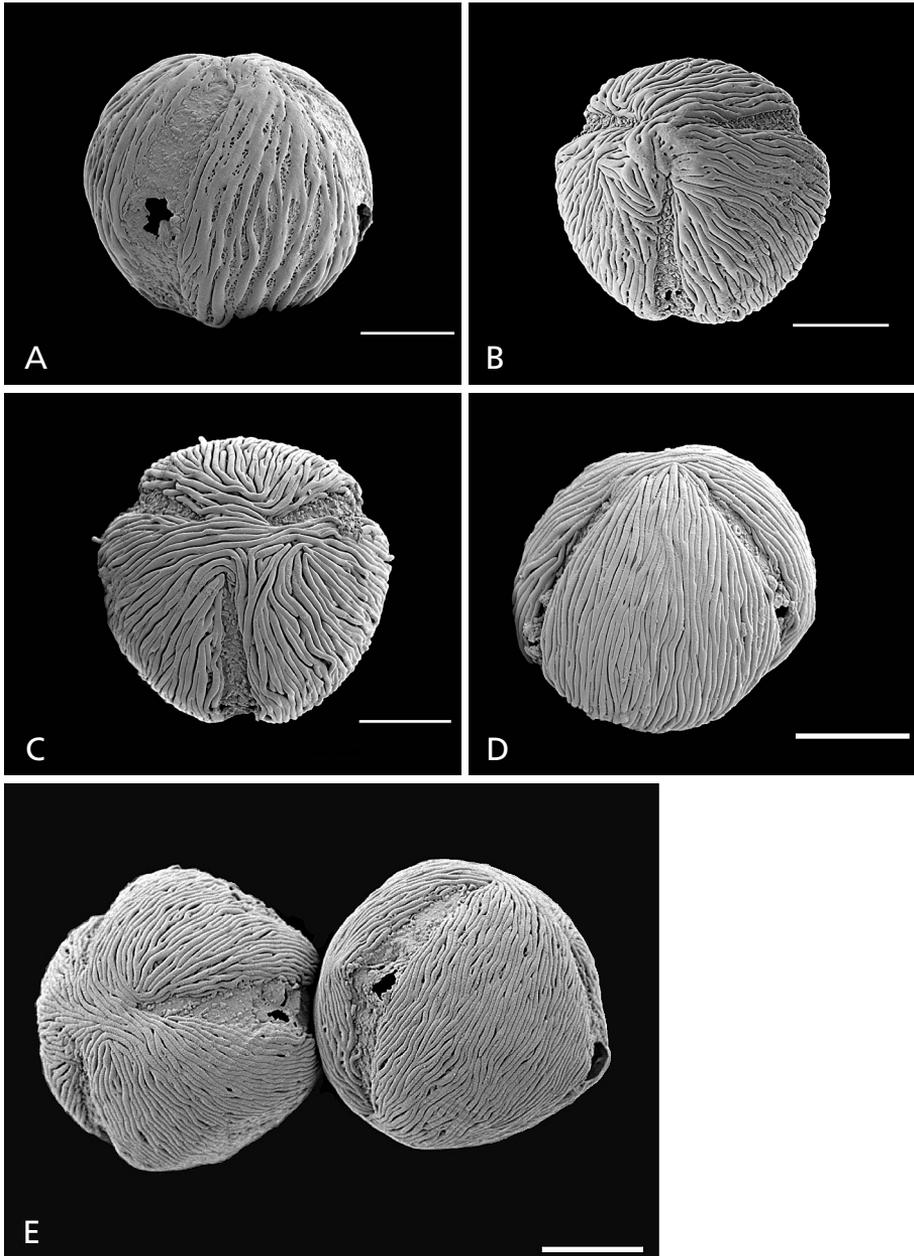
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FIG. 2. Scale bars are 10 microns. **A** *Hymenostegia floribunda*. SEM of whole grain in equatorial view showing broader apertures and semi-tectate striate surface; **B** *Talbotiella eketensis*. SEM of whole grain in oblique polar view showing narrow apertures and tectate striate surface; **C** *Talbotiella sp. nov. 1*. SEM of whole grain in oblique polar view showing narrow apertures and tectate striate surface; **D** *T. sp. nov. 4*. SEM of whole grain, equatorial view also showing narrow apertures and tectate striate surface; **E** *Hymenostegia bretelei*. SEM of whole grains showing narrow apertures and tectate striate surface.

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**7 Summary of characters examined in this study**

A summary of the morphological and palynological evidence presented in this paper is given in Table 5. With respect to the characters historically used to distinguish *Talbotiella* and *Hymenostegia* (Table 1) i.e. bud scale persistence, bracteole shape and persistence, and petal number, the status of *Talbotiella* is unchanged. However, with the exclusion of eight species from *Hymenostegia sensu lato* and the reassessment of petal number, the more narrowly circumscribed *Hymenostegia sensu stricto* becomes morphologically more homogenous for bud scale persistence and petal number.

TABLE 5. Summary of the revised and extended character set relevant to the determination of the generic limits of *Hymenostegia sensu stricto* and *Talbotiella*, including, for comparison, the character states of the four undescribed species and the misplaced *H. breteleri*.

| Characters                            | <i>Hymenostegia sensu stricto</i><br>(excluding<br><i>H. breteleri</i> ) | <i>Hymenostegia breteleri</i>                       | <i>Talbotiella</i> | Undescribed species |
|---------------------------------------|--|---|--------------------|---------------------|
| Persistent imbricate bud scales       | always present   |   |                    |                     |
| Persistent narrow petaloid bracteoles | sometimes present  | always present                                      | always present     | sometimes present   |
| Petals                                | 2–3  | 0   | 0                  | 0                   |
| Pollen                                | apertures broad, ornamentation semi-tectate and striate                  | apertures narrow, ornamentation tectate and striate |                    |                     |

**8 Decision to maintain *Talbotiella* as distinct from *Hymenostegia sensu stricto***

The character combination of free auriculate stipules, 1–3 glands on the distal part of the leaflet, glands absent from the proximal part, appressed puberulous indumentum on the lower leaflet surface indumentums, and a canaliculate leaf rachis is shared by the species of *Hymenostegia sensu stricto*, *H. breteleri*, *Talbotiella* spp. and the four undescribed species. Based on these characters alone, a case could be made for combining *Talbotiella* with *Hymenostegia sensu stricto* and *H. breteleri* and including the undescribed species within *Hymenostegia*. However, given the absence of petals in *Talbotiella*, *Hymenostegia breteleri* and the undescribed species, along with pollen possessing narrow apertures and a tectate surface, and in light of the results from the molecular studies, we have decided to uphold *Talbotiella* as distinct. The undescribed species are all apetalous and pollen sampled from two of the undescribed species matches that of *Talbotiella*, as does the pollen of the apetalous *Hymenostegia breteleri*.

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We therefore consider it best to place the undescribed species in *Talbotiella* and we propose transferring *Hymenostegia breteleri* to *Talbotiella*, thus expanding this genus from three to eight species.

### 9 The relationship of *Talbotiella* to *Hymenostegia sensu stricto*

Although we have chosen to maintain *Hymenostegia sensu stricto* and *Talbotiella* as distinct, their relationship remains unclear. The shared vegetative characters (listed above) could be interpreted as indicating a sister group relationship, but due to lack of resolution from the Bayesian analysis of the *rbL* sequence data that interpretation is neither supported nor refuted (Fig. 1) and the results of the *trnL* studies of Bruneau *et al.* (2001) were no less equivocal. Moreover, without a more extensive morphological phylogenetic study that includes a larger number of outgroup genera, we can not rule out the possibility that these shared characters are not synplesiomorphies. An analysis of Bayesian consensus topologies uncovered evidence that *Hymenostegia sensu stricto* and *Talbotiella* may not be sisters (Lunenburg, 2006), which lends support to maintaining *Talbotiella* as distinct. A combined molecular and morphological phylogenetic analysis of Caesalpinioideae (Herendeen *et al.*, 2003) did not place *Talbotiella* (represented by *T. gentii*) as sister to a clade comprising the five sampled species of *Hymenostegia sensu stricto* including the type *H. floribunda*, but instead placed *Hymenostegia afzelii* (ex *Hymenostegia*) as sister to *Hymenostegia sensu stricto* species with limited support.

### 10 Summary of results

*Talbotiella* can be distinguished from *Hymenostegia sensu stricto*.

*Hymenostegia sensu lato*, to which 16 species are currently assigned, is a heterogeneous assemblage.

*Hymenostegia sensu stricto* comprises seven species, *H. floribunda* (the type), *H. felcis*, *H. klainei*, *H. neoaubrevillei*, *H. normandii*, *H. mundungu* and *H. pellegrinii*.

*Hymenostegia breteleri* is misplaced in *Hymenostegia* and should be transferred to *Talbotiella*.

The species misplaced in, and eventually to be excluded from *Hymenostegia* (ex *Hymenostegia* species) are *H. afzelii*, *H. aubrevillei*, *H. bakeriana*, *H. brachyura*, *H. gracilipes*, *H. laxiflora*, *H. ngounyensis* and *H. talbotii*.

The eight ex *Hymenostegia* species do not appear to comprise a natural group.

### 11 Future research plans

Based on the results presented here, we plan to pursue the following activities. We will publish a revision of *Talbotiella* to include 8 species, three of which are already described in the genus, four will be newly described and one species will be transferred from *Hymenostegia*. The pollen data set will be expanded by undertaking wider sampling and recording more characters. We will build a widely sampled *trnL* dataset and add key taxa to the *rbL* dataset, ultimately to be analysed in combination in an effort to resolve to determine the correct placement of ex *Hymenostegia* species and to elucidate the relationship between *Talbotiella* and *Hymenostegia sensu stricto*. We plan also to publish a revision of *Hymenostegia sensu stricto*.

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Clarifying the generic limits of *Talbotiella* and *Hymenostegia*

APPENDIX 1. Voucher details for *rbcL* sequences adapted from Lunenburg (2006). GenBank ID is reported for taxa when relevant.

| Taxon   | Voucher                    | GenBank ID. or Herbarium code |
|---|----------------------------|-------------------------------|
| <i>Afzelia quanzensis</i> Welw.                       | <i>Goyder</i> 3727         | WAG; YA                       |
| <i>Anthonotha macrophylla</i> P. Beauv.               | <i>Wieringa</i> 4590       | WAG; LBV                      |
| <i>Bauhinia candicans</i> Benth.                      |                            | Z70161                        |
| <i>Berlinia occidentalis</i> Keay                     | <i>Jongkind</i> 2068       | GC; WAG                       |
| <i>Brownea ariza</i> Benth.                           |                            | Z70158                        |
| <i>Brownea coccinea</i> Jacq.                         |                            | Z70159                        |
| <i>Brownea</i> sp. nov.                               |                            | U74186                        |
| <i>Cercis siliquastrum</i> L.                         | <i>Wieringa</i> 5680       | WAG                           |
| <i>Connarus conchocarpus</i> F. Muell.                |                            | U06798                        |
| <i>Crudia gabonensis</i> Pierre ex De Wild.           | <i>Wieringa</i> 2585       | LBV; WAG                      |
| <i>Cynometra ananta</i> Hutch. & Dalziel              | <i>Wieringa</i> 4296       | WAG                           |
| <i>Cynometra iripa</i> Kostel.                        |                            | AY289677                      |
| <i>Cynometra letestui</i> (Pellegr.) J. Léonard       | <i>Breteler</i> 13966      | LBV; WAG                      |
| <i>Cynometra lujae</i> De Wild.                       | <i>van Valkenburg</i> 3006 | LBV; WAG                      |
| <i>Cynometra mannii</i> Oliv.                         | <i>van Valkenburg</i> 3028 | LBV; WAG                      |
| <i>Cynometra</i> sp.                                  | <i>van Andel</i> 4214      | WAG; YA                       |
| <i>Hymenostegia afzelii</i> (Oliv.) Harms 1           | <i>Breteler</i> 13352      | WAG                           |
| <i>Hymenostegia afzelii</i> (Oliv.) Harms 2           | <i>van Andel</i> 4244      | WAG; YA                       |
| <i>Hymenostegia aubrevillai</i> Pellegr.              | <i>de Kruif</i> 668        | WAG                           |
| <i>Hymenostegia bakeriana</i> Hutch. & Dalziel        | <i>van der Burgt</i> 587   | WAG; YA                       |
| <i>Hymenostegia brachyura</i> (Harms)                 | <i>Zenker</i> 4481         | WAG; YA                       |
| J. Léonard  |                            |                               |
| <i>Hymenostegia felicis</i> (A.Chev.) J. Léonard 1    | <i>Wieringa</i> 2581       | LBV; WAG                      |
| <i>Hymenostegia felicis</i> (A.Chev.) J. Léonard 2    | <i>Wieringa</i> 2841       | LBV; WAG                      |
| <i>Hymenostegia felicis</i> (A.Chev.) J. Léonard 3    | <i>Jacques-Félix</i> 5129  | WAG; YA                       |
| <i>Hymenostegia gracilipes</i> Hutch. & Dalziel       | <i>Merello</i> 1299        | GC; WAG                       |
| <i>Hymenostegia klainei</i> Pierre ex Pellegr. 1      | <i>Wieringa</i> 4714       | LBV; WAG                      |
| <i>Hymenostegia klainei</i> Pierre ex Pellegr. 2      | <i>Wieringa</i> 2575       | LBV; WAG                      |
| <i>Hymenostegia klainei</i> Pierre ex Pellegr. 3      | <i>Wieringa</i> 5137       | LBV; WAG                      |
| <i>Hymenostegia mundungu</i> (Pellegr.)               | <i>Devred</i> 2640         | BR; WAG                       |
| J. Léonard  |                            |                               |
| <i>Hymenostegia neoaubrevillei</i> J. Léonard         | <i>Breteler</i> 14793      | LBV; WAG                      |
| <i>Hymenostegia ngounyensis</i> Pellegr. 1            | <i>Wieringa</i> 2579       | LBV; WAG                      |
| <i>Hymenostegia ngounyensis</i> Pellegr. 2            | <i>Wieringa</i> 4493       | LBV; WAG                      |
| <i>Hymenostegia normandii</i> Pellegr. 1              | <i>Breteler</i> 13943      | LBV; WAG                      |
| <i>Hymenostegia normandii</i> Pellegr. 2              | <i>Wieringa</i> 2208       | WAG; YA                       |
| <i>Hymenostegia pellegrinii</i> (A. Chev.)            | <i>Breteler</i> 15602A     | LBV; WAG                      |
| J. Léonard  |                            |                               |
| <i>Hymenostegia</i> cf. <i>pellegrinii</i> (A. Chev.) | <i>Wieringa</i> 3771       | LBV; WAG                      |
| J. Léonard  |                            |                               |
| <i>Lebruni dendron leptanthum</i> (Harms)             | <i>Wieringa</i> 1659       | LBV; WAG                      |
| J. Léonard 1  |                            |                               |
| <i>Lebruni dendron leptanthum</i> (Harms)             | <i>Allogho</i> 20          | LBV; WAG                      |
| J. Léonard 2  |                            |                               |

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|  |                                      |            |
|--|--------------------------------------|------------|
| <i>Loesenera gabonensis</i> Pellegr.                           | Wieringa 4542                        | LBV; WAG   |
| <i>Macrolobium acaciifolium</i> Benth.                         |                                      | U74191     |
| <i>Neochevalierodendron stephanii</i><br>(A. Chev.) J. Léonard | <i>Breteler</i> 13262                | LBV; WAG   |
| <i>Normandiodendron bequaertii</i> (De Wild.)<br>J. Léonard    | <i>J. J. F. E. de Wilde</i><br>11209 | LBV; WAG   |
| <i>Plagiosiphon discifer</i> Harms                             | <i>Wieringa</i> 2316                 | WAG; YA    |
| <i>Plagiosiphon gabonensis</i> (A. Chev.)<br>J. Léonard        | <i>Wieringa</i> 4400                 | LBV; WAG   |
| <i>Plagiosiphon longitubus</i> (Harms)<br>J. Léonard           | not recorded                         | WAG        |
| <i>Plagiosiphon multijugus</i> (Harms)<br>J. Léonard           | <i>Wieringa</i> 3813                 | LBV; WAG   |
| <i>Plagiosiphon</i> sp. nov.                                   | <i>Breteler</i> 12828                | LBV; WAG   |
| <i>Polygala amara</i> L.                                       |                                      | Z70175     |
| <i>Polygala chamaebuxus</i> L.                                 |                                      | Z70176     |
| <i>Rourea coccinea</i> (Thonn. ex Schumach.)<br>Benth.         |                                      | AF308704   |
| <i>Saraca palembanica</i> (Miq.) Baker                         | <i>Breteler</i> 13509                | WAG        |
| <i>Scorodophloeus fischeri</i> (Taub.)<br>J. Léonard           | <i>Faulkner</i> 4025                 | WAG        |
| <i>Scorodophloeus zenkeri</i> Harms 1                          | <i>Breteler</i> 14073                | LBV; WAG   |
| <i>Scorodophloeus zenkeri</i> Harms 2                          | <i>Wieringa</i> 5067                 | LBV; WAG   |
| <i>Scorodophloeus zenkeri</i> Harms 3                          | <i>Breteler</i> 11111                | LBV; WAG   |
| <i>Talbotiella gentii</i> Hutch. & Greenway                    | <i>Jongkind</i> 1940                 | GC; WAG    |
| <i>Talbotiella</i> sp. nov 1                                   | <i>Letouzey</i> 10940                | K; P; YA   |
| <i>Talbotiella</i> sp. nov 2                                   | <i>van der Burgt</i> s.n.            | K; WAG; YA |
| <i>Talbotiella</i> sp. nov 3-1                                 | <i>van der Burgt</i> 601             | K; WAG; YA |
| <i>Talbotiella</i> sp. nov 3-2                                 | <i>van der Burgt</i> 708             | K; WAG; YA |
| <i>Tamarindus indica</i> L.                                    |                                      | Z70160     |
| <i>Zenkerella citrina</i> Taub.                                | <i>Cheek</i> 7614                    | K; WAG; YA |