

Taxonomic changes in C_3 *Cyperus* (Cyperaceae) supported by molecular data, morphology, embryography, ontogeny and anatomy

Isabel Larridon^{1,*}, Marc Reynders¹, Wim Huygh¹, Kenneth Bauters¹, Alexander Vrijdaghs², Olivier Leroux³, A. Muthama Muasya⁴, David A. Simpson⁵ & Paul Goetghebeur¹

¹Ghent University, Department of Biology, Research Group Spermatophytes, K.L. Ledeganckstraat 35, BE-9000 Gent, Belgium

²K.U.Leuven, Institute of Botany and Microbiology, Laboratory of Plant Systematics, Kasteelpark Arenberg 31, BE-3001 Leuven, Belgium

³Ghent University, Department of Biology, Research Group Pteridology, K.L. Ledeganckstraat 35, BE-9000 Gent, Belgium

⁴University of Cape Town, Botany Department, Rondebosch 7700, South Africa

⁵Royal Botanic Gardens, Kew, Richmond, Surrey, UK-TW9 3AB, United Kingdom

*Author for correspondence: isabel.larridon@ugent.be

Background and aims – Recent molecular studies validate a broad definition of *Cyperus* (Cyperaceae) uniting genera previously scattered in Cyperoideae. First indication of their affinity with *Cyperus* was obtained through embryography. *Cyperus* consists of a paraphyletic C_3 *Cyperus* and monophyletic C_4 *Cyperus*. In this study, we aim to check and clarify the putative positions of the segregate genera in C_3 *Cyperus*. Additional information is given and remarks are made on the position of some as yet unplaced species or sections in the C_3 *Cyperus* phylogeny.

Methods – Embryos of *Cyperus constanzae* and *C. gardneri* were cleared and drawn. Inflorescences of selected C_3 *Cyperus* species were investigated using scanning electron and light microscopy. Histochemical tests were performed to assess the presence of suberin in the ‘corky’ tissue of the nutlets of *Cyperus pectinatus*.

Key results – Embryography not only supports tribal classification in Cyperoideae, it is also phylogenetically informative in C_3 *Cyperus*. Morphology and ontogeny support molecular phylogenetic results suggesting the inclusion of the segregate genera in C_3 *Cyperus* as new sections or in established sections, and confirm the need to broaden the circumscription of some of these sections.

Conclusion – Although less diverse than C_4 *Cyperus*, C_3 *Cyperus* includes clades which evolved an exceptional morphological diversity compared to its limited species numbers. The segregate genera *Courtoisina* (deciduous spikelets), *Kyllingiella* (spirally-arranged glumes) and *Oxycaryum* (spirally-arranged glumes and dorsiventrally flattened dimerous gynoecia), and the taxon *Anosporum* (recognised at sectional, subgeneric or generic level) are here included in C_3 *Cyperus* (= *Cyperus* subg. *Anosporum*) as sections or included in an existing section (*Kyllingiella* is included in *Cyperus* sect. *Leucocephali*). A formal taxonomic revision is presented with relevant new names and combinations, synonyms, diagnoses and identification keys.

Key words – Anatomy, *Cyperus*, Cyperaceae, embryography, molecular phylogeny, morphology, ontogeny, taxonomy.

INTRODUCTION

In the tropics and subtropics, *Cyperus* is the largest genus in the family Cyperaceae. *Cyperus* s. str. includes c. 700 species (Govaerts et al. 2011). Our recent molecular phylogenetic studies validate a broad definition of *Cyperus* uniting genera previously scattered in Cyperoideae (Simpson et al. 2007, Muasya et al. 2009a, Larridon et al. 2011b). The seminal embryographical study by Van der Veken (1965) gave the first

indication of a close relationship between these taxa. After studying the embryos of 342 Cyperoideae species, Van der Veken (1965) not only concluded that the uniformity of the embryos of *Cyperus* species supports the wide concept of the genus, but he also revealed the presence of embryos of the *Cyperus*-type in many taxa previously placed near *Scirpus* (e.g. *Ascolepis*, *Ficinia*, *Isolepis*, *Lipocarpha*, *Kyllingiella* and *Oxycaryum*). Van der Veken (1965) studied the embryos of thirty C_3 *Cyperus* species. Using maximum likelihood and

Bayesian analyses of nrDNA (ETS1f) and cpDNA (*rpl32-trnL* and *trnH-psbA*) sequence data, Larridon et al. (2011b) concluded that the *Cyperus* clade consists of a paraphyletic C_3 *Cyperus* (the *Cyperus* clade species using C_3 photosynthesis linked with eucyperoid vegetative anatomy) in which a monophyletic C_4 *Cyperus* is nested (uniting the *Cyperus* clade species using C_4 photosynthesis linked with chlorocyperoid vegetative anatomy). In C_3 *Cyperus*, five major clades are recognisable (fig. 1) (Larridon et al. 2011b). Clade 1 can be divided in three subclades largely corresponding to *Cyperus* sect. *Haspani*, *C.* sect. *Incurvi* and *C.* sect. *Diffusi*. The other major clades respectively correspond to: (clade 2) an entirely New World *C.* sect. *Luzuloidei* sensu Denton (1978), (clade 3) a highly diverse clade including *C.* sect. *Fusci*, *C.* sect. *Pseudanosporum* and *C.* sect. *Anosporum*, and the segregate genera *Courtoisina* and *Oxycaryum*, (clade 4) *C.* sect. *Alternifolii*, and (clade 5) *C.* sect. *Leucocephali* and the segregate genus *Kyllingiella*. The morphological diversity of *Cyperus* translates into a large number of published names. Compared to C_4 *Cyperus*, a smaller number of names of genera and of subdivisions of genera were described in C_3 *Cyperus* (Huygh et al. 2010, Larridon et al. 2011a, Reynders et al. 2011). Of the names of genera and of subdivisions of genera described for C_3 *Cyperus*, a surprisingly large number relate to a single, relatively small clade (fig. 1, clade 3). The number of names published for taxa belonging to clade 3, reflects morphological diversity of this clade.

Based on molecular data (Muasya et al. 2002, 2009a), two clades are recognised in Cyperaceae. Traditionally, Cyperaceae were described as having distichously organised spikelets and trimerous flowers without a perianth (e.g. Kükenthal 1936). However, Muasya et al. (2002, 2006, 2007, 2009a, 2009b) and Vrijdaghs et al. (2005, 2006, 2009) demonstrated that spirally organised spikelets and flowers with at least remnants of a perianth occur in the *Ficinia* clade in Cyperaceae. In the *Cyperus* clade, given that segregate genera such as *Oxycaryum* and *Kyllingiella* are nested within it (Muasya et al. 2002, 2009a, Larridon et al. 2011b), spirally organised spikelets also occur. "Perianthless flowers" still hold, although in this ontogenetic study, we investigated: (1) the flexibility of the spikelet structure in C_3 *Cyperus* s. str. and its segregate genera *Courtoisina*, *Oxycaryum* and *Kyllingiella* to establish the range of variation on the spikelet model as proposed by Vrijdaghs et al. (2010), (2) the variation in spikelet and floral structure present in the segregate genera, and (3) the variation in spikelet and floral structure from the developmental standpoint. The nature of the 'corky' tissue surrounding the nutlets of *Cyperus pectinatus* Vahl was studied using histochemical techniques.

The molecular phylogenetic hypothesis of Larridon et al. (2011b) demonstrated the need to adapt the current infra-generic classification of *Cyperus* as a whole, and more specifically of C_3 *Cyperus*, to accommodate several segregate genera (i.e. *Courtoisina*, *Oxycaryum* and *Kyllingiella*). In addition, several species need to be moved between different sections. This paper provides the necessary formal nomenclatural and taxonomic changes and adds further morphological, embryographical and ontogenetic support for these taxonomic changes.

Taxonomic history

As mentioned above, a surprisingly large number of taxa relate to clade 3 of the molecular phylogenetic hypothesis of Larridon et al. (2011b) (fig. 1), i.e. *Cyperus* sect. *Anosporum* (Pax) Nees, *Cyperus* sect. *Pseudanosporum* C.B. Clarke, *Courtoisina* Soják, and *Oxycaryum* Nees. Although the species of this clade have been placed in a number of different segregate genera and / or subdivisions of *Cyperus* (or even *Scirpus* in the case of *Oxycaryum cubense* (Poepp. & Kunth) Palla) to reflect the morphological diversity of this clade, they have some characters in common. For example, species of *C.* sect. *Anosporum*, *C.* sect. *Pseudanosporum* and *Oxycaryum* have nutlets with corky thickenings and *Courtoisina* and *Oxycaryum* have a tendency towards globose spikelet-clusters (fig. 2D & E). The other taxa introduced here are *C.* sect. *Leucocephali* Cherm. ex Kük., *Kyllingiella* R.W. Haines & Lye, *C.* sect. *Dichostylis* sensu Kükenthal (1936), and *C.* sect. *Graciles* (Benth.) Kük.

Cyperus* sect. *Anosporum* and *C.* sect. *Pseudanosporum – Nees (1834a) established *Anosporum* Nees as a monotypic genus based on the species *Cyperus monocephalus* Roxb. This species differs from *Cyperus* s. str. by its unusual habit and its nutlets which are surrounded by a corky tissue. Various authors, unknowingly, described other monotypic genera based on the same conspicuous species (*Hydroschoenus* Zoll. & Moritzi, *Trentepohlia* Boeck.). A second species, *Cyperus pectinatus* Vahl, served as type for the genus *Atomostylis*. The two species described in this genus are now both seen as synonyms of *C. pectinatus*.

Boeckeler (1869, 1870) included several more species in *Anosporum* based on a similarity of the nutlets, including *Anosporum pallidum* Boeck. [= *Cyperus platystylis* R.Br.] and *Anosporum cubense* (Poepp. & Kunth) Boeck. [= *Oxycaryum cubense*]. Most authors at that time included *Oxycaryum* in *Scirpus* because of its spirally-arranged glumes.

Both Nees (1834a) and Boeckeler (1869) considered the corky thickenings of the nutlet to be a perigynium. This influenced Nees (1834a) to include *Anosporum* in the tribe Hypolytrae. However, Boeckeler (1869) placed *Anosporum* close to *Cyperus*. Clarke (1884) showed the perigynium theory to be incorrect. As Clarke (1884) is a survey of the Indian *Cyperus* species, he treated *Cyperus cephalotes* Vahl as the only species of *Cyperus* subg. *Anosporum*. In addition, Clarke (1884) described a new monotypic *Cyperus* section *Pseudanosporum* for the only other Asian species included in *Anosporum* by Boeckeler (1869), i.e. *Cyperus platystylis*. Clarke (1884) agreed with Steudel (1854) in placing *C. platystylis* somewhere near Kunth's *Alternifolii*, of which it has the inflorescence, digitate spikelets and subexalate rachilla. However, in the same paper he remarked that even assuming that the corkiness of the nutlets is adaptive, there is much to connect *C. platystylis* with *Anosporum*. Clarke (1884) stated that in his opinion *Anosporum* should not be maintained as separate from *Cyperus* if *C. platystylis* is included in it as it does not have any of the traits which characterise *Anosporum* (the pedicel, the permanent style or the entire stigma), the only clearly shared character being the corkiness of the nutlet.

In recent years most botanists shared the view of Kükenthal (1936), who regarded *Cyperus cephalotes*, *C. co-*

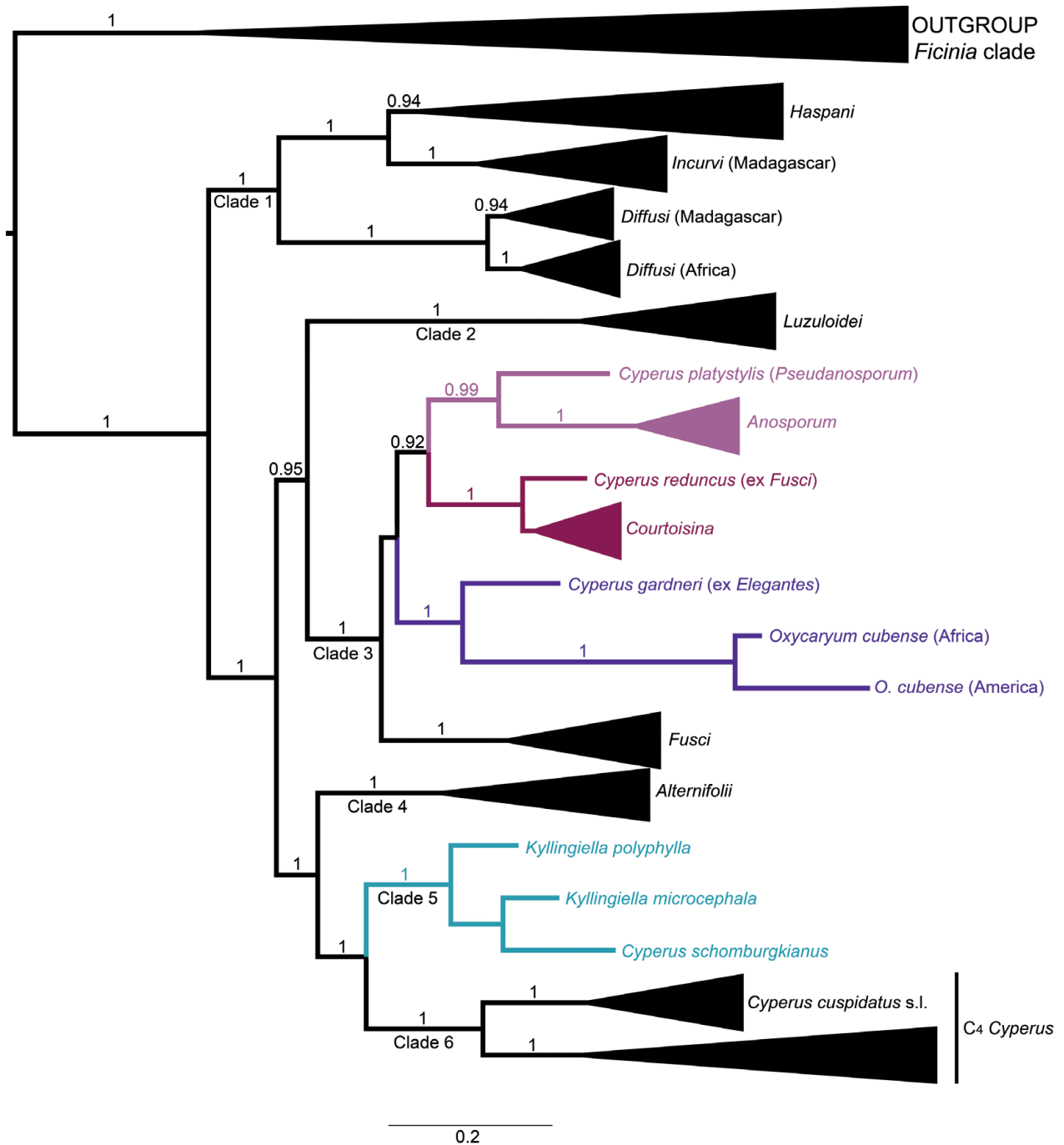


Figure 1 – Simplified 50% majority consensus multiple-locus BI-GTR+I+ Γ tree with the associated posterior probabilities (PP) values based on fig. 2 of Larridon et al. (2011b). Only PP values above 85% are shown.

lymbetes Kotschy & Peyr. and *C. pectinatus* as belonging to a section *Anosporum* in *Cyperus*. However, Lye (1981) stated that *Anosporum* is sufficiently different from *Cyperus* to warrant generic separation, at least when such genera as *Alinula*, *Mariscus*, *Kyllinga*, *Pycreus*, *Remirea* and *Torulinium* are accepted. Later, Haines & Lye (1983) treated *Anosporum* at subgeneric level in *Cyperus*. Lye (1981), like Boeckeler (1869) and Chermeson (1924) before him, considered the possibility of a relationship of *Anosporum* with *Oxycaryum*

based on the similarity of their nutlets. Goetghebeur (1986) considered glume arrangement to be a more important character than corkiness of the nutlets.

Courtoisina – The genus *Courtoisina* was first established under the name *Courtoisia* by Nees (1834a) to accommodate the Indian species previously known as *Kyllinga cyperoides* Roxb. Clarke (1894) combined the African species *Cyperus assimilis* Steud. in *Courtoisina*. However, the name *Courtoisina* Nees (Nees 1834a) is a younger homonym of *Cour-*

toisia Marchand (Lichenes) (Marchand 1830). Soják (1979), Raizada & Bennet (1981) and Rauschert (1982) published new names and combinations for *Courtoisia* Nees, most of which proved superfluous. Wilson (1983) protested with good reason against the publication of superfluous names. When renaming the genus, Soják (1979) combined *Courtoisia cyperoides* (Roxb.) Soják, but failed to combine *Courtoisia assimilis* (Steud.) C.B. Clarke, nom. illeg. Maquet (1988) later published the correct combination for this species, *Courtoisia assimilis* (Steud.) Maquet. Rauschert (1982) published the superfluous and illegitimate name *Pseudomariscus* and made the equally illegitimate combination *P. cyperoides* (Roxb.) Rauschert. As with Soják (1979), the other known species was left unnamed. However, Rauschert (1982) did make the combination *P. olivaceus* (Boeck.) Rauschert for *Oxycaryum cubense*. Raizada & Bennet (1981) published superfluous new names for both the genus and its two species. The proposal by Vorster (1986) to conserve *Courtoisia* Nees against *Courtoisia* Marchand was not accepted at the nomenclatural sessions during the 14th International Botanical Congress in Berlin (1987). The name *Courtoisia* Soják should be used (Brummitt 1989). Most recent authors consider *Courtoisia* to be a distinct genus (e.g. Goetghebeur 1986, 1998, Vorster 1996, Govaerts et al. 2007, 2011), although some consider it to be a part of *Cyperus* s. lat. (Haines & Lye 1983, Lye 1983, 1992). The most obvious characters used to support *Courtoisia* at generic rank are the strongly flattened spikelets which disarticulate as a unit when mature, leaving the spikelet bract and prophyll behind and the conspicuously winged glumes.

Lye (1983) made the combination *Cyperus* subg. *Courtoisia* (Nees) Lye, and later (Lye 1992) he made the illegitimate combination *Cyperus* subg. *Courtoisia* (Soják) Lye for the same taxon. Publishing the name *Cyperus* subg. *Courtoisia* (Nees) Lye was unfortunate, because although the generic name *Courtoisia* Nees is an illegitimate later homonym, the subgeneric name *Cyperus* subg. *Courtoisia* is legitimate with priority from its date of publication (1983) (Huygh et al. 2010). Consequently, it is the correct name for the taxon at subgeneric rank in *Cyperus*, although *Courtoisia* Soják is the correct name at generic rank.

Oxycaryum – The genus *Oxycaryum*, either considered as monotypic, or sometimes divided into several closely related taxa (Palla 1908), is widely distributed. A great number of synonyms have been published in other genera as *Anosporum*, “*Crepidocarpus*”, *Cyperus*, *Isolepis*, *Kyllinga*, *Mariscus* and *Scirpus*. Such inconsistent interpretations show that this plant unites characters which are more or less typical for one of these genera.

Oxycaryum cubense was first described in the tribe Scirpeae s. lat. as *Scirpus cubensis* Poepp. & Kunth because of its spirally-arranged glumes. However, the genus *Scirpus*, as interpreted by Linnaeus (1753), and accepted with some modifications by later authors (e.g. Boeckeler 1868–1877, Clarke 1908, Chermeson 1937), proved to be a very heterogeneous assemblage of species. Since the embryographical study of Van der Veken (1965) and the division of *Scirpus*, *Oxycaryum* is included in the Cyperae.

As mentioned above, Boeckeler (1869), Chermeson (1924) and later Lye (1981) suggested a possible relationship

of *Anosporum* with *Oxycaryum* based on the corky nutlets. Van der Veken (1965) mentioned a certain similarity of the embryos of both taxa. Goetghebeur (1986) considered *Oxycaryum* to be related to *Cyperus* itself, of which he believed it to be an early evolutionary lineage based on the spirally arranged glumes. However, Goetghebeur (1986) does not support uniting *Oxycaryum* with *Anosporum* because of their differing morphology (nutlet morphology excepted).

Cyperus* sect. *Leucocephali – Steudel (1854) described *Cyperus pulchellus* R.Br. as a new species *Sorostachys kyllingioides* Steud. (based on a different type specimen) in a separate genus *Sorostachys*. Only Lye (1981) accepted this genus, including only two species, *Cyperus leucocephalus* Retz. and *Cyperus pulchellus*. Lye (1981) placed *Sorostachys* close to *C₃ Cyperus* and possibly even to *Kyllingiella* (Haines & Lye 1978). Later, Lye (1983) reduced *Sorostachys* to a subgenus in *Cyperus*.

Clarke (1884) incorrectly placed *C. leucocephalus* in sect. *Platystachyi*, based on the presence of *C. sphaerocephalus* var. *leucocephalus* Kunth [= *C. niveus* var. *leucocephalus* (Kunth) Fosberg] in Kunth's *Platystachyi* (Kunth 1837). As a consequence, Clarke (1884) also placed *Sorostachys* in synonymy of sect. *Platystachyi*. Based on Clarke's (1884) mistake, Kern (1974) lectotypified *Cyperus* sect. *Platystachyi* with *C. leucocephalus* Retz. However, Larridon et al. (2011a) superseded Kern's (1974) choice, by giving preference to *C. niveus*. This is because *Cyperus niveus* was included in the original circumscription of *C. sect. Platystachyi* given by Kunth (1837) and its characters fit the description of this group, in contrast to *C. leucocephalus*. Simpson (1990) clearly explained the differences between sections *Leucocephali* and *Platystachyi*. Furthermore, *C. sect. Leucocephali* and *C. sect. Platystachyi*, as originally circumscribed, both form well-defined natural groups in *Cyperus* and following the subgeneric classification of Goetghebeur (1998) they respectively belong in *C. subg. Anosporum* (*C₃* photosynthesis – eucyperoid anatomy) and *C. subg. Cyperus* (*C₄* photosynthesis – chlorocyperoid anatomy) and are in so not closely related.

Kükenthal (1936) validated Chermeson's (1931) *C. sect. Leucocephali*. However, at the same time, Kükenthal (1936) reduced the name *Sorostachys* to the synonymy of sect. *Platystachyi*, but placed its only species (*S. kyllingioides*) in synonymy of *C. leucocephalus* in sect. *Leucocephali*. This confusion is probably also the result of Clarke's (1884) error.

Simpson (1990) includes seven species in his revision of *C. sect. Leucocephali*. He considered *C. pulchellus* and *C. leucocephalus* as separate species, and includes three of the others also included by Kükenthal (1936), i.e. *C. schomburgkianus* Nees, *C. tenerrimus* J.Presl & C.Presl, and *C. michoacanensis* Britton ex C.B. Clarke. *C. zanzibarensis* C.B. Clarke (accepted species name, Govaerts et al. 2007, 2011) is placed in the synonymy of *C. pulchellus*, while *C. coronarius* (Vahl) Kunth (accepted species name, Govaerts et al. 2007, 2011) is placed in the synonymy of *C. leucocephalus* and the recently described *C. microglumis* D.A. Simpson (Simpson 1990) and *C. nayaritensis* G.C. Tucker (Tucker 1983) are also included. Since Simpson's (1990) publication, two additional species of this section were described by Simpson, i.e. *Cyperus androhibensis* D.A. Simpson (Simpson 1992) from Madagascar

and *Cyperus brumadoi* D.A.Simpson (Simpson 1993) from Brazil.

Kyllingiella – Steudel (1842) described *Kyllinga microcephala* Steud. from Ethiopia. This species resembles *Kyllinga* in several respects (white capitate inflorescence and general habit). However, it differs in having spirally-arranged glumes. Richard (1850) renamed the species *Isolepis kyllingoides* A.Rich. Boeckeler (1870) in his turn transferred this plant to *Scirpus* as *Scirpus kyllingoides* (A.Rich.) Boeck. Most authors regarded this plant as a *Scirpus*. Clarke (1893) associated this species in *Scirpus* with another *Cyperus* species which often has spirally-arranged glumes, i.e. *Scirpus michelianus* L. [= *Cyperus michelianus* (L.) Delile].

Based on the results of e.g. Van der Veken's (1965) embryographical study (*Cyperus*-type embryo) and Druyts-Voets (1970) anatomical study (eucyperoid stem and leaf anatomy), Haines & Lye (1978) established the genus *Kyllingiella* based on the species *Kyllingiella microcephala* (Steud.) R.W.Haines & Lye. As accepted by Govaerts et al. (2007, 2011), *Kyllingiella* includes four species.

Cyperus* sect. *Dichostylis sensu Kükenthal (1936) – Huygh et al. (2010) explained that the name *Dichostylis* P.Beauv. ex T.Lestib. (Lestiboudois 1819: 39) is illegitimate since in its protologue another name (*Echinolytrum* Desv. (Desvaux 1808) [= *Fimbristylis* Vahl]) was cited in synonymy. As circumscribed by Kükenthal (1936) this is a very heterogeneous group of species, and included two confirmed *C₄* *Cyperus* species *Cyperus meeboldii* Kük. and *C. michelianus* (L.) Link (Bruhl & Wilson 2007). However, Kükenthal (1936) also placed four *C₃* *Cyperus* species in this section (*C. humilis* Kunth, *C. seslerioides* Kunth, *C. tweediei* C.B.Clarke and *C. uncinulatus* Schrad. ex Nees). A last species, *C. hilarensis* Steud., was mentioned by Kükenthal as uncertain with possible affinity to *C. uncinulatus*. Since then, two more species have been described with possible affinity to *C. uncinulatus*: *C. arsenei* O'Neill & Ben.Ayers and *C. microbrunneus* G.C.Tucker.

Cyperus* sect. *Graciles – Bentham (1878: 254) published his *Graciles* as a group of unspecified rank under the not validly published name "*Cyperus* sect. *Eucyperus*". He diagnosed "*Cyperus* sect. *Eucyperus*" as follows: "Spikelets flat, the [rachis] not winged or rarely with an exceedingly narrow border. Style 3-cleft. Nut equally triquetrous." and "*Cyperus* [unranked] *Graciles*" as: "Spikelets spreading, pale-colored, in a single sessile cluster or solitary. Glumes obtuse or very shortly pointed. Nuts short." Bentham (1878) included five species, i.e. *Cyperus tenellus* L.f., *C. gracilis* R.Br., *C. enervis* R.Br., *C. debilis* R.Br. and *C. laevis* R.Br.

Kükenthal (1936: 292) formally published this taxon at sectional rank and included eight species in *Cyperus* sect. *Graciles*. Blake (1939) published a thorough revision of *C. sect. Graciles*, in which he used a more natural circumscription for this section. After correspondence, Kükenthal (1943) accepted Blake's opinions. Three species included by Kükenthal (1936) in *C. sect. Graciles* were no longer included by Blake (1939). Two of these, i.e. *Cyperus tenellus* L.f. and *C. leucoloma* Nees, have since been moved to the genus *Isolepis*, as *I. levynsiana* Muasya & D.A.Simpson and *I. leucoloma* (Nees) C.Archer respectively (Archer 1998; Muasya

et al. 2002, 2006, 2007). A third species included in *C. sect. Graciles* by Kükenthal (1936), *Cyperus trichodes* Griseb., was excluded most likely based on its deviant distribution in Jamaica, while all other *C. sect. Graciles* species are limited to north and east Australia, and some of its surrounding islands. Furthermore, Blake (1939) had a quite different view on the synonymy and rank of some of the taxa included in *C. sect. Graciles*.

MATERIAL AND METHODS

Plant material and morphology

We examined a large number of herbarium specimens (from the herbaria B, BM, BR, GENT, EA, K, MO, P, TAN, U, UPS, WAG mainly; abbreviations according to Holmgren et al. 1990), supplemented with own observations in the field, and from collections in the Ghent University Botanical Garden. Additional information on species and (type) specimens was obtained from literature (incl. protologues) and the databases <http://plants.jstor.org/>, <http://www.tropicos.org/> and Govaerts et al. (2011). Images of spikelets and nutlets were taken with a Nikon SMZ800 stereoscopic microscope, equipped with a Nikon digital camera DXM1200 (Nikon, Tokyo, Japan). The images were edited with Adobe Photoshop CS3 (Adobe Systems Inc., San Jose, USA). The macroscopic photos were taken during expeditions in the field.

Embryography

The embryos of two species were studied and drawn, based on the methods described in Van der Veken (1965). For *Cyperus gardneri* Nees, embryos were studied and drawn from the specimen *Schessl* 3316 (GENT), and for *Cyperus contanzae* Urb. from the specimen *Ekman* 6879 (K). These embryos were compared with the embryos of *C₃* *Cyperus* species studied by Van der Veken (1965). Table 1 lists the species of which the embryographs are displayed in fig. 3. The embryos of clade 3 species (fig. 1) (Larridon et al. 2011b) were assembled and overlaid onto the Bayesian inference tree to trace their morphological evolutionary transformations (fig. 4).

Ontogeny

Inflorescences of the species studied were collected in the field and at the Ghent University Botanical Garden (table 2) and subsequently fixed in FAA (70% ethanol, acetic acid, 40% formaldehyde, 90/5/5). Spikelets and floral buds were dissected in 70% ethanol under a Wild M3 (Leica Microsystems AG, Wetzlar, Germany) stereo microscope equipped with a cold-light source (Schott KL1500; Schott-Fostec LLC, Auburn, NY, USA). The prepared material was washed twice with 70% ethanol for 5 min and then placed in a mixture (1/1) of 70% ethanol and DMM (dimethoxymethane) for 5 min. Subsequently, the material was transferred to 100% DMM for 20 min, before it was CO₂ critical point dried using a CPD 030 critical point dryer (BAL-TEC AG, Balzers, Liechtenstein). The dried samples were mounted on aluminium stubs using Leit-C and coated with gold with a SPI-Module™ Sputter Coater (SPI Supplies, West-Chester, PA, USA). Images were



Table 1 – List of the species of which the embryographs are displayed in fig. 3.

The classification used for the sections is that of Kükenthal (1936), but the correct names are used for his sections (Larridon et al. 2011a). For the segregate genera we refer to Goetghebeur (1998) and Govaerts et al. (2007, 2011). Three relevant *C₄ Cyperus* species included are indicated.

Supraspecific taxon	Species
<i>C. sect. Alternifolii</i>	<i>C. alternifolius</i> L.
<i>C. sect. Anosporum</i>	<i>C. pectinatus</i> Vahl
<i>C. sect. Cyperus</i>	<i>C. esculentus</i> L. (<i>C₄</i>)
<i>C. sect. Dichostylis</i> sensu Kükenthal (1936)	<i>C. humilis</i> Kunth, <i>C. seslerioides</i> Kunth, <i>C. uncinulatus</i> Schrad. ex Nees, <i>C. michelianus</i> (L.) Link (<i>C₄</i>)
<i>C. sect. Diffusi</i>	<i>C. ajax</i> C.B. Clarke, <i>C. diffusus</i> Vahl
<i>C. sect. Elegantes</i>	<i>C. constanzae</i> Urb., <i>C. elegans</i> L. (<i>C₄</i>), <i>C. gardneri</i> Nees
<i>C. sect. Fusci</i>	<i>C. dichrostachyus</i> Hochst. & A. Rich., <i>C. difformis</i> L., <i>C. haematocephalus</i> Boeck. ex C.B. Clarke, <i>C. fuscus</i> L., <i>C. reduncus</i> Hochst. ex Boeck., <i>C. submicrolepis</i> Kük., <i>C. unicolor</i> Boeck.
<i>C. sect. Graciles</i>	<i>C. gracilis</i> R.Br., <i>C. tetraphyllus</i> R.Br.
<i>C. sect. Haspani</i>	<i>C. decidiuus</i> Boeck., <i>C. haspan</i> L.
<i>C. sect. Incurvi</i>	<i>C. fertilis</i> Boeck., <i>C. mapanioides</i> C.B. Clarke, <i>C. simplex</i> Kunth
<i>C. sect. Leucocephali</i>	<i>C. tenerrimus</i> J. Presl & C. Presl
<i>C. sect. Luzuloidei</i>	<i>C. eragrostis</i> Lam., <i>C. incomtus</i> Kunth
<i>C. sect. Pseudanosporum</i>	<i>C. platystylis</i> R.Br.
<i>Courtoisina</i>	<i>Courtoisina assimilis</i> (Steud.) Maquet, <i>Courtoisina cyperoides</i> (Roxb.) Soják
<i>Kyllingiella</i>	<i>Kyllingiella microcephala</i> (Steud.) R.W. Haines & Lye
<i>Oxycaryum</i>	<i>Oxycaryum cubense</i> (Poepp. & Kunth) Palla

obtained on a Jeol JSM-6360 (Jeol, Tokyo) at the Laboratory of Plant Systematics (K.U. Leuven). Since in *Cyperus* s. lat. most spikelets have many flowers, and consequently in order to avoid the use of abstract numbers, (flower subtending) glumes are numbered from young (1) to old (x).

Anatomy

For detailed anatomical observation of mature nutlets, FAA-fixed material was dehydrated in a graded ethanol series, embedded in Technovit 7100 resin (Heraeus Kulzer, Wehrheim, Germany), sectioned, stained and mounted following Leroux et al. (2007). Phloroglucinol/HCl staining was performed on hand-cut sections using 2% (w/v) phloroglucinol in 95% (v/v) ethanol for 5 min, and subsequently mounting in 33% (v/v) hydrochloric acid. Sections were observed with a Nikon Eclipse E600 microscope and images were recorded using a Nikon digital camera DXM1200.

For determination of suberin presence we applied a berberine/aniline blue fluorescent staining procedure as described by Brundett et al. (1988). Sections were first stained in 0.1% (w/v) berberine hemi-sulphate (Sigma; C.I. 75160) for 1 hour. After thorough washing, sections were stained with 0.5% (w/v) aniline blue (Sigma, C.I. 42755) for 30 min, washed with distilled water, and mounted in a glycerol-

based anti-fade solution (Citifluor AF1, Citifluor Ltd., UK). Immunofluorescence was observed with an epifluorescence microscope equipped with UV-illumination (Olympus BX-51). Untreated sections were observed as control for intrinsic autofluorescence.

RESULTS

Habit and habitat

The taxa treated in this paper and the habitats in which they occur are illustrated in fig. 2. *Cyperus pectinatus*, *Courtoisina cyperoides* and *Oxycaryum cubense* and their related species occur in wetlands. *Courtoisina cyperoides* grows rooted in mud, e.g. in swamps (fig. 2C) and in rice fields (fig. 2D). *Cyperus pectinatus* (fig. 2B) and *Oxycaryum cubense* (fig. 2F) grow in floating mats in open water. *Cyperus pulchellus* (*Cyperus* sect. *Leucocephali*) and its related species have a preference for seasonally dry grasslands (fig. 2G) which is atypical for *C₃ Cyperus*. Species of *C. sect. Leucocephali* and the segregate genus *Kyllingiella* are characterised by the presence of whitish capitate inflorescences (fig. 2H) and show adaptations to their dryer environment (often thickened base and/or remaining old leaf sheaths).

◀ **Figure 2** – A, inflorescence of *Cyperus pectinatus* (picture taken by M. Reynders in Madagascar); B, habitat of *C. pectinatus* (picture taken by W. Huygh in Madagascar); C, habitat and D, inflorescence of *Courtoisina cyperoides* (pictures taken by A.M. Muasya in Madagascar); E, inflorescence and F, habitat of *Oxycaryum cubense* (pictures taken by R. Carter in Lowndes County, Georgia, U.S.A.); G, habitat and H, inflorescence of *Cyperus pulchellus* (pictures taken by W. Huygh in Madagascar).

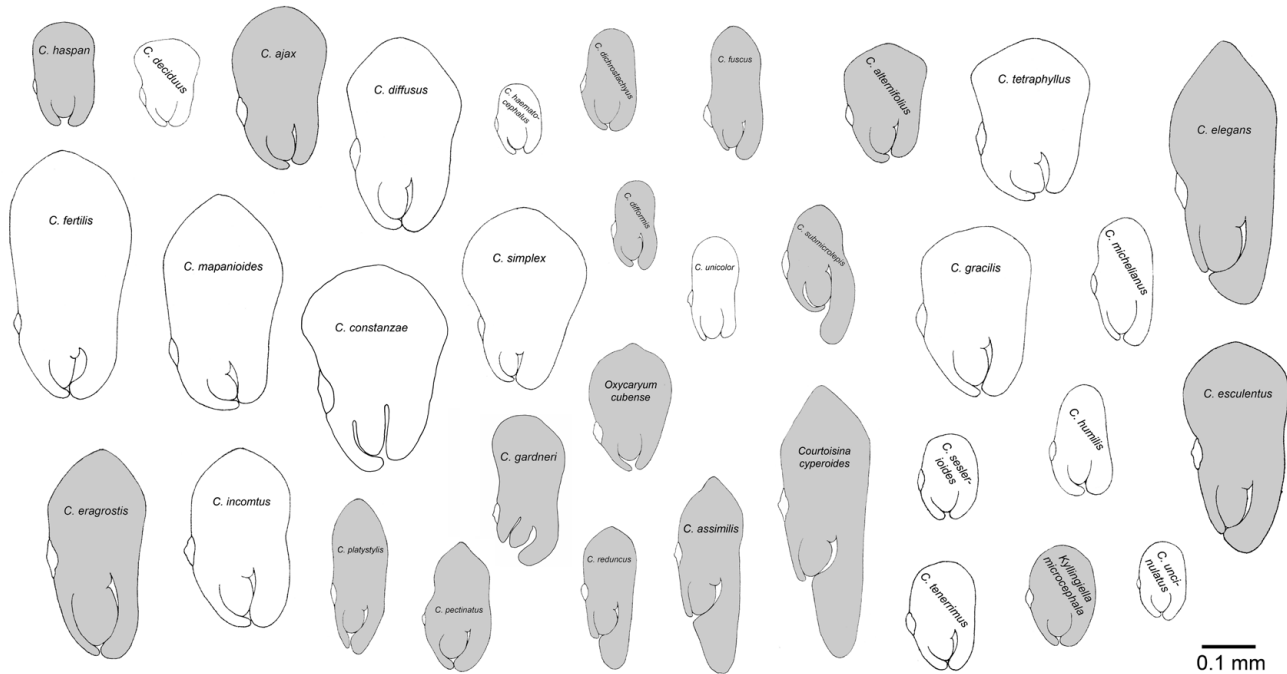


Figure 3 – Embryographs of *C. constanzae* (Ekman 6879, K) and *C. gardneri* (Schessl 3316, GENT) (own data) and relevant species studied by Van der Veken (1965). Species of which the embryos are in grey were included in the molecular phylogenetic study of Larridon et al. (2011b).

Embryography

The embryos of 31 *C*₃ *Cyperus* species and of three relevant *C*₄ *Cyperus* species (*C. elegans*, *C. esculentus* L. and *C. michelianus*) are displayed in fig. 3 and listed in table 1. The embryographs of *C. constanzae* and *C. gardneri* were newly produced for this study, the other 32 were published in Van der Veken’ study (1965). The embryographs are shown according to their known (grey = included in the molecular study of Larridon et al. 2011b) or inferred relationships.

The embryos of *C. sect. Haspani* species are small and inconspicuous in shape. In *C. sect. Diffusi*, *C. sect. Incurvi* and *C. sect. Luzuloidei*, the embryos are noticeably larger and have a slightly asymmetrical development of the coleoptile. The embryo of *C. constanzae* (placed in a section with *C. elegans* (*C*₄) by Kükenthal 1936) shows the most resemblance to the embryos of species of *C. sect. Diffusi* and *C. sect. Incurvi*. The embryograph of *C. elegans* is also shown; its shape and size are typical for most *C*₄ *Cyperus* species (illustrated here by the embryograph of the *C*₄ *Cyperus* species *C. esculentus*, lectotype of the name *Cyperus* L.).

The embryos of *C. sect. Pseudanosporum*, *C. sect. Anosporum*, *C. reduncus* Hochst. ex Boeck., *Courtoisina*, *C. gardneri*, *Oxycaryum* and *C. sect. Fusci* are overlaid onto clade 3 of the Bayesian inference tree of Larridon et al. (2011b) (figs 1 & 4). The embryo of *Cyperus reduncus* is very similar to that of two *Courtoisina* species (characterised by the strongly asymmetrical development of the coleoptile). The embryos of *Courtoisina* and *Cyperus reduncus* share further similarities with those of *C. sect. Anosporum* and *C. sect. Pseudanosporum* sensu Kükenthal (1936) and with those

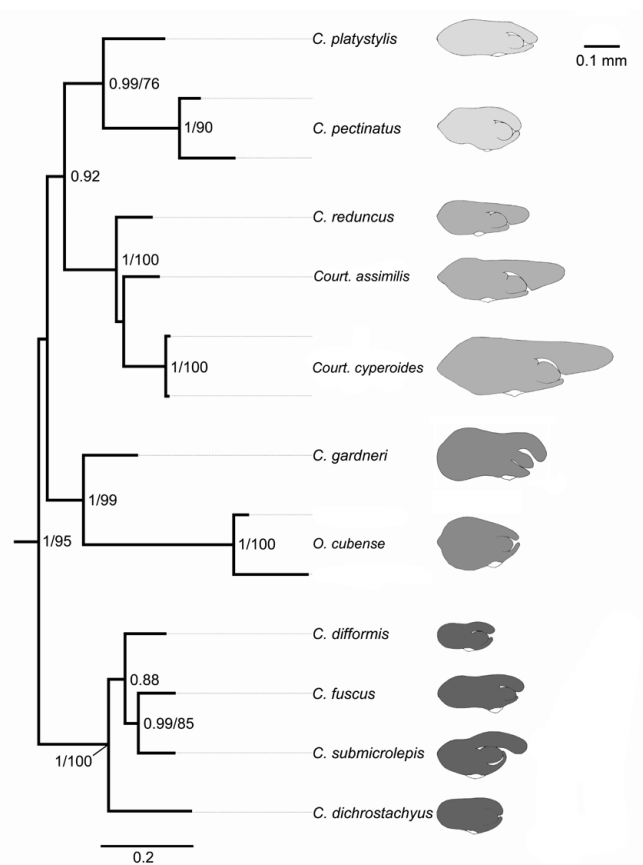


Figure 4 – Embryographs overlaid onto clade 3 (*Anosporum–Courtoisina–Oxycaryum–Cyperus* sect. *Fusci* clade) of the Bayesian inference tree of Larridon et al. (2011b).

Table 2 – Voucher data and origin of the C_3 *Cyperus* species used in the ontogenetic study.

Species	Voucher	Origin
<i>Courtoisina assimilis</i> (Steud.) Maquet	Larridon et al. 2009-0001 (GENT)	Kenya
<i>Courtoisina cyperoides</i> (Roxb.) Soják	Larridon et al. 2010-0261 (GENT)	Madagascar
<i>Cyperus colymbetes</i> Kotschy & Peyr.	Mwachala 341 (EA)	Kenya
<i>Cyperus pectinatus</i> Vahl	Larridon et al. 2010-0265 (GENT)	Madagascar
<i>Cyperus pulchellus</i> R.Br.	Muasya 2131 (EA)	Kenya
<i>Kyllingiella polyphylla</i> (A.Rich.) Lye	Muasya 2435 (EA)	Kenya
<i>Oxycaryum cubense</i> (Poepp. & Kunth) Palla	Mwachala 340 (EA)	Kenya

of *Oxycaryum cubense* and *C. gardneri*. The embryos of the species of *C.* sect. *Fusci* are also very similar; a small embryo with a tendency towards an asymmetrical development of the coleoptile.

The embryos of *C. gracilis* and *C. tetraphyllus* (*C.* sect. *Graciles*) show resemblance both to the embryo of *C. alternifolius* (shape) and to some of the embryos of *C.* sect. *Diffusi* and *C.* sect. *Incurvi* (size). *Cyperus tenerrimus* and *Kyllingiella microcephala* have embryos which are very similar in shape and size. The embryos of *C. humilis*, *C. seslerioides* and *C. uncinulatus* are rather small and show resemblance both to the embryos of *C. tenerrimus* and *K. microcephala* and to the smaller embryos of *C.* sect. *Fusci* species (*C. haematocephalus*, *C. difformis* and *C. dichrostachyus*). The embryo of *C. humilis* is conspicuously shaped. The embryograph of *C. michelianus* is also displayed in fig. 6 to illustrate its difference to the embryos of the C_3 *Cyperus* species of *C.* sect. *Dichostylis* sensu Kükenthal (1936).

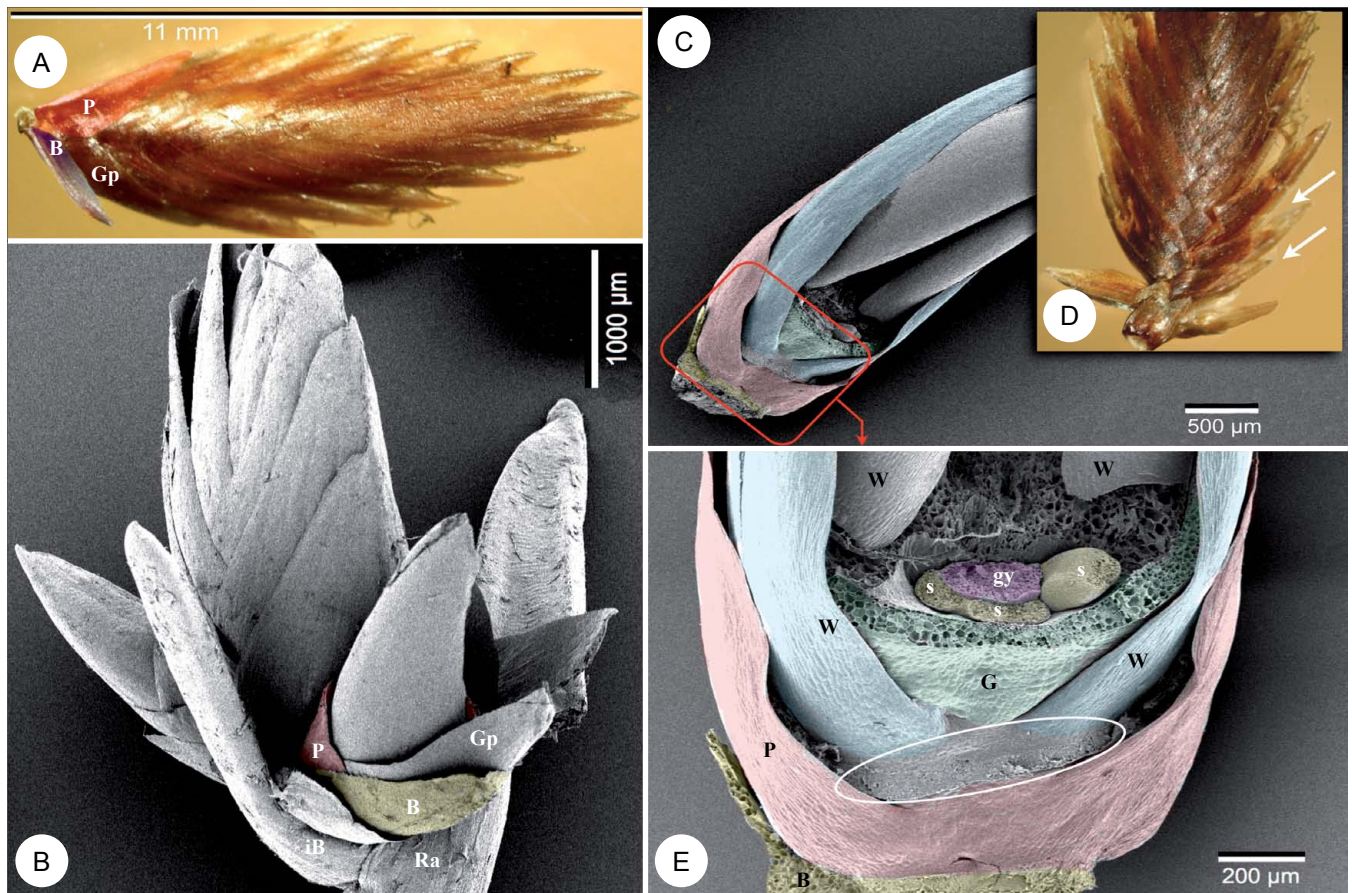
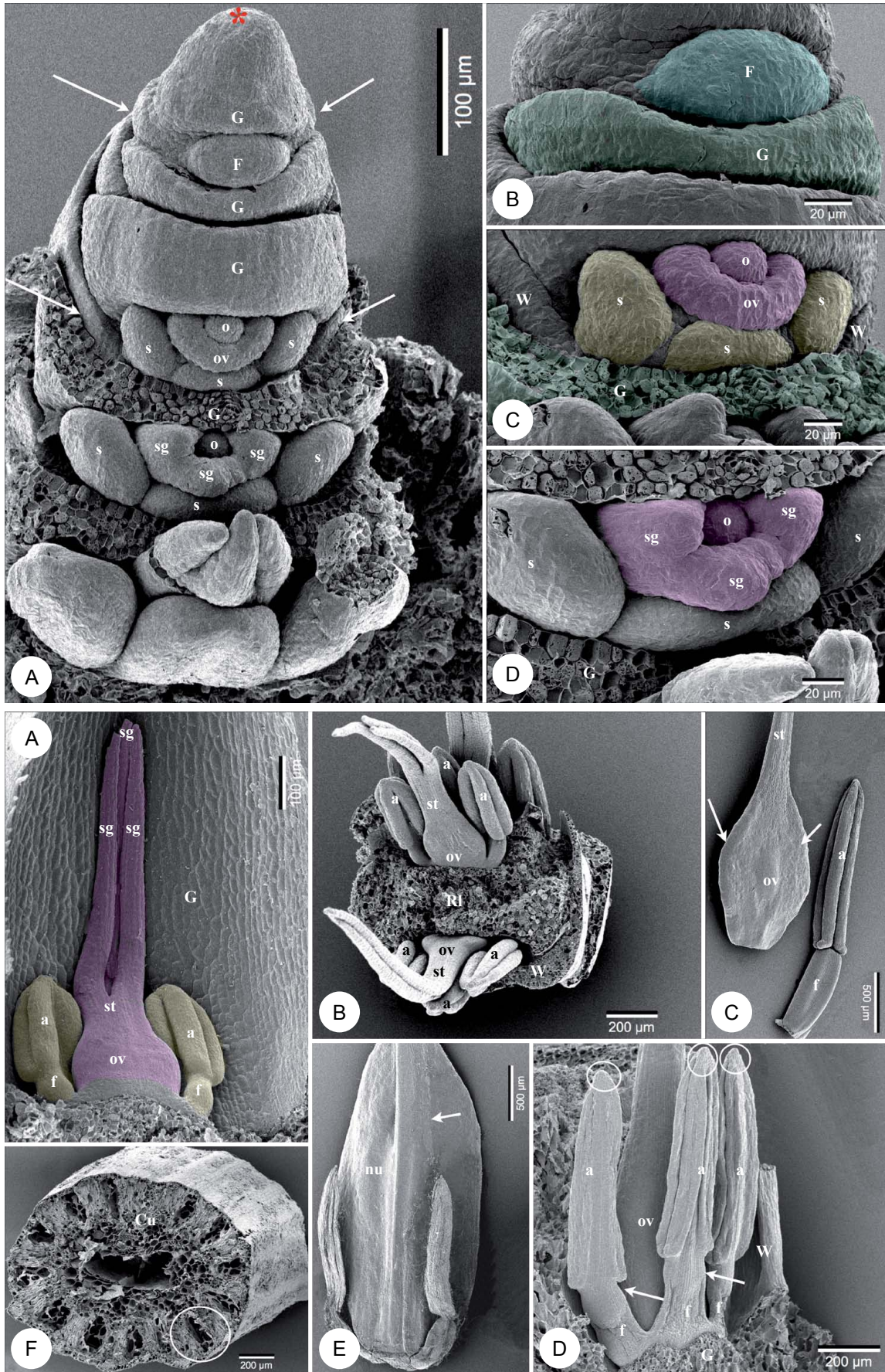


Figure 5 – SE micrographs and macroscopic images of spikelets in *Cyperus pectinatus*. A, spikelet subtended by a bract, with proximally the spikelet prophyll, followed by numerous glumes; B, part of partial inflorescence with a rachis and involucre bract, and some spikelets (the prophyll of one of the spikelets is coloured red, the bract subtending the spikelet yellow); C–E, proximal part of a spikelet, with in yellow, the bract subtending the spikelet, in red the spikelet prophyll [proximally, several glumes are empty (D, arrowed); alternating with the prophyll, only a scar of the proximal glume can be observed (E, encircled); the next glume is coloured in blue; the wings of this glume envelop the alternate, higher glume (coloured green); in the axil of the green coloured glume, the scars of floral parts are visible (stamens and gynoecium, coloured respectively yellow and purple)].

Abbreviations: B, bract; G, glume; Gp, proximal glume; gy, gynoecium; iB, involucre bract; P, prophyll; Ra, rachis; s, stamen; W, wing.



◀ **Figure 6** – SE micrographs of the earliest floral ontogenetic stages in *Cyperus pectinatus*. A, distal part of a developing spikelet with glumes subtending a flower at different developmental stages; the spikelet apex is open, and immediately below it, successively and alternately, new glume primordia appear, so that the oldest glumes and flowers are situated proximally [at both sides of each flower, the wings of the alternate, higher glume are visible (arrowed)]; B, detail of new glume primordium (coloured green), with in its axil a yet undifferentiated flower primordium (coloured blue); C, later stage of floral development, with already visible three stamen primordia (coloured yellow), and a primordial gynoeceium (coloured purple) consisting of an annular ovary primordium surrounding a central ovule primordium; D, idem as in “C”, later developmental stage; the ovary wall is growing up and enveloping the central ovule; on the top of the ovary wall, two adaxially situated and one basial stigma primordia appear.

Abbreviations: F, flower primordium; G, glume (primordium); o, ovule primordium; ov, ovary wall primordium; s, stamen (primordium); sg, stigma primordium; W, wing; *, rachilla apex.

◀ **Figure 7** – SE micrographs of the floral ontogeny in *Cyperus pectinatus*. A, adaxial view of a developing flower; style and stigma branches are growing (purple), while the formation of anther and filament in the two stamens (yellow) is completed; B, apical view of a section through the middle part of a developing spikelet [two alternate flowers are visible, and the wing of a higher glume (arrowed)]; C, semi-mature pistil and stamen [along the ribs of the pistil, formation of cork is starting (arrowed)]; D, lateral-abaxial view of semi-mature flower with three stamens [on the top of each anther, a small apiculus is formed (encircled); below the anthers, the connective continues in the upper part of the filament (arrowed); at this stage, filaments are fused at their bases]; E, nutlet with three persistent withered stamens (notice that the stamens in these samples remain small with respect to the gynoeceium); F, section through a hollow culm, with large peripheral cavities. Abbreviations: a, anther; Cu, culm; f, filament; G, glume; nu, nutlet; ov, ovary wall primordium; RI, rachilla; sg, stigma primordium; st, style; W, wing.

Morphology and spikelet and floral ontogeny

Cyperus* sect. *Anosporum* and *C. sect. Pseudanosporum – Spikelets of *Cyperus pectinatus* and *C. colymbetes* are distichously organised (figs 5 & 8). Lateral spikelets are subtended by a bract (fig. 5A & B), have a spikelet prophyll (fig. 5A–C), and the first glumes are empty (fig. 5D). In *C. pectinatus*, the proximal glume can be dehiscent, with only a scar of it remaining in the spikelet (fig. 5E). The spikelet of *C. pectinatus* and *C. colymbetes* has an indeterminate rachilla (fig. 6A, fig. 8A & B). Immediately below the rachilla apex, new glumes originate alternately (fig. 6A, fig. 8A & B). Soon, in the axil of a newly originated glume, a flower primordium appears (figs 6B & 8B). The flower primordium differentiates into two adaxially situated and one abaxially situated stamen primordia, the latter being slightly retarded (figs 6C & 8C). At this stage, a gynoeceium is originating from an annular ovary wall primordium surrounding a central ovule primordium (figs 6C & 8C). Next, on the top of the raising ovary wall, opposite the stamen primordia, three stigma primordia appear (figs 6D & 8D). Subsequently, the stamen primordia differentiate into filament and anther, while the ovary wall envelops the central ovule, forming a style. The stigma branches grow up, protruding highly above the stamens (fig. 7A & B, fig. 8D & E). At this stage, the formation of a corky tissue along the ribs of the ovary begins (fig. 7C). On the top of the anthers, a small, unobscure apiculus is formed (fig. 7D & E). In the specimens studied, the stamens remain small compared to the gynoeceium (fig. 7E). The culm is hollow, and large peripheral cavities are formed (fig. 7F).

Figure 9 shows the nutlets of the three species included in *Cyperus* sect. *Anosporum* by Kükenthal (1936), *C. cephalotes* (fig. 9A), *C. colymbetes* (fig. 9B) and *C. pectinatus* (fig. 9C), and of the single species of *C. sect. Pseudanosporum*, *C. platystylis* (fig. 9D). Corky thickenings are obvious on the nutlets of all four species. In *C. cephalotes*, *C. colymbetes* and *C. pectinatus* the thickenings are concentrated at the base of the nutlets (fig. 9A–C), in *C. platystylis* the corky tissue is more evenly present along the three ridges of the trigonous nutlet (fig. 9D).

A transverse section through a mature nutlet of *C. pectinatus* shows the embryo surrounded by a sclerified pericarp, as well as two lateral ridges consisting of parenchymatous cells (fig. 9E). To confirm the ‘corky’ nature of these lateral ridges we performed a berberine/aniline blue fluorescent staining procedure, which has widely been used to stain suberised and lignified cell walls (Brundrett et al. 1988). As suberin is the main constituent of cork this dye was used to check the presence of suberin in the lateral ridges. Berberine/aniline blue stained cell walls in the ridges yellowish green (fig. 9F), whereas unstained control sections only displayed weak autofluorescence (fig. 9G), suggesting that cell walls in the ridges are suberised and/or lignified. The negative phloroglucinol/HCl test (data not shown) and the absence of blue-autofluorescence in the parenchymatous cells of the ridges (fig. 9H) further suggested that these are non-lignified. In conclusion, these experiments suggest that the ridges of the nutlets of *C. pectinatus* are suberised and that the nutlets can indeed be called ‘corky’.

Courtoisina* and *Cyperus reduncus – In *Courtoisina cyperoides*, spikelets are grouped in clusters, each subtended by a bract (fig. 10A). A spikelet cluster results from prophyll branching, i.e. in the spikelet prophyll, a secondary, tertiary etc. axis originates (fig. 10B–D). In both species, glumes have pronounced wings and a conspicuous mucro (e.g. in fig. 10E). The glumes are distichous upon an indeterminate rachilla (e.g. in fig. 11A) and subtend each a flower. The flower consists of a trimerous ovary and three stamens, which, at the early ontogenetic stages, grow faster than the gynoeceium (fig. 11B), but later the developing stigma branches protrude above the stamens (fig. 11C). The ovary develops into a long trimerous nutlet (fig. 11D).

The spikelets and nutlets of *Cyperus reduncus* (fig. 12A & B), *Courtoisina assimilis* (fig. 12C & D) and *Courtoisina cyperoides* (fig. 12E & F) are shown in fig. 12. The fusiform shape of the nutlets of these species is unusual in Cyperaceae. The glumes of all three species are mucronate. The spikelets in all three species are deciduous as a unit at maturity. However, in *Cyperus reduncus* the spikelets also break up easily in between the glumes.

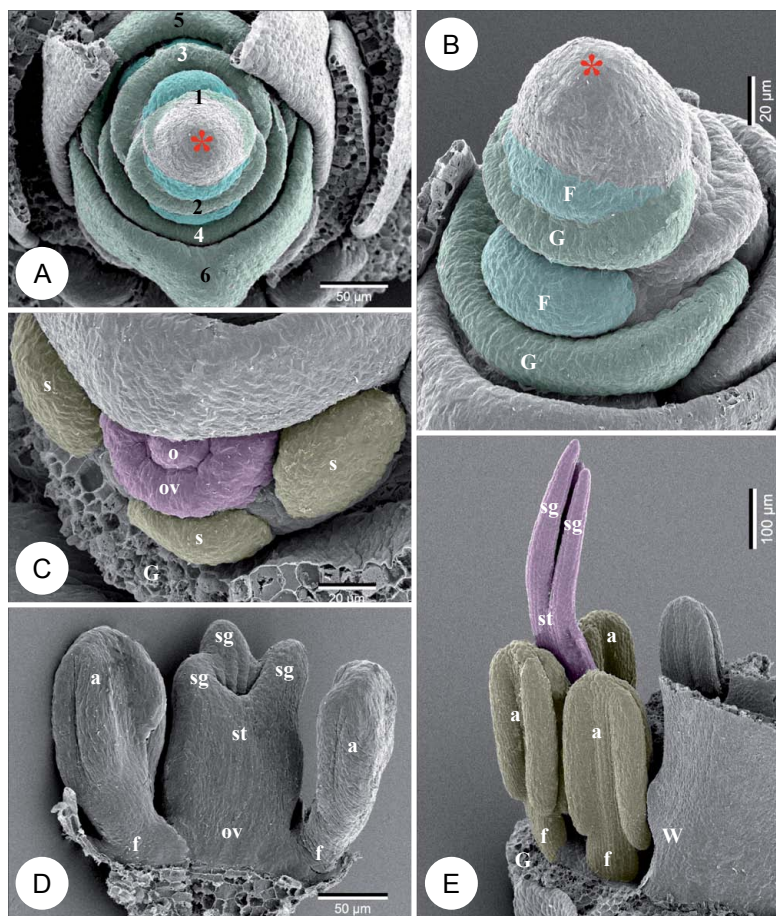


Figure 8 – SE micrographs of the floral ontogeny in *Cyperus colymbetes*. A, apical view of a distichously organised spikelet with indeterminate rachilla apex, with glumes and the flowers they subtend at different developmental stages (“1” is the most recent glume primordium); B, detail of the distal part of a spikelet, with the open rachilla apex and two glumes (green) with each in the axil an undifferentiated flower primordium (blue); C, detail of a developing flower at early ontogenetic stage; D, adaxial view of a developing flower; at this stage, the rising ovary wall envelopes the central ovule, and two adaxial and one abaxial stigma primordia are present on the top of it; the stamen primordia are differentiating into filament and anther; E, lateral view of a developing flower (stamens are coloured yellow, the gynoecium purple; a wing of a higher, alternate glume is visible).

Abbreviations: a, anther; f, filament; F, flower primordium; G, glume (primordium); o, ovule primordium; ov, ovary wall primordium; s, stamen; sg, stigma primordium; st, style; W, wing; *, rachilla apex.

Oxycaryum* and *Cyperus gardneri – The spikelets of *Oxycaryum cubense* are spirally organised, with numerous glumes, each subtending a flower (fig. 13A & B). Along the rims of the glumes, hairs with a length of more than 0.5 mm grow (fig. 13C). The rachilla is indeterminate (fig. 13B). New glumes originate immediately below the rachilla apex in a tristichous arrangement, and in the axil of a new glume, soon a flower primordium appears (fig. 13D & E). The flower primordium differentiates into three stamen primordia, two adaxial and an abaxial one, and an annular ovary wall primordium surrounding a central ovule primordium (fig. 13F). On the top of the ovary wall, two laterally situated stigma primordia appear (fig. 14A). The stigma primordia grow out into stigma branches, soon protruding above the developing stamens (fig. 14B–E). Simultaneously, the stamen primordia differentiate into filament and anther. On the top of the anthers, a conspicuous apiculus is formed (fig. 14D). At this stage, the glumes are well developed, with a large mucro (fig. 14E). Subsequently, the style and stigma branches elongate further, being forced to fold within the available space within the glume subtending the flower, with the stamens remaining relatively small (fig. 14F & G).

Figure 15 shows a spikelet and nutlets of *Cyperus gardneri* (fig. 15A & B) and a spikeletcluster and nutlet of *Oxycaryum cubense* (fig. 15C & D). In *C. gardneri*, the glumes are distichously arranged and the nutlets are trigonous (trimerous gynoecium). In *O. cubense*, the glumes are spirally-arranged and the nutlets appear awkwardly flattened (dorsiventrally

flattened dimerous gynoecium). Both species show corky thickenings on the nutlets (fig. 15B & D). The branching pattern and general appearance of the inflorescences of these species also shows similarities.

Cyperus* sect. *Leucocephali* and *Kyllingiella – In *Cyperus pulchellus*, the spikelets are organised in clusters, each cluster being subtended by a bract (fig. 16A). A cluster originates by prophyll branching, where in the axil of the prophyll of the main spikelet a secondary spikelet originates, which at its turn has a tertiary spikelet in the axil of its prophyll, and so on (fig. 16B & C). The glumes are distichously placed, with each flower surrounded by the wings of the alternate, higher glume (fig. 16D & E).

In *Kyllingiella polyphylla*, spikelets have spirally-arranged, elongate glumes which envelop the whole spikelet (fig. 17A). The rachilla is indeterminate, and immediately below its apex, new glumes originate in a spiral sequence (fig. 17B & C). Soon, in the axil of a new glume, a flower primordium originates, which differentiates into a stamen primordium and a floral apex (fig. 17C–E). The stamen primordium enlarges, becoming as large as the developing gynoecium, followed by the formation an anther and filament (fig. 18A & B). Meanwhile, the ovary wall envelops the central ovule, and on its top, two lateral, or three (two adaxially and one abaxially situated) stigma primordia are visible (fig. 18B–E). When there are three stigma branches, this can also be the result of the splitting of one of the two originally formed stigma branches (fig. 18E). Flowers can also have two stamens (fig.

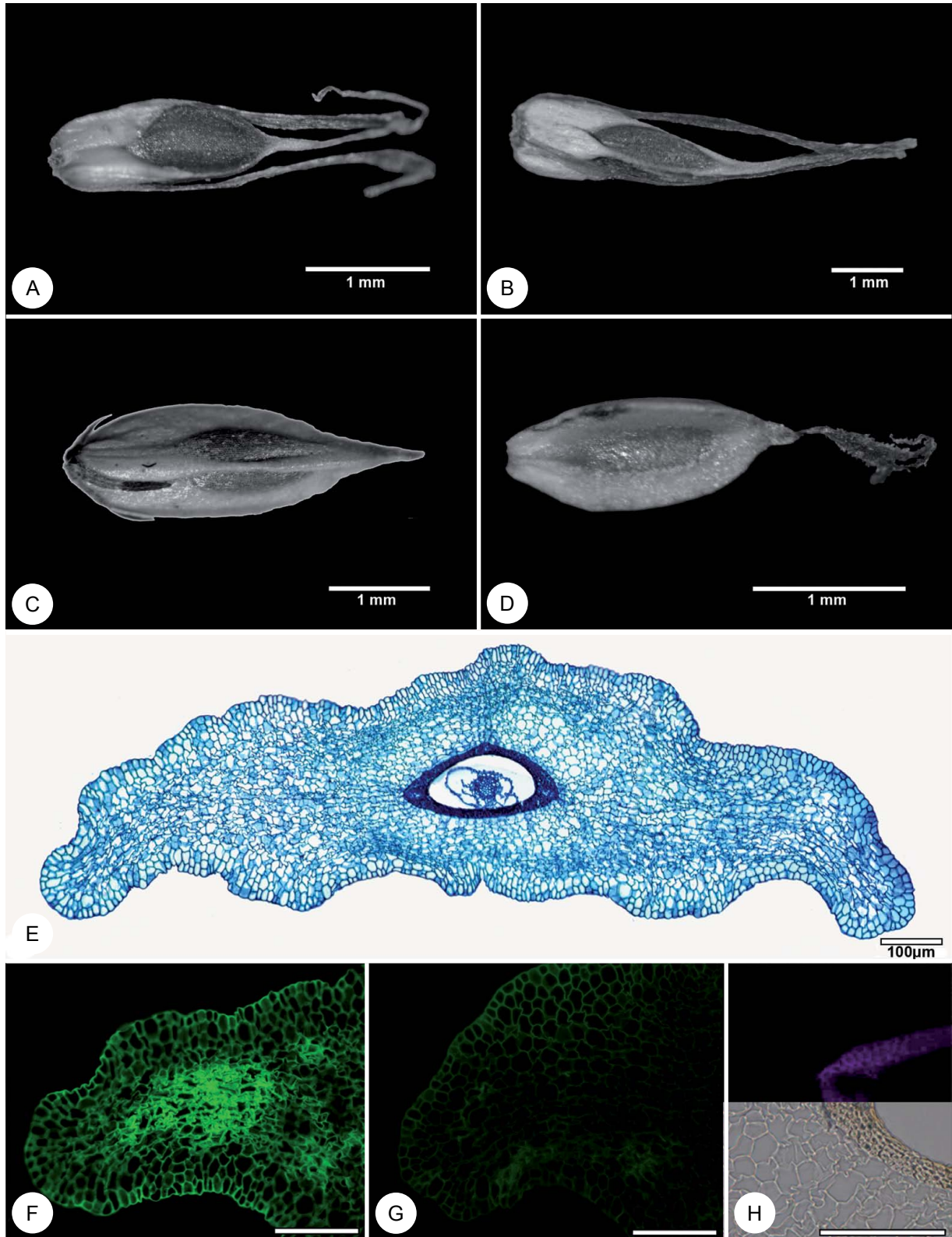
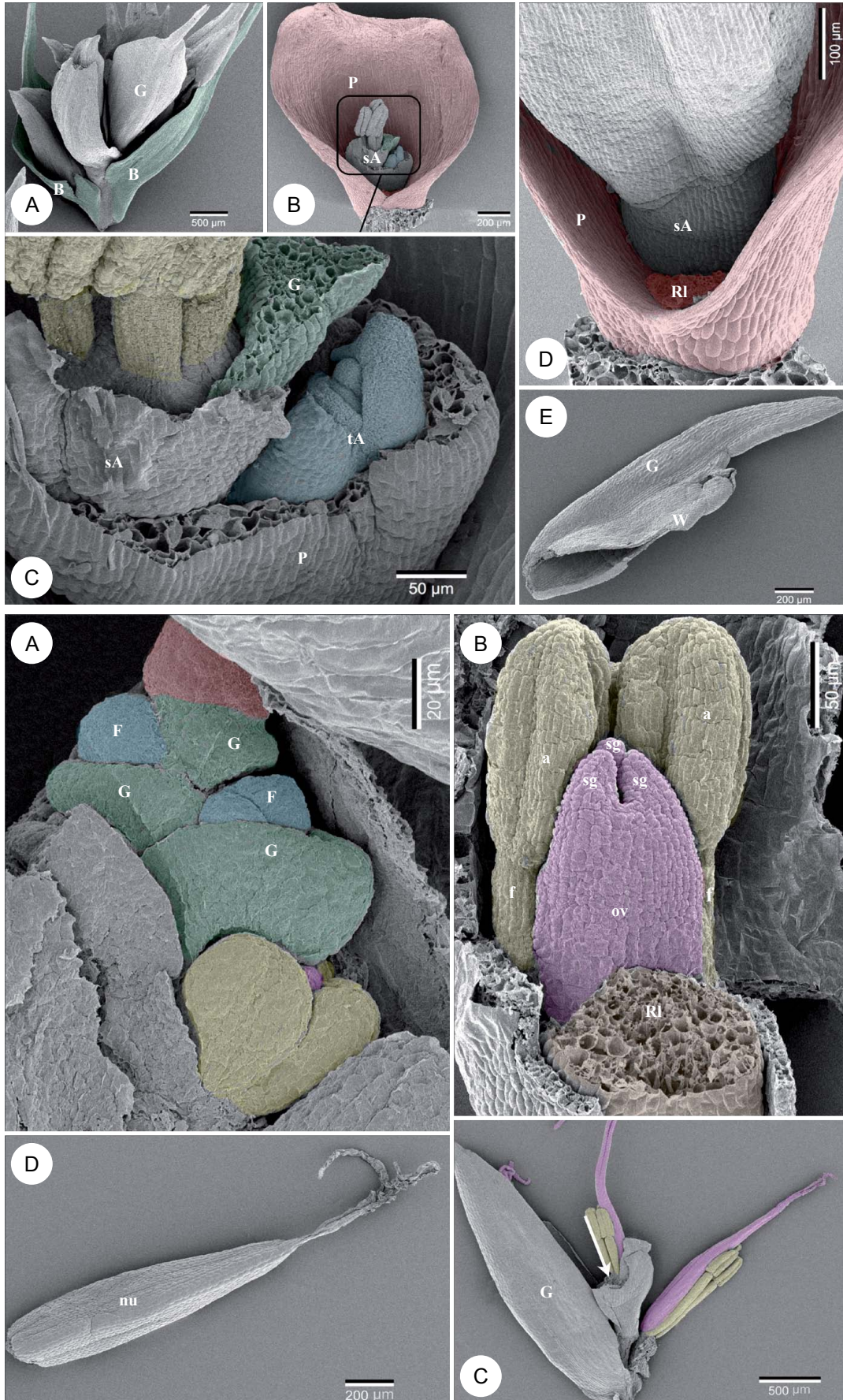


Figure 9 – A, nutlet with undivided style and two remaining stamens of *C. cephalotes* (Heckman 166, K); B, nutlet with part of style and two stamens remaining of *C. colymbetes* (Denny 1283, GENT); C, nutlet of *C. pectinatus* (De Wolf 92-86, GENT); D, nutlet of *C. platystylis* (Goetghebeur 6684, K); E, transverse section through a mature nutlet of *C. pectinatus* (Larridon et al. 2010-0265, GENT); F, berberine-aniline blue stained section showing yellowish green stained cell walls; G, unstained control sections showing weak autofluorescence; H, combined image showing blue autofluorescence of lignified sclerenchyma (top panel) and bright-field image of the same section (bottom panel).



◀ **Figure 10** – SE micrographs of the spikelet structure and development in *Courtoisina cyperoides*. A, two bracts (green), each subtending a spikelet-cluster; B–C, spikelet prophyll (red), subtending a secondary spikelet (sA) of which the proximal part is visible [the prophyll of the secondary axis (not coloured) at its turn subtends a tertiary spikelet (tA, blue)]; D, detail of prophyll branching, the prophyll and rachilla of the main spikelet are coloured in red; E, glume with conspicuous mucro.

Abbreviations: B, bract; G, glume; P, prophyll; RL, rachilla; sA, secondary axis (or spikelet); tA, tertiary axis; W, wing.

◀ **Figure 11** – SE micrographs of the spikelet structure and floral development in *Courtoisina assimilis*. A, distal part of a developing spikelet with the apical zone of the spikelet (red), several distichously placed glumes (green), and the flower primordia each glume subtends (blue); the lowest flower has already three stamen primordia (yellow) and a primordial gynoeceium (purple); B, adaxial view of a developing flower, with on the top of the ovary wall three stigma primordia; at this stage, filaments and anthers are formed; C, part of a spikelet; D, nutlet with persistent style and withered stigma branches (the arrow indicates where the glume is cut).

Abbreviations: a, anther; f, filament; F, flower primordium; G, glume; nu, nutlet; ov, ovary wall primordium; RL, rachilla; sg, stigma primordium.

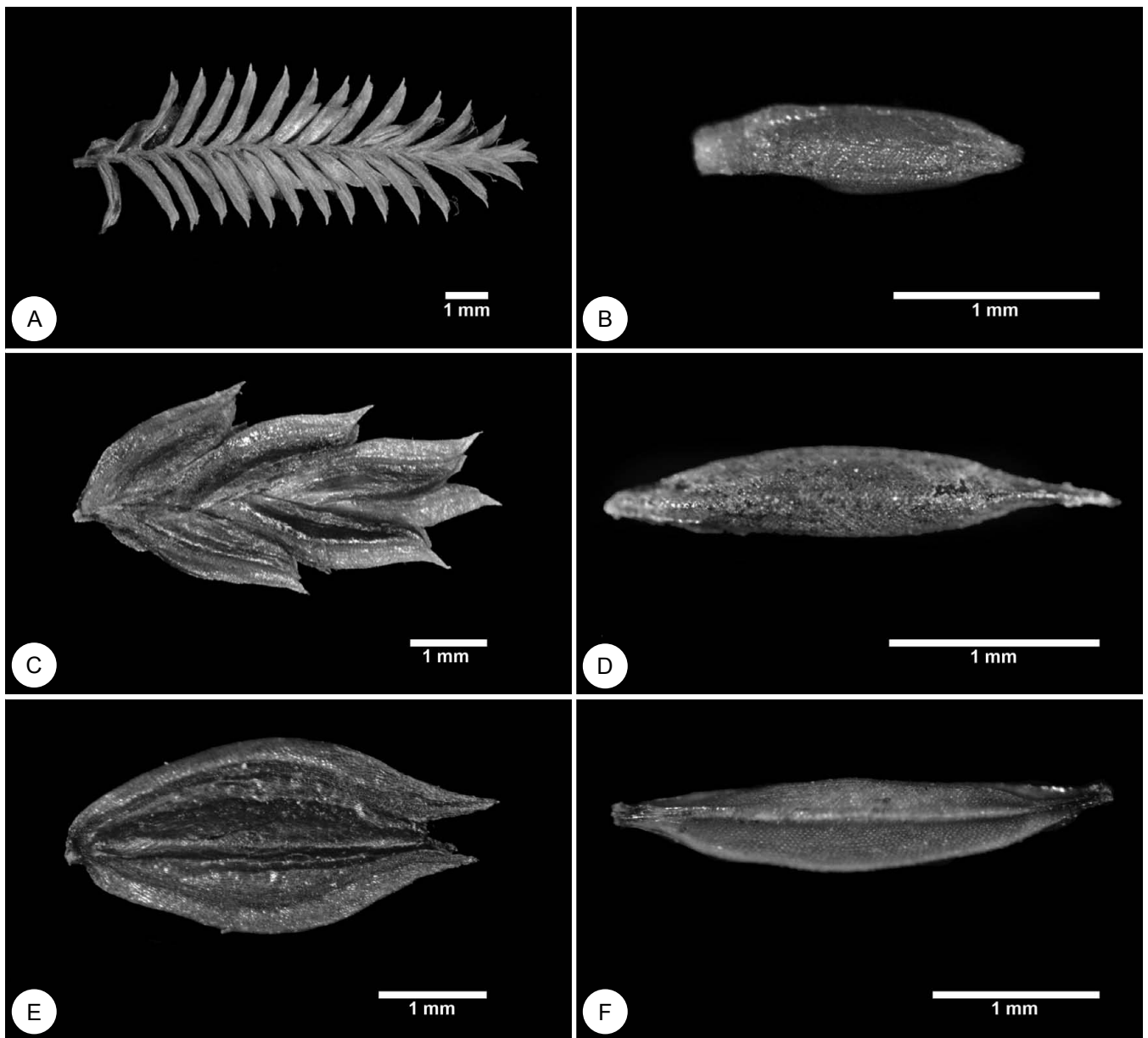
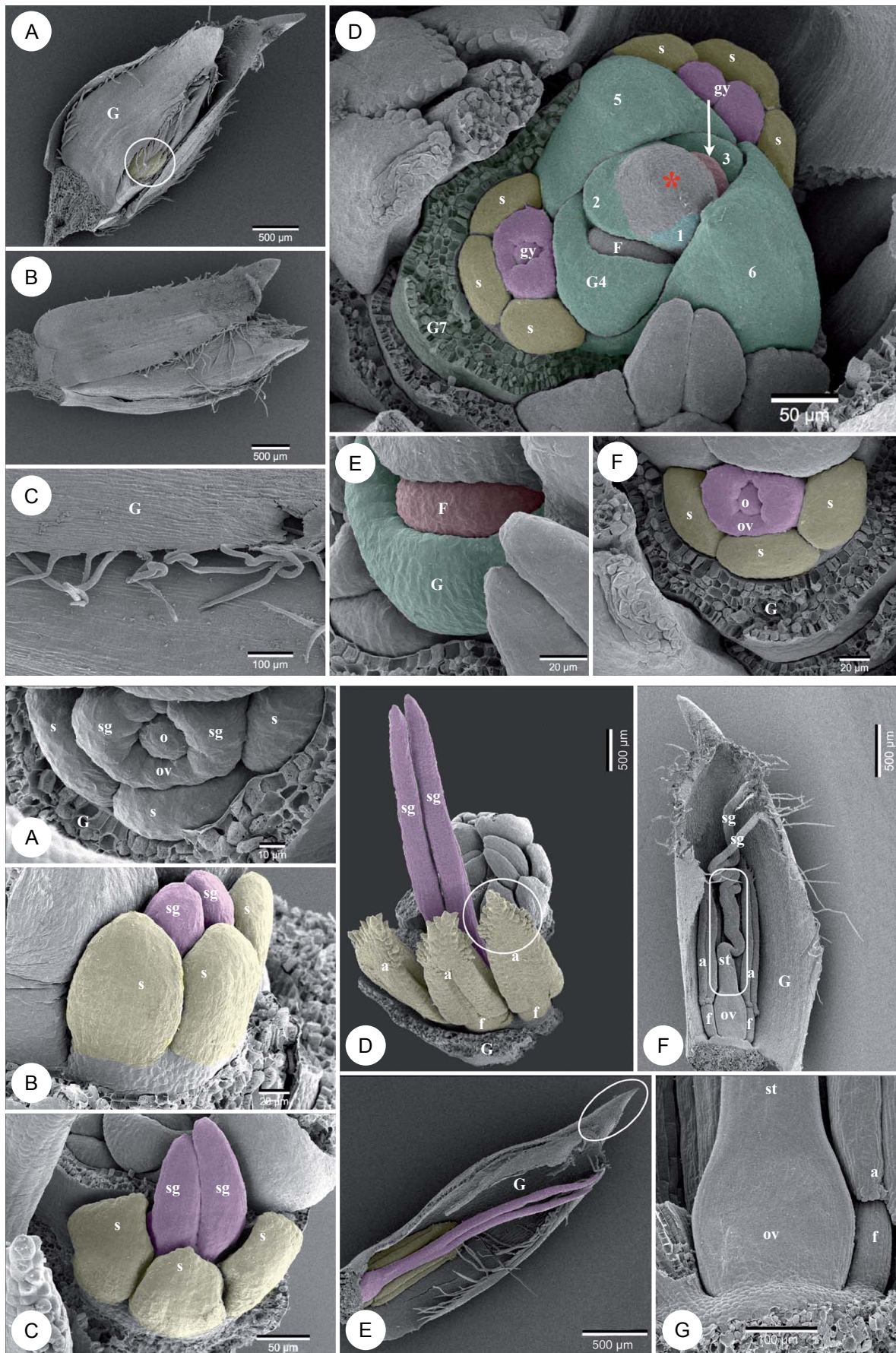


Figure 12 – A, spikelet and B, nutlet of *Cyperus reduncus* (Madsen 6136, GENT); C, spikelet and D, nutlet of *Courtoisina assimilis* (Hooper & Townsend 1588, GENT); E, spikelet and F, nutlet of *Courtoisina cyperoides* (Malaisse & Goetghebeur 161, GENT).



◀ **Figure 13** – SE micrographs of the spikelet structure and floral development in *Oxycaryum cubense*. A–B, spikelets [encircled is a developing flower of which the stamens (yellow) are visible after removing a glume]; C, rim of a glume, with long, curled hairs; D, apical view of a developing spikelet [six (primordia of) intact glumes (green) and the scar of a seventh (G7) are visible, each subtending a flower (primordium); the most recently formed glume immediately under the rachilla apex is coloured blue, the first flower primordium (in the axil of the third glume, arrowed) is coloured red]; E, detail of glume (green) subtending a flower primordium (red); F, apical view of a developing flower, with three stamen primordia (yellow) and an annular ovary wall primordium surrounding a central ovule primordium (purple). Abbreviations: F, flower primordium; G, glume; gy, primordial gynoeceium; o, ovule primordium; ov, ovary wall primordium; s, stamen; sg, stigma primordium; *, rachilla apex.

◀ **Figure 14** – SE micrographs of the floral development in *Oxycaryum cubense*. A, apical view of a developing flower (two stigma primordia originate laterally on the top of the annular ovary wall primordium); B–D, lateral-abaxial view of a developing flower [at these successive stages, the stamen primordia (yellow) start differentiating into anther and filament; the stigma primordia are growing up, forming stigma branches (purple); on the top of each anther, a conspicuous apiculus is formed (encircled)]; E, adaxial view of a semi-mature flower and the glume that subtends it [the glume has a large mucro (encircled)]; at this stage, the gynoeceium (purple), with a long style, is larger than the stamens]; F, idem, at a later stage [the style (encircled) has become so long that style and stigma branches are folded within the available space]; G, detail of the ovary and style base. Abbreviations: a, anther; f, filament; G, glume; gy, primordial gynoeceium; o, ovule primordium; ov, ovary wall primordium; s, stamen; sg, stigma primordium; st, style.

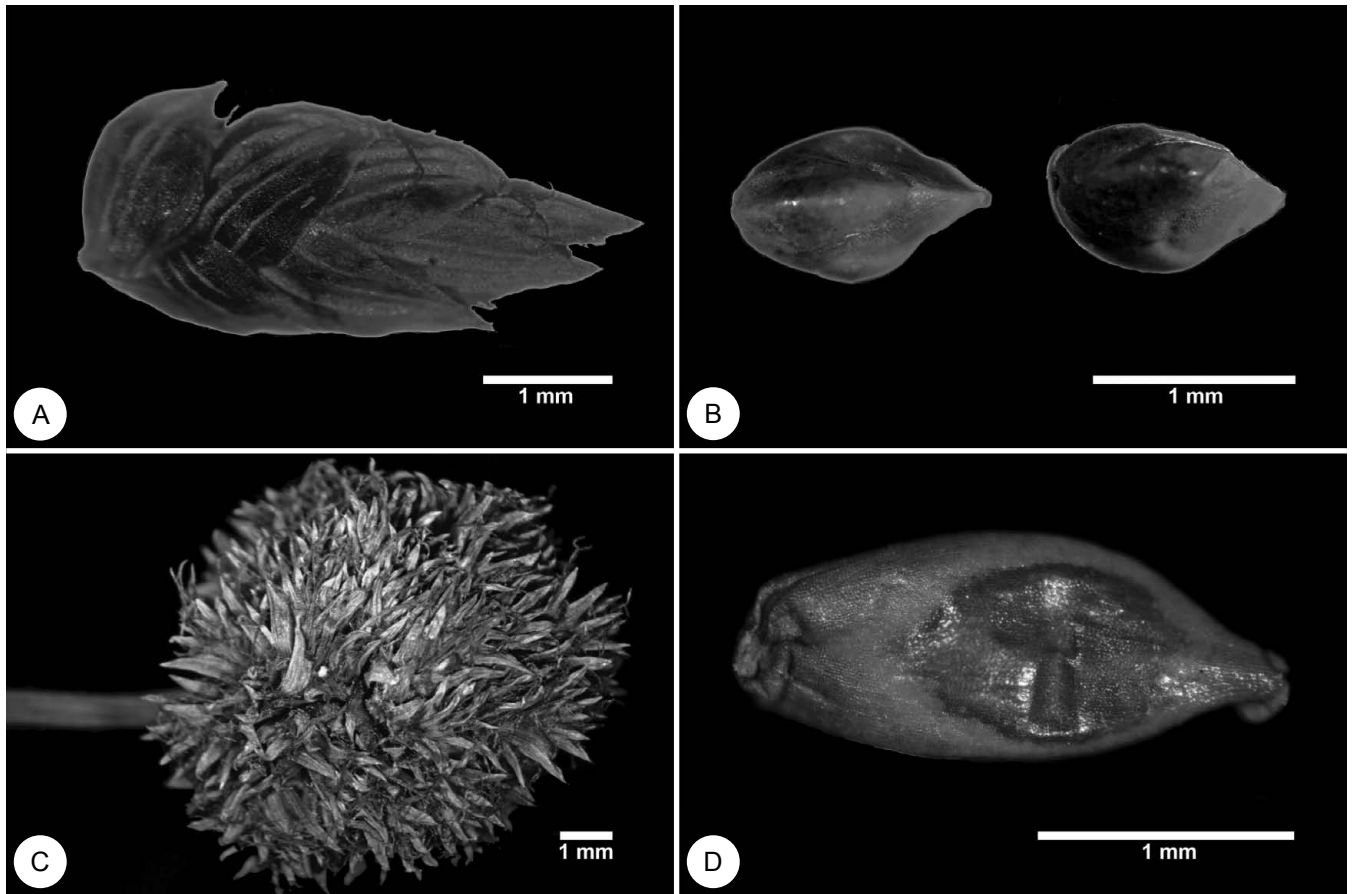


Figure 15 – A, spikelet and B, nutlet of *Cyperus gardneri* (Schessl 3316, GENT); C, partial inflorescence of *Oxycaryum cubense* (Guillen et al. 2257, GENT); D, nutlet of *O. cubense* (Kalliola et al. 2257, GENT).

18C) or two stamen primordia of which only one develops (fig. 18F). The nutlet is obovate (fig. 18G).

DISCUSSION

Spikelet structure

All spikelets studied in C_3 *Cyperus* concur with the spikelet model as proposed by Vrijdaghs et al. (2010). Compared

with our previous study in the C_4 species of *Pycneus* and *C. laevigatus* L. (Vrijdaghs et al. 2011), in the distichous species studied, concaulescence and epicaulescence are less conspicuously present. On the other hand, the flexibility of primordia in the axil of a glume to develop into either a flower or into a secondary spikelet is present C_3 *Cyperus* as well. In *Courtoisina cyperoides* and *Cyperus pulchellus*, prophyll branching occurs, which indicates that prophylls, even in Cyperaceae, still have the potential to form a primordium in their

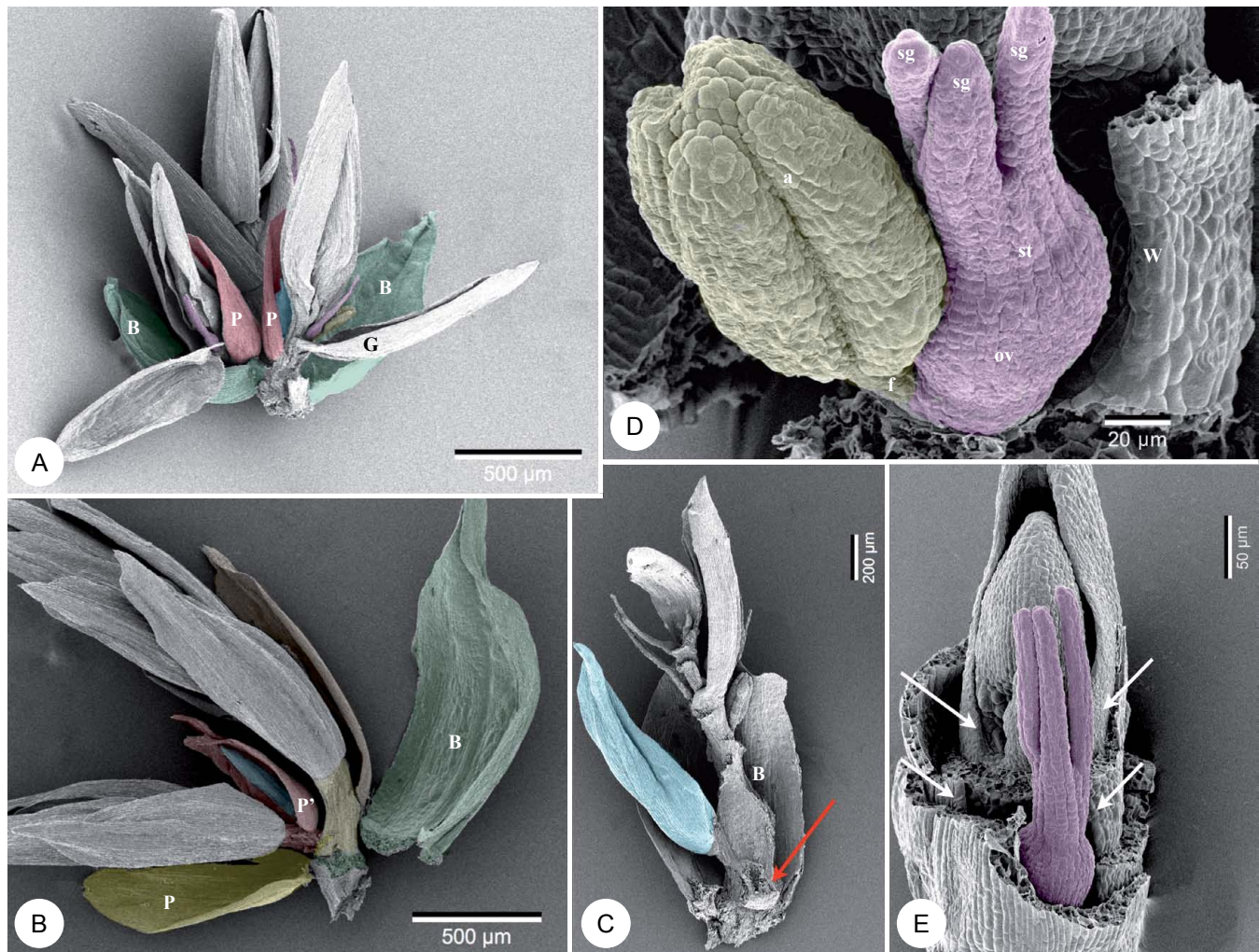


Figure 16 – SE micrographs of spikelet and floral development in *Cyperus pulchellus*. A, two bracts with spikelet clusters resulting from prophyll branching; B, detail of spikelet cluster, with main axis (yellow) in bract (green) [in the prophyll of the main axis (yellow, P), a secondary axis is present (red); in the prophyll of the secondary axis (red, P'), a tertiary axis (blue) can be seen]; C, detail of a spikelet with a secondary spikelet (blue) in the axil of the spikelet prophyll (removed, scar arrowed); D, abaxial view of a developing flower [a single stamen (yellow), a gynoeceum with three stigma branches (purple), and a wing of the higher, alternate flower is visible]; E, abaxial view of the gynoeceum (purple) of a flower of which the stamen is removed [higher, and mostly hidden, is a younger flower (glume removed) and distally a glume hiding the apical part of the spikelet; the wings of the alternate, higher glumes are visible (arrowed)]. Abbreviations: a, anther; B, bract; f, filament; G, glume; ov, ovary wall primordium; P, spikelet prophyll; P', secondary spikelet prophyll; s, stamen; sg, stigma primordium; st, style; W, wing.

axil, and that this primordium can be developed into a secondary axis (spikelet). Prophyll branching in C_3 *Cyperus* was already described by Guarise & Vegetti (2008) for *Cyperus* sect. *Luzuloidei*. In most Cyperoideae, the spikelet prophyll is empty, with exception of Dulichieae and Caricae, where the spikelet prophyll subtends a flower. Whether primordia subtended by a glume (and we consider the spikelet prophyll as a first glume) develop into flower or axis depends on phytohormonal regulation (Smith 1967). One might expect that: (1) presence or absence of a primordium in the axil of a glume/prophyll, (2) development of a primordium subtended by a glume/prophyll into flower or secondary spikelet, in all Cyperoideae are regulated by the same underlying genetic and developmental programmes. In Cyperaceae, the branching flexibility at spikelet level is high compared with the other

cyperoid subtaxa, by prophyll branching or by dedoublement of the spikelet primordium itself, or by the formation of secondary spikelets in the axil of glumes observed in *Pycreus pumilus* (L.) Nees (Vrijdaghs et al. 2011). This slightly blurs the cyperoid spikelet concept as “ultimate inflorescence branch” (Vrijdaghs et al. 2010). In *Cyperus pectinatus*, the prophyll as well as the proximal glumes are empty. Moreover, the first glume alternating with the prophyll may be dehiscent. In such spikelets, an apparently unusual disposition of the prophyll and first glumes can be observed (fig. 5C & E).

Floral ontogeny

All flowers in C_3 *Cyperus* concur with the general cyperoid floral ontogenetic model as proposed by Vrijdaghs et al.

(2009). The perianth is totally absent. Observed conspicuous reduction tendencies in androecium and gynoecium are the reduction of number of stigma branches and of stamens. In *Oxycaryum cubense* and *Kyllingiella polyphylla*, the stigma branches can be reduced from three to two (here, the word “reduction” is perhaps misleading, since in our opinion, it is rather a reorganisation of the gynoecium due to the development of the ovary wall from an annular primordium and to the ontogeny of the vascular bundles which link from the floral organ primordia to the stele; Reynders et al. accepted). In the latter species, the number of stigma branches can be two or three, and if three, this can be either by development from three stigma primordia, or by development from two stigma primordia of which one undergoes splitting during its development (fig. 18B, D & E). In *K. polyphylla*, the number of stamens varies between one and two. Here, a literal meaning can be given to the term “reduction” as shown in figure 19F, where two stamen primordia are formed, but only one develops into a stamen. In *Cyperus pulchellus*, the number of stamens is apparently fixed to one. In the other species studied, like in many other cyperoid species, the development of the abaxial stamen, especially at early ontogenetic stages, may be retarded a little bit with respect to the development of the two adaxial stamens (fig. 16D, fig. 17D & E).

Cyperus sect. *Anosporum* and *C.* sect. *Pseudanosporum*

Based on molecular phylogenetic data (fig. 1) (Larridon et al. 2011b), *Cyperus* sect. *Anosporum* and *C.* sect. *Pseudanosporum* are very closely related. *Cyperus platystylis* is the sister species of *C. pectinatus*. Possibly, *C. platystylis* is an intermediate on the evolutionary lineage leading from a more typical *Cyperus* morphology to the more specialised morphology of the three species included in *C.* sect. *Anosporum* by Kükenthal (1936), i.e. *C. cephalotes*, *C. colymbetes* and *C. pectinatus*. Morphological resemblance between all four species (e.g. tightly imbricate rather glossy and thick glumes), their shared habitat preference (wetlands, fig. 2B) and their adaptations to this habitat (corky nutlets, fig. 9; air cavities, fig. 7F), and embryology (figs 3 & 4) all support the inclusion of *C.* sect. *Pseudanosporum* in a broader circumscribed *C.* sect. *Anosporum* (see Taxonomic treatment). These corky thickenings allow the nutlets to float. The corky nutlets of these species are often distributed inside their glumes and with the short stamens still attached to the base of the nutlet; this might give the nutlets even more buoyancy (air bubble?).

Courtoisina

Although the habit of the two *Courtoisina* species corresponds with that of *Cyperus* s. str., authors as Goetghebeur (1986, 1998), Vorster (1996), Govaerts et al. (2007, 2011) recognised *Courtoisina* as a distinct genus based on the combination of several differentiating characters. The characters identifying *Courtoisina* include spikelets disarticulating as a unit when mature leaving the spikelet bract and prophyll behind, winged glumes, and an unusually differentiated *Cyperus*-type embryo. However, one other *C₃ Cyperus* species, i.e. *Cyperus reduncus* (included in *Cyperus* sect. *Fusci* by Kükenthal 1936), closely resembles the two *Courtoisina* species. It shares the therophytic habit, typical yellowish green

colour, the long flaccid leaves and leaf-like primary involucre bracts, and the spikelets disarticulating as a unit when mature, leaving the spikelet bract and prophyll behind. Additionally, in *Cyperus reduncus*, the rachilla of the spikelet can easily be broken at any point between glumes. In this species the nutlets are still distributed separately (nutlet = unit of dispersal). In *Courtoisina assimilis* and *Courtoisina cyperoides* the glumes closely envelop the few or single maturing nutlets. Furthermore, the glumes of the two *Courtoisina* species are clearly winged (fig. 12C & E), helping wind-distribution of the spikelet as a unit (spikelet = unit of dispersal). Though the glumes of *Cyperus reduncus* lack the conspicuous wings (fig. 12A), they are otherwise very similar to those of *Courtoisina*, but there are more glumes per spikelet. Also, *Cyperus reduncus* shares the oddly elongated nutlets (fig. 12B, D & F) and the unusually differentiated *Cyperus*-type embryo (strongly asymmetrical development of the coleoptile, figs 3 & 4) with *Courtoisina*.

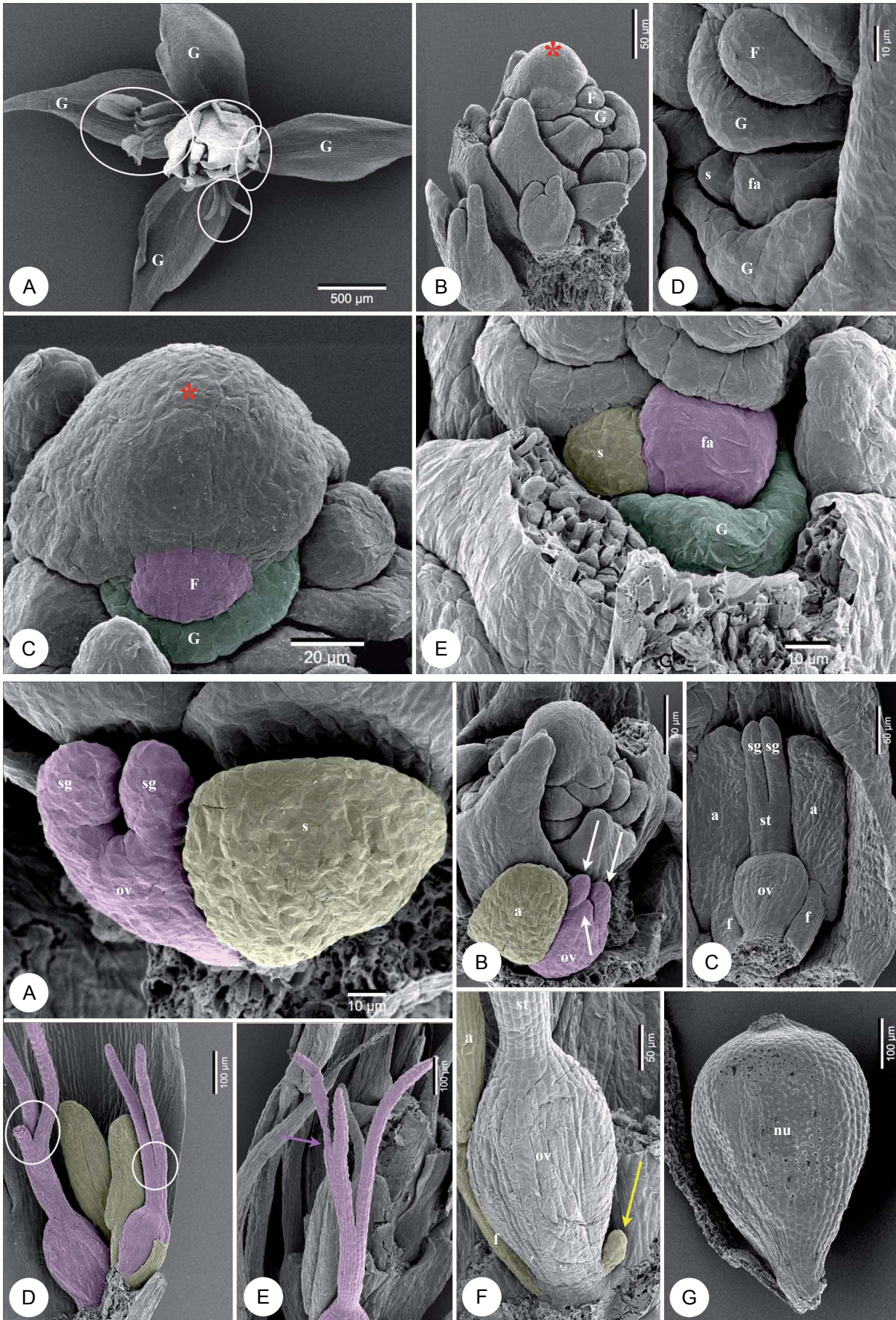
The molecular phylogenetic hypothesis of Larridon et al. (2011b) (figs 1 & 4), confirms the very close relationship of *Courtoisina* and *Cyperus reduncus*, and verifies its phylogenetic position in *C₃ Cyperus*. Consequently, in the formal taxonomic treatment (see below) the two previously recognised *Courtoisina* species are included in *Cyperus* and put in their own section together with *Cyperus reduncus*. The characters previously used to separate *Courtoisina* from *Cyperus* have recently been shown to be of little taxonomic value (Muasya et al. 2009a, 2009b). These characters are homoplasies; they have arisen multiple times in different *Cyperus* lineages. For example, deciduous spikelets occur not only in the two *Courtoisina* species and *Cyperus reduncus*, but also in another, not closely related *C₃ Cyperus* species, *Cyperus deciduus* Boeck., and in many *C₄ Cyperus* species. Winged glumes, another “*Courtoisina* character”, also occur in different, unrelated lineages of the *Cyperus* clade like *Ascolepis* and *Kyllinga*.

Unlike Clarke (1893), Kükenthal (1936), Podlech (1960), and Gordon-Gray (1995), we consider the infraspecific distinction between the African and Asian specimens of *Courtoisina cyperoides* unjustified. These authors defended a distinction at infraspecific rank (subspecies or variety) by the presence of an excurving mucro of c. 0.5 mm present in the African specimens, but absent in the Asian specimens of *Courtoisina cyperoides*. However, in the type specimen of *Courtoisina cyperoides* (Wallich 3537, from India) the debated mucros are clearly present.

Based on biogeography and morphology we place the origin of the section in Africa, where *Cyperus reduncus* most closely resembles its related *C₃ Cyperus* species. *Courtoisina cyperoides* and *Courtoisina assimilis* represent further evolutionary steps away from the typical *Cyperus* characters (reduction of the number of glumes, conspicuously winged midrib). As mentioned above, the glumes of *Courtoisina cyperoides* from some Asiatic specimens illustrate the loss of the generally present mucros.

Oxycaryum and *Cyperus gardneri*

As mentioned above, *Oxycaryum cubense* was included in different genera based on its aberrant morphology (spirally-arranged glumes and dimerous dorsiventrally flattened gyn-



◀ **Figure 17** – SE micrographs of spikelet and floral development in *Kyllingiella polyphylla*. A, apical view of a spikelet, with spirally placed glumes, each subtending a flower (encircled); B, detail of the distal part of a spikelet, with the spikelet apex, and several glumes, each subtending a flower, at different developmental stages; C, detail of spikelet apex; D, detail of two glumes, each with a flower primordium, at successive stages; E, detail of a glume (green), with a flower primordium differentiating into a floral apex (purple) and a lateral stamen primordium (yellow).

Abbreviations: F, flower primordium; fa, floral apex; G, glume; s, stamen; *, rachilla apex.

◀ **Figure 18** – SE micrographs of spikelet and floral development in *Kyllingiella polyphylla*. A–C, detail of a developing flower at three successive stages [the stamen primordium (yellow) starts differentiating into filament and anther; the ovary wall (purple) is covering the central ovule, and on its top two laterally positioned stigma primordia grow out]; D–E, gynoecea with two and three stigma branches (encircled), and splitting of one of the stigma branches (arrowed); F, flower with a not further developing stamen primordium (arrowed); G, nutlet, with persistent withered filament.

Abbreviations: a, anther; f, filament; nu, nutlet; ov, ovary wall; s, stamen; sg, stigma branch (primordium); st, style.

oecea / nutlets, figs 2E, 13, 14 & 15). However, the two key characteristics used to recognise *Oxycaryum* have originated multiple times in *Cyperus* (e.g. Muasya et al. 2009a, 2009b, Reynders et al. accepted, Vrijdaghs et al. 2011). A reversal to spiral glume arrangement (as found in the *Ficinia* clade) has occurred several times in the *Cyperus* clade (usually distichous glume arrangement), i.e. in *Oxycaryum cubense* and *Kyllingiella* (*C₃ Cyperus*) and in *Cyperus michelianus* (*C₄ Cyperus*). Dimerous dorsiventrally flattened nutlets also originated multiple times independently in the *Cyperus* clade, i.e. in *Oxycaryum cubense* and in various *C₄ Cyperus* lineages. Consequently, there is clear justification to include *Oxycaryum* in *C₃ Cyperus*. The use of the *C₃* photosynthetic pathway (linked with eucyberoid anatomy), the presence of a *Cyperus*-type embryo (figs 3 & 4), and its phylogenetic position in *C₃ Cyperus* (fig. 1) (Larridon et al. 2011b) further substantiate this inclusion. Molecular phylogenetical data (fig. 1) (Larridon et al. 2011b) also indicate a close relationship with *Cyperus gardneri*, a species morphologically resembling *Oxycaryum cubense* to some extent: somewhat contracted inflorescence, corky nutlets (fig. 15B), and a similar embryo (figs 3 & 4). In the taxonomic treatment below, the genus *Oxycaryum* is combined into *Cyperus* at sectional rank including *Oxycaryum cubense* and *C. gardneri*.

Cyperus sect. *Leucocephali* and *Kyllingiella*

The species of *Cyperus* sect. *Leucocephali* and those of the small genus *Kyllingiella* show a marked resemblance in habit (small to medium-sized grasslike plants with a thickened base and a pale-coloured capitate inflorescence, fig. 2H & G). Also, they share a preference for seasonally dry open grasslands; this is rather unusual for *C₃ Cyperus* species which generally prefer forests and marshes. In this context, the phylogenetic position of *C. sect. Leucocephali* and *Kyllingiella* as sister clade to the *C₄ Cyperus* clade (fig. 1) (Larridon et al. 2011b) might indicate a transitional stage towards *C₄ Cyperus* physiology which is reflected by their enhanced drought resistance. The only character to uphold *Kyllingiella* as a distinct genus is the spiral arrangement of its glumes. As mentioned above, recent studies (Muasya et al. 2002, 2006, 2007, 2009a, 2009b, Simpson et al. 2007, Larridon et al. 2011b) showed that the presence of the spirally-arranged glumes is not a phylogenetically informative character, as this glume arrangement arose many times in Cyperaceae. Also in *Cyperus pulchellus*, the glume arranged is not entirely distichous (fig. 16A, B &

E). Therefore, *Kyllingiella* is included here in *C₃ Cyperus*, and more specifically into *C. sect. Leucocephali*.

In 1990, Simpson published a revision of *C. sect. Leucocephali* including seven species. Since then, he described two additional species (Simpson 1992, 1993) in this section. In 1992, when Simpson described *C. androhibensis*, it was the first recorded specimen of *C. sect. Leucocephali* in Madagascar. However, due to several recent finds of *C. pulchellus* in Madagascar, we now feel *C. androhibensis* should not be upheld as a separate species. In our opinion, the type (and only) specimen of *C. androhibensis* is an aberrant / not very well developed specimen of *C. pulchellus*. Consequently, *C. androhibensis* is here placed in synonymy of the widely distributed *C. pulchellus*.

Cyperus sect. *Dichostylis* sensu Kükenthal (1936) p.p.

Although possessing a small, congested, globose inflorescence with numerous spikelets as *Cyperus* sect. *Leucocephali*, Kükenthal (1936) nor Simpson (1990) considered *Cyperus seslerioides* to belong in *C. sect. Leucocephali*. Kükenthal (1936) placed *C. seslerioides* in his '*C. sect. Dichostylis*'. Simpson (1990) did not include *C. seslerioides* in *C. sect. Leucocephali* because of its ovate-lanceolate, excurrent glumes and trigonous achenes. However, some similarity can be seen between the embryos of *Cyperus seslerioides* and the embryos of *C. tenerimus* and *Kyllingiella microcephala* (fig. 3).

Several other *C₃ Cyperus* species were included in *C. sect. Dichostylis* sensu Kükenthal (1936) by Kükenthal or have since been described: *C. humilis*, *C. tweediei*, *C. uncinulatus*, *C. arsenei*, *C. microbrunneus* and possibly *C. hilairenus*. It should be mentioned that the *C₃* photosynthetic pathway has only been confirmed in *C. humilis*, *C. seslerioides* and *C. uncinulatus* (Bruhl & Wilson 2007). Tucker (1983) placed his new species *C. microbrunneus* in *C. sect. Dichostylis* sensu Kükenthal (1936) based on its small size, narrow leaves, densely capitate, rayless inflorescence, oblong-lanceolate spikelets, one stamen per flower and small stipitate achenes. Although the species included in *C. sect. Dichostylis* sensu Kükenthal (1936) definitely share some characters, this group of species is also obviously heterogeneous / polyphyletic as it includes both *C₃* and *C₄ Cyperus* species. Molecular phylogenetic study is required to determine the relationships between the species in this group and their phylogenetic position in *Cyperus*.

Table 3 – A preliminary classification of C₃ *Cyperus*.
For more details on the nomenclature and typification of the sections see Larridon et al. (2011a).

<i>Cyperus</i>	C ₃ <i>Cyperus</i> <i>Cyperus</i> subg. <i>Anosporum</i>	Clade 1	<i>Cyperus</i> sect. <i>Haspani</i> <i>Cyperus</i> sect. <i>Incurvi</i> (probably polyphyletic) <i>Cyperus</i> sect. <i>Diffusi</i>
		Clade 2	<i>Cyperus</i> sect. <i>Luzuloidei</i>
		Clade 3	<i>Cyperus</i> sect. <i>Anosporum</i> <i>Cyperus</i> sect. <i>Courtoisina</i> <i>Cyperus</i> sect. <i>Oxycaryum</i> <i>Cyperus</i> sect. <i>Fusci</i>
		Clade 4	<i>Cyperus</i> sect. <i>Alternifolii</i>
		Clade 5	<i>Cyperus</i> sect. <i>Leucocephali</i>
		Unplaced C ₃ <i>Cyperus</i>	<i>Cyperus</i> sect. <i>Graciles</i> <i>Cyperus</i> sect. <i>Dichostylis</i> sensu Kük. p.p. / <i>Cyperus</i> sect. <i>Humiles</i> <i>Cyperus</i> sect. <i>Radiantes</i> Selected species (see table 4 of Larridon et al. 2011b).
C ₄ <i>Cyperus</i> <i>Cyperus</i> subg. <i>Cyperus</i>	Clade 6	Unresolved, includes more than 500 <i>Cyperus</i> s.str. species and nine segregate genera (Huygh & Reynders et al. unpubl. data).	

***Cyperus constanzae* Urb.**

Kükenthal (1936) included *Cyperus constanzae* in *C. sect. Glutinosi* Kük., nom. illegit. As explained by Larridon et al. (2011b), the correct name for this section is *C. sect. Elegantes* C.B. Clarke (Clarke 1883: 288). Kükenthal (1936) included six species in this section, four species use the C₄

photosynthetic pathway and two species (*C. constanzae* and *C. gardneri*) use C₃ photosynthesis (Bruhl & Wilson 2007, Larridon et al. 2011b). Molecular phylogenetic study revealed a close relationship of *C. gardneri* with *Oxycaryum cubense* (fig. 1) (Larridon et al. 2011b). However, the position of *C. constanzae* in C₃ *Cyperus* remains unknown. The embryo of *C. constanzae* shows most resemblance to the embryos of species of *C. sect. Diffusi* and *C. sect. Incurvi* (fig. 3). Based on its general morphology such a relationship is possible, but molecular phylogenetic confirmation is necessary to place this taxon in its correct section.

Cyperus* sect. *Graciles

This section was not included in the molecular study of Larridon et al. (2011b). For seven of the 11 species the photosynthesis type was confirmed as C₃ (Bruhl & Wilson 2007, Larridon et al. 2011b). Although Blake (1939) suggested a relationship of *Cyperus* sect. *Graciles* with *C. sect. Haspani*, this is unlikely since the embryos of the *C. sect. Graciles* species included in this study do not at all resemble those of *C. sect. Haspani* (fig. 3). The embryos of *C. gracilis* and *C. tetraphyllus* show much more resemblance both to the embryo of *C. alternifolius* (shape) and to some of the embryos of *C. sect. Diffusi* and *C. sect. Incurvi* (size) (fig. 3). Based on embryographical data alone, it is impossible to clearly indicate the phylogenetic position of *C. sect. Graciles*. Furthermore, the morphology of the species of *C. sect. Graciles* does not show obvious similarities with just one of the *Cyperus* sections mentioned above. Molecular phylogenetic confirmation is needed here.

TAXONOMIC TREATMENT

***Cyperus* sect. *Anosporum* (Nees) Pax** (Pax 1887: 107) – *Anosporum* Nees (Nees 1834a: 287) – *Cyperus* subg. *Anosporum* (Nees) C.B. Clarke (Clarke 1884: 34) – Type: *Cyperus monocephalus* Roxb. [= *Cyperus cephalotes* Vahl]. *Hydroschoenus* Zoll. & Moritzi (Moritzi 1846: 95). *Trentepohlia* Boeck., nom. rej. (Boeckeler 1858: 249). *Cyperus* sect. *Pseudanosporum* C.B. Clarke (Clarke 1884: 117) – *Cyperus* sect. *Natantes* C.B. Clarke, nom. illegit. (Clarke 1893: 597). *Cyperus* sect. *Cephalotes* J.V. Suringar, nom. illegit. (Suringar 1898: 76). *Cyperus* sect. *Nudicaules* Cherm., nom. invalid. (Chermezon 1922: 3).

Diagnosis – Perennials, adapted to an aquatic (often floating) lifestyle. Glumes tightly imbricate, rather glossy and thick. Style unbranched, shortly branched or more deeply branched. Nutlets dark surrounded by paler corky tissue (at least on angles and at apex).

Habitat – Growing in swamps or pools, either floating in deep water or emergent with roots in mud.

Distribution – Species 4, tropical Africa, Asia and Australia.

Species

1. *Cyperus cephalotes* Vahl (Vahl 1805: 311) – *Anosporum cephalotes* (Vahl) Kurz (Kurz 1876: 159) – Type: India, Nico-

Key to the species of *Cyperus* sect. *Anosporum*

1. Leaves reduced to their leaf-sheaths; involucre bracts 1–2 short, rigid and rather sharp.....2
- 1'. Leaves not reduced.....3
2. Culms 3–5 mm thick, sharply triangular to winged; involucre bract 1.....*C. colymbetes*
- 2'. Culm 0.5–2 mm thick, rounded-angular; involucre bracts 1–2.....*C. pectinatus*
3. Bracts 3–5 leaf-like, 5–30 cm long; inflorescence capitate.....*C. cephalotes*
- 3'. Bracts 4–12 leaf-like, 30–80 cm long; inflorescence anthelate.....*C. platystylis*

bar Islands, *Vahl* s.n. (holo-: C).

Cyperus monocephalus Roxb. (Roxburgh 1820: 193) – *Anosporum monocephalum* (Roxb.) Nees (Nees 1834a: 287).

Cyperus monocephaloides Roxb. ex Nees, nom. invalid. (Nees 1834b: 92).

Hydroschoenus kyllingioides Zoll. & Moritzi (Moritzi 1846: 95).

Trentepohlia bifoliata Boeck. (Boeckeler 1858: 249).

Cyperus hookerianus Thwaites (Thwaites 1864: 342).

Cyperus monogynus Boeck. (Boeckeler 1868: 565).

Cyperus natans Buch.-Ham. ex C.B. Clarke, nom. invalid. (Clarke 1884: 34).

Ungeria monocephala (Roxb.) Nees ex C.B. Clarke, nom. invalid. (Clarke 1884: 34).

Ficinia foliaceobracteata H. Pfeiff. (Pfeiffer 1921: 35).

Cyperus cephalotes var. *grandiceps* Kük. (Kükenthal 1943: 4).

Distribution – Tropical Asia to Northeastern Australia.

Description – Lye (1981: 187).

2. *Cyperus colymbetes* Kotschy & Peyr. (Kotschy & Peyr. 1867: 49) – *Anosporum colymbetes* (Kotschy & Peyr.) Boeck. (Boeckeler 1869: 26) – Original type: Sudan, Bahrel-Ghasal, *Tinne* s.n., (holo-: W, destroyed during the war, Kotschy & Peyr. 1867: t. XXIV).

Distribution – Sudan to Mozambique, Madagascar.

Description – Lye (1981: 188).

3. *Cyperus pectinatus* Vahl (Vahl 1805: 298) – *Anosporum pectinatum* (Vahl) Lye (Lye 1981: 188) – Type: Guinea, Dahomey, Ouidah, *Isert* s.n. (holo-: C).

Cyperus nudicaulis Poir. (Poiret 1806: 240) – *Anosporum nudicaule* (Poir.) Boeck. (Boeckeler 1869: 26).

Atomostylis cyperiformis Steud. (Steudel 1855: 315).

Atomostylis flavescens Steud. (Steudel 1855: 315).

Distribution – Tropical and Southern Africa, Madagascar.

Description – Lye (1981: 188).

4. *Cyperus platystylis* R.Br. (Brown 1810: 214) – Type: Australia, New South Wales, Hawkesbury, *Brown* 5907 (holo-: BM).

Cyperus pallidus Nees, nom. illegit. (Nees 1834b: 79) – *Anosporum pallidum* Boeck. (Boeckeler 1870: 412).

Cyperus fluitans Buch.-Ham. ex C.B. Clarke, nom. invalid. (Clarke 1884: 118).

Distribution – Tropical and subtropical Asia, Australia.

Description – Kern (1974: 618).

Cyperus* sect. *Courtoisina (Soják) Larridon, **comb. nov.** – *Courtoisina* Soják, *Časopis Národního muzea, řada přírodovědecká* 148: 193. 1979 (Soják 1979) – *Courtoisina* Nees, nom. illegit., non Marchand (1830) (Nees 1834a: 286) – *Indocourtoisia* Bennet & Raizada, nom. illegit. (Raizada & Bennet 1981: 432) – *Pseudomariscus* Rauschert, nom. illegit. (Rauschert 1982: 559) – *Cyperus* subg. *Courtoisina* (Nees) Lye (Lye 1983: 230) – *Cyperus* subg. *Courtoisina* (Soják) Lye, nom. illegit. (Lye 1992: 52) – Type: *Cyperus pseudokyllingioides* Kük. as nomen novum of *Courtoisina cyperoides* (Roxb.) Nees (*Kyllinga cyperoides* Roxb.).

Diagnosis – Medium-sized therophytes yellowish green with long flaccid leaves and leaf-like primary involucre bracts, strongly flattened spikelets which disarticulate as a unit when mature leaving the spikelet bract and prophyll behind, glumes often conspicuously winged (except in *C. reduncus*). Some authors (Haines & Lye, 1983; Goetghebeur, 1998) report a strong odour (curry scent).

Habitat – Often growing on temporarily wet sandy soils.

Distribution – Species 3, widely distributed in tropical Central, East and South Africa, one also in Madagascar, India and Southeast Asia.

Species

1. *Cyperus assimilis* Steud. (Steudel 1842: 584) – *Courtoisina assimilis* (Steud.) C.B. Clarke (Clarke 1894: 596) – *Mariscus assimilis* (Steud.) Podlech (Podlech 1960: 523) – *Indocourtoisia assimilis* (Steud.) Bennet & Raizada (Raizada & Bennet 1981: 432) – *Courtoisina assimilis* (Steud.) Maquet (Maquet 1988: 265). – Type (designated here): Ethiopia, *Schimper* 1252 (lecto-: B; isolecto-: BR, G, GOET, HEID, K, L, M, P, S, STU, WAG).

Distribution – Ethiopia to South Africa, Madagascar.

Description – Haines & Lye (1983: 174).

2. *Cyperus pseudokyllingioides* Kük. (Kükenthal 1936: 501) – *Kyllinga cyperoides* Roxb. (Roxburgh 1820: 182) – *Mariscus cyperoides* (Roxb.) A. Dietr. (Dietrich 1832: 348) – *Courtoisina cyperoides* (Roxb.) Nees (Nees 1834a: 286) – *Cyperus pseudokyllingioides* Kük. var. *pseudokyllingioides* (Kükenthal 1936: 501) – *Courtoisina cyperoides* (Roxb.) Soják (Soják 1979: 193) – *Indocourtoisia cyperoides* (Roxb.) Bennet & Raizada (Raizada & Bennet 1981: 432) – *Pseudomariscus cyperoides* (Roxb.) Rauschert (Rauschert 1982: 559) – Type (lectotype designated here): India, *Wallich* 3537 (holo-: ?; isolecto-: P).

Cyperus kleinianus Hochst. ex Steud., nom. invalid. (Steudel 1854: 71).

Key to the species of *Cyperus* sect. *Courtoisina*

1. Glumes winged, 2–4(–12) per spikelet.....2
- 1'. Glumes not winged, 5–25 per spikelet.....*C. reduncus*
2. Glumes 2(–3) per spikelet.....*C. pseudokyllingioides*
- 2'. Glumes 4(–12) per spikelet.....*C. assimilis*

Key to the species of *Cyperus* sect. *Oxycaryum*

1. Glumes distichously-arranged, style-branches 3, nutlets trigonous (tropical and subtropical America).....*C. gardneri*
- 1'. Glumes spirally-arranged, style-branches 2, nutlets dorsiventrally plano-convex (tropical and subtropical America and Africa).....*C. blepharoleptos*

Courtoisia cyperoides var. *africana* C.B. Clarke, nom. invalid. (Clarke 1893: 596).

Cyperus pseudokyllingioides var. *africanus* C.B. Clarke ex Kük. (Kükenthal 1936: 501).

Distribution – Himalaya to Indo-China, Chad to South Africa, Madagascar.

Description – Haines & Lye (1983: 175).

3. *Cyperus reduncus* Hochst. ex Boeck. (Boeckeler 1868: 580) – Type: Ethiopia, Schimper s.n. (holo-: B, destroyed during the war?; iso-: M).

Cyperus aristatus Hook.f. & Thomson ex C.B. Clarke, nom. invalid. (Clarke 1884: 90).

Distribution – Chad to South Africa, Madagascar.

Description – Haines & Lye (1983: 160).

Cyperus* sect. *Oxycaryum (Nees) Larridon, **comb. nov.** – *Oxycaryum* Nees, in Martius, Flora Brasiliensis 2(1): 90. 1842 (Nees 1842) – *Scirpus* sect. *Oxycaryum* (Nees) Beetle (Beetle 1944: 263) – Type: *Oxycaryum schomburgkianum* Nees [= *Cyperus blepharoleptos* Steud.].

“*Crepidocarpus* Klotzsch ex Boeck.”, nom. invalid. (Boeckeler 1870: 414).

“*Scirpus* sect. *Cubenses* Cherm.”, nom. invalid. (Chermezon 1937: 156).

Diagnosis – Aquatic, often floating plants. Inflorescence anthelate (with partial inflorescences capitate) to capitate. Spikelets with several distichously or spirally-arranged glumes. Stamens 3. Style 3-fid or 2-fid. Nutlet trigonous or slightly dorsiventrally flattened, conspicuously corky.

Habitat – Floating in water or growing in wet soil.

Distribution – Species 2, tropical and subtropical America and Africa.

Species

1. *Cyperus blepharoleptos* Steud. (Steudel 1854: 28) – Type: Senegal, Leprieur s.n. (holo-: P00462624; iso-: P00462625, P00462626).

Scirpus cubensis Poepp. & Kunth (Kunth 1837: 172) – *Anosporum cubense* (Poepp. & Kunth) Boeck. (Boeckeler 1869:

26) – *Oxycaryum cubense* (Poepp. & Kunth) Palla (Palla 1908: 169) – Type: Cuba, Poeppig s.n. (holo-: ?; iso-: P).

Oxycaryum schomburgkianum Nees (Nees 1842: 90) – Type: Guyana, Schomburgk 371 (holo-: W; iso-: BM, K, P).

Mariscus foliosissimus Steud. (Steudel 1854: 65).

Courtoisia olivacea Boeck. (Boeckeler 1861: 331) – *Pseudomariscus olivaceus* (Boeck.) Rauschert (Rauschert 1982: 559).

Scirpus ablepharus Griseb. (Grisebach 1866: 240) – *Anosporum ablepharum* (Griseb.) Maury (Maury 1890: 125).

“*Crepidocarpus cubensis* (Poepp. & Kunth) Klotzsch ex Boeck.”, nom. invalid. (Boeckeler 1870: 414).

Anosporum cubense var. *gracile* Boeck. (Boeckeler 1870: 414) – *Scirpus cubensis* var. *gracilis* (Boeck.) Beetle (Beetle 1944: 146).

Isolepis echinocephala Oliv. (Oliver 1875: 167).

Anosporum schinzii Boeck. (Boeckeler 1888: 46) – *Oxycaryum schinzii* (Boeck.) Palla (Palla 1908: 169).

Crepidocarpus schinzii Klotzsch ex Boeck., nom. invalid. (Boeckeler 1888: 46).

Anosporum paraguayense Maury (Maury 1890: 124) – *Oxycaryum paraguayense* (Maury) Palla (Palla 1908: 169) – *Scirpus cubensis* var. *paraguayensis* (Maury) Kük. ex Barros (Barros 1935: 150) – *Scirpus paraguayensis* (Maury) Herter (Herter 1943: 161) – *Oxycaryum cubense* f. *paraguayense* (Maury) Pedersen (Pedersen 1995: 138).

Anosporum piliferum Maury (Maury 1890: 124) – *Oxycaryum piliferum* (Maury) Palla (Palla 1908: 169) – *Scirpus piliferus* (Maury) Pickel (Pickel 1937: 124).

Oxycaryum guianense Palla (Palla 1908: 169).

“*Kyllinga scirpina* Rchb. ex C.B. Clarke”, nom. invalid. (Clarke 1894: 620).

Distribution – Tropical and subtropical Africa, America.

Description – Lye (1971: 282–284).

2. *Cyperus gardneri* Nees (Nees 1842: 34) – Type: Brazil, Gardner 1213 (holo-: BM; iso-: G, K, NY, P, TCD, US).

Distribution – Cuba, Southeastern Mexico to Northeastern Argentina.

Description – Diego-Pérez et al. (2001: 18, in Spanish).

Key to the species of *Cyperus* sect. *Leucocephali*

1. Glumes distichously-arranged.....2
- 1'. Glumes spirally-arranged.....9
2. Inflorescence ± dense (sub-)globose cluster of spikelets; stamen 1 (tropical Old World and Australia).....3
- 2'. Inflorescence ± dense (sub-)globose cluster of spikelets or more loose half-globose cluster of spikelets; stamens 1, 2 or 3 (Neotropics).....5
3. Leaf-blades 0.4–0.6 mm wide; spikelets 2–5.5 × ± 1 mm; glumes 0.8–1 × 0.4–0.5 mm; achene widely obovoid or subglobose, 0.3–0.4 × 0.25–0.4 mm (Somalia).....*C. microglumis*
- 3'. Leaf-blades usually > 0.6 mm wide; spikelets > 1 mm wide; glumes > 1.2 mm long; achenes > 0.5 mm long.....4
4. Spikelets 4–8 × 1–2 mm wide; glumes 1.2–1.5 × 0.3–0.4 mm; achenes 0.5–0.8 × 0.2–0.3 mm (tropical Old World and Australia).....*C. pulchellus*
- 4'. Spikelets 2.5–6.5 × 2–2.5 mm; glumes 1.5–2.5 × ± 0.6 mm; achenes 1.2–1.6 × 0.3–0.4 mm (Indian Subcontinent, Indo-China).....*C. leucocephalus*
5. Inflorescence with up to 12 spikelets; achene ellipsoid, distinctly trigonous, 0.9–1.3 × 0.5–0.6 mm (Mexico).....*C. michoacanensis*
- 5'. Inflorescence with more than 12 spikelets; achene narrowly cylindrical, cylindrical, obovoid or subglobose, obscurely trigonous, 0.2–0.4 mm wide.....6
6. Inflorescence bracts usually 5–8; inflorescence usually a loose half-globose cluster of spikelets; glumes 1.45–2 × 0.8–1 mm, prominently nerved; stamen 1 (Central America to Colombia)..
.....*C. tenerrimus*
- 6'. Inflorescence bracts 3–4(–5); inflorescence a dense, congested cluster of spikelets; glumes indistinctly nerved or nerveless; stamens 2 or 3.....7
7. Stamens 3; glumes 2.3–3.6 × 0.8–1.2 mm; nutlet 1.2–1.7 × ± 0.3 mm, dark brown to black; plants often flowering male and female separately (protandry) (South America).....*C. schomburgkianus*
- 7'. Stamens 2.....8
8. Glumes 2.1–2.6 × 0.6–1.2 mm; nutlet 1–1.3 × 0.3–0.4 mm, dark brown; mature anthers and gynoecia present at the same time (Mexico).....*C. nayaritensis*
- 8'. Glumes 1.7–2 × 0.6–0.8 mm; nutlet 0.5 × 0.2 mm, pale brown to dark grey brown; plants sometimes flowering male and female separately (protandry) (Brazil).....*C. brumadoi*
9. Inflorescence greenish; glumes 2–2.5 mm long including a 0.5 mm long recurved mucro.....
.....*C. spiralis*
- 9'. Inflorescence whitish; glumes not mucronate.....10
10. Inflorescence head (2–)3(–4) mm in diam.; spikelets ± 2 mm long.....*C. acholiensis*
- 10'. Inflorescence head larger; spikelets longer.....11
11. Culms 5–40 cm × 0.2–0.5 mm; inflorescence head 3–8 × 3–5 mm; nutlets 0.5–0.8 mm long.....
.....*C. kyllingiella*
- 11'. Culms 30–62 cm × 0.7–1.5 mm; inflorescence head 3–7 × 5–9 mm; nutlets 1.3–1.7 mm long.....
.....*C. simpsonii*

Cyperus* sect. *Leucocephali [Chermezon 1931: 17, nom. nud.] Cherm. ex Kük. (Kükenthal 1936: 276) – *Cyperus* [unranked] *Leptolepides* Boeck. (Boeckeler 1868: 588) – *Cyperus* [unranked] *Leptolepides* [unranked] *Capitati* Boeck. (Boeckeler 1868: 588) – Type: *Cyperus leucocephalus* Retz. *Sorostachys* Steud. (Steudel 1854: 71) – *Cyperus* subg. *Sorostachys* (Steud.) Lye (Lye 1983: 230). *Kyllingiella* R.W.Haines & Lye (Haines & Lye 1978: 176).

Diagnosis – Small to medium-sized grass-like plants with a pale-coloured head-like inflorescence of numerous small spikelets and small, narrow, membranous glumes.

Habitat – Open, seasonally dry habitats, especially grasslands.

Distribution – 12 species, wide distribution throughout the tropics.

Species

1. ***Cyperus acholiensis*** Larridon, **nom. nov.** – *Kyllingiella ugandensis* R.W.Haines & Lye (Haines & Lye 1978: 177), non *Cyperus ugandensis* Chiov. – Type: Uganda, Kertland 111 (holo-: MHU).

Distribution – Kenya, Tanzania, Uganda.

Description – Haines & Lye (1978: 177).

2. ***Cyperus brumadoi*** D.A.Simpson (Simpson 1993: 701) – Type: Brazil, Bahia, *Carvalho, Brito & Santos* 2617 (holo-: CEPEC; iso-: K).

Distribution – Brazil.

Description – Simpson (1993: 701).

3. ***Cyperus kyllingiella*** Larridon, **nom. nov.** – *Kyllinga microcephala* Steud. (Steudel 1842: 597) – *Isolepis kyllingi-*

oides A.Rich., nom. illegit. (Richard 1850: 502) – *Scirpus microcephalus* (Steud.) Dandy (Dandy 1956: 366) – *Scirpus kyllingioides* (A.Rich.) Boeck., nom. illegit. (Boeckeler 1870: 733) – *Isolepis microcephala* (Steud.) Lye (Haines & Lye 1971: 480) – *Kyllingiella microcephala* (Steud.) R.W.Haines & Lye (Haines & Lye 1978: 176), non *Cyperus microcephalus* R.Br. – Type: Ethiopia, *Schimper* 650 (holo-: P; iso-: BR, G, K, MO, P, S, WAG).

Distribution – Tropical and southern Africa, Indian subcontinent.

Description – Haines & Lye (1983: 142).

4. *Cyperus leucocephalus* Retz. (Retzius 1788: 11) – *Sorostachys leucocephalus* (Retz.) Lye (Lye 1981: 190) – Type: India, *König* s.n. (holo-: LD).

Scirpus coronarius Vahl (Vahl 1805: 261) – *Isolepis coronaria* (Vahl) Roem. & Schult. (Roemer & Schultes 1817: 113) – *Cyperus coronarius* (Vahl) Kunth (Kunth 1837: 44). *Kyllinga pierreana* E.G.Camus (Camus 1910: 290).

Distribution – Northeastern India, Bangladesh, Myanmar, Thailand, Vietnam.

Description – Simpson (1990: 494).

5. *Cyperus michoacanensis* Britton ex C.B.Clarke (Clarke 1908: 5) – Type: Mexico, *Pringle* 3427 (holo-: VT; iso-: K, NY).

Cyperus patzcuarensis C.B.Clarke ex Kük., nom. invalid. (Kükenthal 1936: 277).

Distribution – Mexico.

Description – Simpson (1990: 500).

6. *Cyperus microglumis* D.A.Simpson (Simpson 1990: 492) – Type: Somalia, *Beckett* 217 (holo-: K; iso-: EA).

Distribution – Somalia.

Description – Simpson (1990: 492).

7. *Cyperus nayaritensis* G.C.Tucker (Tucker 1983: 161) – Type: Mexico, Nayarit, *Feddema* 418 (holo-: DUKE; iso-: ENCB, MICH).

Distribution – Mexico.

Description – Simpson (1990: 499).

8. *Cyperus pulchellus* R.Br. (Brown 1810: 213) – *Sorostachys pulchellus* (R.Br.) Lye (Lye 1981: 189) – Type: Australia, *Brown* 5917 (holo-: K; iso-: L).

Sorostachys kyllingioides Steud. (Steudel 1854: 71) – *Cyperus sorostachys* Boeck., nom. superfl. (Boeckeler 1868: 588). *Cyperus zanzibarensis* C.B.Clarke (Clarke 1901: 323).

Cyperus androhibensis D.A.Simpson (Simpson 1992: 745).

Distribution – Tropical Africa, Madagascar, India, Philippines, northern Australia.

Description – Simpson (1990: 490).

9. *Cyperus schomburgkianus* Nees (Nees 1840: 393) – Type: Guyana, *Schomburgk* 810 (holo-: B, destroyed during the war; iso-: BM, G, K, TCD).

Cyperus leucanthus Schrad. ex Nees (Nees 1842: 18) – *Cyperus schomburgkianus* var. *leucanthus* (Schrad. ex Nees) Kük. (Kükenthal 1936: 277).

Cyperus schomburgkianus var. *trilobatus* Kük. (Kükenthal 1936: 277).

Distribution – South America: Bolivia (*Beck* 25586; LPB, GENT), Brazil, Guyana, Venezuela.

Description – Simpson (1990: 495).

10. *Cyperus simpsonii* (Muasya) Larridon, **comb. nov.** – *Kyllingiella simpsonii* Muasya, *Kew Bulletin* 57: 997. 2002 (Muasya 2002) – Type: Tanzania, *Ole Sayalel* 5320 (holo-: EA; iso-: K).

Distribution – Democratic Republic of Congo, Tanzania, Zambia.

Description – Muasya (2002: 997).

11. *Cyperus spiralis* Larridon, **nom. nov.** – *Isolepis polyphylla* A.Rich. (Richard 1850: 503) – *Kyllingiella polyphylla* (A.Rich.) Lye (Haines & Lye 1983: 143), non *Cyperus polyphyllus* Vahl – Type: Ethiopia, *Quartin Dillon* s.n. (holo-: P; iso-: P).

Distribution – Ethiopia to east tropical Africa.

Description – Haines & Lye (1983: 143).

12. *Cyperus tenerrimus* J.Presl & C.Presl (Presl & Presl 1828: 166) – Type: Mexico, *Haenke* s.n. (holo-: PR).

Cyperus cymbiformis Liebm. (Liebmann 1850: 208).

Cyperus wawrai Boeck. (Boeckeler 1874: 363).

Distribution – Central America: Mexico, Guatemala, Nicaragua, El Salvador, Costa Rica, Panama; South America: Colombia.

Description – Simpson (1990: 497–498).

CONCLUSIONS

The segregate genera *Courtoisina*, *Oxycaryum* and *Kyllingiella* are here included in *Cyperus*. *Courtoisina* and *Oxycaryum* are combined in *Cyperus* as sections, whereas *Kyllingiella* is included in an expanded *Cyperus* sect. *Leucocephali*. *Cyperus* sect. *Pseudanosporum* is placed in synonymy of *C.* sect. *Anosporum*. The inclusion of these segregates in *C₃ Cyperus* (*Cyperus* subg. *Anosporum*) is based on the phylogenetic hypothesis presented by Larridon et al. (2011b) (fig. 1), and is here corroborated using morphology, embryology, spikelet and floral ontogeny, and anatomy. Table 3 presents a preliminary classification of *C₃ Cyperus*.

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