

# BOLETÍN DEL CENTRO DE INVESTIGACIONES BIOLÓGICAS

<b>CALIDAD Y ACTIVIDAD ANTIOXIDANTE EN FRUTOS DE FRESA (FRAGARIA X ANANASSA DUCH) CULTIVAR CHANDLER EN DOS LOCALIDADES DEL ESTADO LARA</b> María Pérez de Camacaro, Maritza Ojeda, Norca Mogollón y Aracelis Giménez.....	6
<b>NOVITATES AGROSTOLOGICAE, V. GENERIC MERGERS IN THE TRIBE OLYREAE (INGLÉS)</b> José Grande.....	19
<b>BIODEGRADACIÓN AERÓBICA DE EFLUENTES DEL PROCESAMIENTO DE PESCADO EN REACTORES POR CARGA</b> Julio César Marín, Abraham Velásquez, Carlos Chinga, Ever Vizueta y Robert Mero	44
Revisión <b>AVANCES EN LAS INVESTIGACIONES GENÉTICAS DE ALOE VERA (L.) BURM.F.</b> Tamara Molero y Maribel Viloria.....	63
<b>INSTRUCCIONES A LOS AUTORES.....</b>	82

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## Novitates Agrostologicae, V. Generic mergers in the tribe Olyreae

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### Abstract

Tribe Olyreae (Poaceae: Bambusoideae), a predominantly American taxon known commonly as “herbaceous bamboos”, shows remarkable inconsistencies in its present generic classification. To further contribute in the proper delimitation of its constituent genera, and based upon an extensive morphological analysis plus bibliographic revision, species previously included in *Olyra* L. group *Ciliatifolia* are transferred to *Agnesia* Zuloaga & Judz., and species previously included in *O.* group *Glaberrima* to *Arberella* Soderstr. & C.E. Calderón. The genera *Parodiolyra* Soderstr. & Zuloaga and *Sucrea* Soderstr. are synonymized under *Raddiella* Swallen and *Raddia* Bertol., respectively. In total, 19 new specific combinations, two generic and two infrageneric synonyms, plus four generic emendations (with emended Latin diagnoses), are proposed. Formal infrageneric taxa of *Olyra* are lectotypified, and its modern generic equivalents are established for the first time. Importance of inflorescence structure in taxonomic delimitation within the tribe is amply discussed. Direct Phylogentic Argumentation (DPA) is proposed as a new method for inferring phylogenies.

**Key words:** Direct Phylogentic Argumentation (DPA); emended diagnoses; generic mergers; Maximum Synapomorphy (MS); new combinations; *Olyra*; Olyreae.

## Novitates Agrostologicae, V. Rearreglos genéricos en la tribu *Olyreae*

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### Resumen

La tribu *Olyreae* (Poaceae: Bambusoideae), un taxón predominantemente americano que agrupa a los denominados “bambúes herbáceos”, muestra notables inconsistencias en su clasificación a nivel genérico. Con el objeto de contribuir en la adecuada delimitación de sus géneros, y tomando como base un extenso análisis morfológico y la revisión de la literatura pertinente, las especies previamente incluidas en *Olyra* L. grupo *Ciliatifolia* son transferidas a *Agnesia* Zuloaga & Judz., aquellas que hasta ahora han sido asignadas a *O.* grupo *Glaberrima* a *Arberella* Soderstr. & C.E. Calderón, y los géneros *Parodiolyra* Soderstr. & Zuloaga y *Sucrea* Soderstr. son sinonimizados bajo *Raddiella* Swallen y *Raddia* Bertol., respectivamente. En total, se proponen 19 combinaciones nuevas a nivel de especie, dos nuevos sinónimos genéricos y dos nuevos sinónimos infragenéricos, mientras que cuatro de los géneros tratados son enmendados a través de una nueva diagnosis latina. Los taxones infragenéricos de *Olyra* que han sido válidamente publicados son lectotipificados, y se establecen por primera vez sus respectivos equivalentes genéricos. La importancia de la estructura de la inflorescencia en la delimitación taxonómica de los géneros de la tribu es discutida de manera amplia. Se propone a la Argumentación Filogenética Directa (AFD) como un nuevo método para la inferencia de filogenias.

**Palabras clave:** Argumentación Filogenética Directa (AFD); combinaciones nuevas; diagnosis emendadas; Máxima Sinapomorfía (MS); *Olyra*; *Olyreae*; rearreglos genéricos.

### Introduction

Tribe *Olyreae* (Poaceae: Bambusoideae) is a predominantly American taxon known commonly as “herbaceous bamboos” (after Calderón and Soderstrom 1980, who also included in this category the Old World *Puelia* Franch., of tribe Arundinarieae, and some basal grasses at present excluded from subfamily Bambusoideae), which is characterized by unisexual spikelets (generally in monoecious inflorescences), low habit, and short life cycle. The tribe has been amply corroborated as monophyletic, with currently accepted classifications placing this group within subfamily Bambusoideae (e.g., Clark et al. 1995, GPWG 2001, Judziewicz and Clark 2007, Kelchner and BPG 2013). Despite this, a

considerable number of genera are fairly artificial, with much variability in both vegetative and reproductive characters (cf. Judziewicz et al. 1999, Grande 2009 and 2015). Diagnostic characters include absence of external ligules and an iteroparous (rarely semelparous) mode of reproduction, with sexes separated into two distinct types of spikelets (namely, male and female spikelets). Classifications in vogue include three subtribes (viz. Buergersiochloinae, Olyrinae and Parianinae; Judziewicz and Clark 2007, Kelchner and BPG 2013).

In the course of a revision of the entire tribe, some inconsistencies were found in the use of certain characters as either diagnostic or putative synapomorphic. Despite an important number of molecular (e.g., Clark et al. 1995, GPWG 2001, Kelchner and BPG 2013, using DNA sequences from GBSSI [or *waxy*], *matK*, *ndhF*, *rbcL*, *rpoC2*, *phyB*, and *trnL-trnF* genes, ITS, ITS2, *atpB-rbcL*, *trnD-trnT* and *trnT-trnL* spacers, and *trnL*, *trnK/matK*, *rpl16* and *rps16* introns), morphoanatomical (Kellogg and Watson 1993, mainly exomorphological), and mixed (Soreng and Davis 1998) cladistic studies, delimitation and relationships of species groupings are still unsatisfactory in an important number of cases.

Ever since Döll (1877) proposed his infrageneric classification of *Olyra* L. (the only genus in the tribe recognized by him) there has been a propensity to classify according to inflorescence structure; the names of his sections, in fact, could be translated literally as “with both sexes at the apex” (*O.* sect. *Acrandrogynae* Döll), “with both sexes along axils” (*O.* sect. *Pleurandrogynae* Döll) and “otherwise arranged” (*O.* sect. *Heterogenicae* Döll). As stated by the late Thomas R. Soderstrom, one of the foremost scholars in the Olyreae “In this tribe the arrangement of spikelets in the inflorescence and disposition of the inflorescences within the plant provide the basic criteria by which genera may be distinguished” (Soderstrom 1980: 495). Regrettably, this complex character shows many transitional forms even within single species (e.g., *Olyra ciliatifolia* Raddi, *O. micrantha* Kunth, *O. obliquifolia* Steud., *Raddia soderstromii* R.P. Oliveira, L.G. Clark & Judz. and *Raddiella kaieeteurana* Soderstr.) and, like habit, minor female antherium ornamentation (including pattern of distribution, but not type of excavations) and pattern of distribution of male/female spikelets along partial inflorescences, constitutes a very variable character of limited taxonomic use. Inflorescence structure, however, has been scarcely studied (most notably by Calderón and Soderstrom (1973), with the assistance of the late eminent plant morphologist Wilhelm Troll), and, as a consequence, taxonomic decisions are uncertain when based solely on it. When properly studied, however, it could serve also as a source of systematic evidence. As an example, is the postulated relationship between *Lithachne* P. Beauv. and *Arberella* Soderstr. & C.E. Calderón, that in recent cladistic works appear as closely related. This relationship was first noted by Soderstrom & Calderón (1979), based on the similar pattern of ramification of the synflorescences, and are further supported by the presence of “thick hairs” toward the base of the palea in female antheria of one of the species of *Lithachne* (viz. the Cuban endemic *L. pineti* (Wright ex Griseb.) Hitchc.; cf. Chase 1935).

Some of *Olyra*'s informal groups (proposed by Judziewicz and Zuloaga 1992, and Grande 2015), in fact, could be considered as different as any other genus in the tribe, and are maintained within *Olyra* on the sole basis of a rather arbitrary combination of characters that heavily rely on inflorescence structure (cf. Grande 2015). The formal system of infrageneric taxa established for *Olyra* (Döll 1877), is perhaps even more artificial, and is reduced to synonymy in the present revision. The observed variability, only when related to more conserved features, like major ornamentation features of female antherium (especially hair type), shape and size of female antherium, morphology of lodicules, type of hilum, pattern of ramification of the inflorescence axes, shape of female pedicels, and, apparently, also some anatomical characters (cf. de Oliveira et al. 2008b, Jesus Junior et al. 2012, Judziewicz and Sepsenwol 2007, Renvoize 1985, Vieira et al. 2002, Zuloaga et al. 1993), and chromosome numbers (as yet to be elucidated for a significant number of non-studied species; for a complete list of published counts see the literature cited in Soderstrom and Zuloaga 1989) could be considered of taxonomic value. Molecular studies, although promising, are still insufficient and based upon a low number of taxa, individuals and/or genes (after the criteria of Petersen et al. 2011) or produce disparate results when based upon different sequences (cf. de Oliveira et al. 2014). In a previous contribution (Grande 2015) some genera and generic groupings are compared based upon putative shared apomorphies; since the submission of that contribution (on may 2012), however, significant progress has been made on the comparative morphology of the group, corroborating previous hypotheses (i.e., those in Soderstrom and Zuloaga 1989, Judziewicz and Zuloaga 1992, and Grande 2011, 2015). As a result, the transfers proposed in the present revision are in order.

Some groups, especially within *Olyra*, deserve further study before proper generic ascription may be fully accomplished. Possible systematic relationships within the tribe are especially interesting, but have received very little or no attention. These include the species with florets (=antheria) generally membranous to cartilaginous, conspicuously covered by macrohairs, and more or less apiculate toward the apex (hitherto included within *Agnesia* Zuloaga & Judz., *Olyra* group *Ciliatifolia*, *Piresia* Swallen and *Piresiella* Judz., Zuloaga & Morrone), those with male spikelets more or less surrounding female spikelets, and with a corresponding characteristic synflorescence arrangement (viz. *Froesiochloa* G.A. Black, *Maclurolyra* C.E. Caderón & Soderstr, and *Rehia* Fijten, also with female antheria covered by cylindrical macrohairs), the remarkably similar inflorescence structure of the Cuban endemics, especially in *Mniochloa* Chase and *Ekmanochloa* Hitchc. (cf. Zuloaga et al. 1993), and the proper delimitation of taxonomically difficult taxa, like remaining *Olyra* and *Pariana* Aubl. (this last genus paraphyletic, even excluding the recent segregate *Parianella* Hollowell, F.M. Ferreira & R.P. Oliveira).

The principal aim of this revision is to validly publish some combinations first suggested in part III of the series (Grande 2015: 19). Four generic concepts are, as a consequence, emended.

## Materials and methods

### Plant material

Herbarium specimens of tribe Olyreae were examined under magnification and carefully dissected only when needed. In addition to the herbaria cited in the nomenclatural paragraphs, the following herbaria were examined: CAR, CICY, CORO, CTES, GUYN, HERZU, MER, MERC, MERF, MY, MYF, UCOB, and UOJ (acronyms after Thiers *s.d.*). For a limited number of taxa (*viz.* *Lithachne pauciflora* (Sw.) P. Beauv., *Olyra latifolia* L., *O. longifolia* Kunth, *O. standleyi* Hitchc., *Pariana radiceflora* Sagot ex Döll *s.l.*, *Raddia guianensis* (Brogn.) Hitchc., *Raddiella esenbeckii* (Steud.) C.E. Calderón & Soderstr., and *O. micrantha* Kunth), fresh material was also available.

### Phylogeny reconstruction, morphological analyses and taxonomy

Standard procedures were followed to examine both fresh and herbarium material (this last including only *exsiccatae*; *cf.* Radford *et al.* 1974). Morphoanatomical characters generally follow the terminology of Calderón and Soderstrom (1973, 1980). Phenotypic characters and character states available both from specimens and literature were considered *a priori* as putative apomorphies when shared by a set of species. Of all possible cladograms, that with the maximum number of synapomorphic characters and character states was selected; in an hypothetical case where two or more trees show the same number of synapomorphic, that (or those) with a greater (assumed) transitional character states in the corresponding transformation series was (or were) selected; if several trees are equally eligible, the tree to be selected should be the strict consensus of all of them, suggesting further study with additional characters. This procedure of relative ranking can be seen as a practical parsimony approach to the Comparative Holomorphological Method (Hennig 1966: 84-133), and is here coined as “Direct Phylogentic Argumentation” (DPA). In contrast with classical parsimony approaches, where evolutionary transitions are *a priori* minimized, in DPA the distribution of shared characters is assumed, after an appropriate comparative analysis, to be maximal; this leads to “Maximum Synapomorphy” (MS) instead of “Maximum Parsimony” (MP) trees. Although here implemented as “manual” (*i.e.*, by the “checking and rechecking” approach, as in classical hennigian argumentation), this method could be further developed with the aid of an explicit (computer-aided) algorithm, at least for the MS statement. In order to prevent a classification based on homoplasies, characters that clearly shows a convergent or parallel nature (*e.g.*, disposition of sexes in the inflorescences cross the genera of the Olyrinae) or are assumed as plesiomorphous (*e.g.*, conjugate condition of the inflorescences, also in the Olyrinae) could



be *a priori* excluded, leading to a character matrix with only putative apomorphies. As was shown by Hennig (1966: 120-122), apomorphies are to be considered as evidence of kinship, when shared by a set of taxa, in the absence of additional evidence (the so-called “auxiliary principle” of Hennig 1966: 121). If all considered characters are assumed as apomorphies, then, the MS statement can be seen as a generalization of the auxiliary principle. In the particular case of the present revision, however, resulting classifications do not change even with the inclusion of the putative homoplasies in the phylogenetic analysis. The only way DPA could be incorrect, in fact, is that congruence based on convergences and parallelisms (known also as homologies; collectively known as homoplasies), and even plesiomorphies are greater than that based on apomorphies, which is clearly a very improbable scenario (*cf.* Hennig 1966: 88-95, and references cited therein). For relative ranking, those clades with the maximum number of synapomorphies in the resulting classification were selected as appropriate taxa; thus, for example, if clade A, comprising species a, b and c, and with autapomorphy 1 shares with clade B, with species d, e and f and autapomorphy 2, synapomorphies 3 and 4, one genus comprising both clades is selected instead of erecting two different genera (*i.e.*, not necessarily one genus for each subclade). As an example of putative transitional character states and their application to tree inference it can be cited the distribution of sexes in inflorescences of *Buergersiochloinae* (basally male and apically female) vs. *Olyrinae* (complex), with intermediate *Parianinae* (male spikelets subtending 0-2 female spikelets in an essentially equivalent way of that of the highly plesiomorphic *Diandrolyra* Stapf [codified as character state “3” in Figure 1]). For absolute ranking determination it is assumed a more or less synchronous time of origin (as in Hennig 1966: 154-193).

Since relationships between several optimal species’ clusters or “genera” (obtained as described above) are as yet poorly understood (*i.e.*, it is not clear which characters are in an apomorphous condition), explicit phylogenetic relationships are omitted for a significant number of currently recognized “genera” in the *Olyrinae*; all of them are included within the “rest of the *Olyrinae*” clade. Autapomorphies and shared characters considered as either homoplasies or symplesiomorphies are not shown in the resulting tree (Figure 1), but are discussed in some detail through the text.

## Nomenclature

Nomenclature follows the Melbourne code rules (McNeill *et al.* 2012). Names are listed alphabetically. Only nomenclatural novelties are considered, and these include basionyms, homotypic synonyms, nomenclatural status and protologue’s

information. Citation of the *exsiccatae* include the herbarium registration number accompanying the corresponding barcode (when present, but deleting the extra zeros placed to the left side). In cases where barcoding is absent, present but without an accompanying number (as in *exsiccatae* from MO), or reference to the original registration number is needed, registration number is offered (when present), but with an hyphen connecting it to the herbarium acronym.

Only validly published names are considered, although comments for those that are only effectively published, including the informal groups of *Olyra* of Judziewicz and Zuloaga (1992) and Grande (2015), are also offered. For a complete list of synonyms, the reader is referred to Judziewicz *et al.* (2000), and for detailed geographical distribution and descriptions, to the general works of Judziewicz *et al.* (1999) and Ohrnberger (1999), revisions of Soderstrom (1981), Soderstrom and Zuloaga (1989) and Zuloaga and Judziewicz (1991), as well as protologues of the thereafter described species. For each accepted genus, its etymology is provided.

Emendation of generic concepts are explicitly indicated by the Latin phrase *hic emendatus*, -a, -um (=here emended), abbreviated as “*hic emend.*”. Emendation is effected to stand out the newly proposed circumscriptions, and do not imply type exclusion or lectotypification (*i.e.*, as defined in McNeill *et al.* 2012, and Turland 2013). Emended diagnoses are offered in Latin, since this is the language in which the diagnostic phrases of the four genera here emended were originally published.

## Results and discussion

After a thorough revision of plant material and literature, several taxonomic and nomenclatural novelties are needed. The new proposed circumscriptions are included below each taxon heading; relevant characters and a discussion on their relationships with nearby groups are also included. A phylogenetic MS cladogram, summarizing gross relationships within tribe Olyreae is shown in Figure 1. Subtribe Buergersiochloinae, restricted to Papuasias and constituted by one genus (*Buergersiochloa* Pilg.) and two species, could be easily differentiated by the inflorescences, consisting of two distinct clusters of dimorphic spikelets, the lower cluster conspicuously ramified and strictly male, the upper scarcely ramified and predominantly female; androecium is similar to that of *Froesiochloa* (core Olyrinae), with both basally fused filaments and more or less basally free thecae, lemmas are long-awned (like in *Ekmanochloa*, but in this last genus only female lemmas are awned) and, like in core Olyrinae male glumes are extremely reduced. Subtribe Parianinae, strictly neotropical, is characterized by the spiciform inflorescences, made up (at least apically) of one to several articles, which are deciduous or not. The Parianinae's articles (also known as gynecandrous whorls) consist of a central (ra-



rely none or two) female spikelet surrounded by a whorl of several male spikelets, the female spikelets sometimes consistently absent from the lower articles. The male spikelets are highly reduced, and subtended by conspicuously developed laminar pedicels, just with a pair of stamens (rarely three) in *Pariana multiflora* R.P. Oliveira, Longhi-Wagner & Hollowell, *Parianella* and *Eremitis* Döll, which are geographically restricted to the Atlantic forests of eastern Brazil, vs. male spikelets conspicuously developed and with 6-40 stamens in *Pariana*, an Amazonian as well as a circumcaribbean genus. Differences between these four taxa are very clear, and current phylogenetic hypotheses highly support their monophyly. Currently, however, genus *Pariana* is paraphyletic, because of the inclusion of *P. multiflora* and *P. parvispica* R.W. Pohl; segregation of these species into one, or even two new genera is highly advisable, but it will not be done here, since their systematic position is a matter of a work, yet to be published, of Fabrício Ferreira (Ferreira et al. 2013). Subtribe Olyrinae have no apparent synapomorphies, the characters that readily differentiate it from the Parianinae are symplesiomorphies shared with the Buergersiochloinae. Excavations in the female antherium could be hypothesized as a synapomorphy for this subtribe, but their presence in Parianinae and Buergersiochloinae are as yet to be elucidated. *Raddiella* and *Diandrolyra* are differentiated from core Olyrinae by the female spikelets generally falling entire, with two points of disarticulation, one above and other below glumes (vs. female glumes persistent, with just one point of disarticulation, above glumes), male glumes more or less developed (vs. male glumes absent), female pedicels not expanded at apex (vs. female pedicels expanded at apex, female spikelets with a basal callus formed by the fusion of the basal portion of the glumes (vs. basal callus absent), and basic chromosome number  $x=9,10$  or their multiples (vs.  $x=11$ , exceptionally  $x=7$  or  $x=12$ , or their multiples). Within core Olyrinae are included *Olyra* group Latifolia (which include *O. latifolia*, the type of genus *Olyra* and subtribe Olyrinae), remaining three genera emended in the present revision (viz. *Agnesia*, *Arberella* and *Raddia* Bertol.) and *Lithachne*. Additional taxa shown in Figure 1 include the Cuban endemics *Ekmanochloa* and *Mniochloa*; these two genera share with *Piresiella* the inflorescence type (simply jugate, either branch with only female or only male spikelets), but in this last genus, female antheria are strikingly different (conspicuously covered by cylindrical macrohairs and with the apex of the lemma apiculate), while epidermal cells (at least abaxially) are simply lobed (vs. conspicuously bilobed to two-toothed), and conspicuous fusoid cells, or their respective lacunae, are present at both sides of the vascular bundles (cf. Zuloaga et al. 1993). Reduced glumes in *Ekmanochloa subaphylla* Hitchc. suggest parallel evolution with *Mniochloa*, also from limestone cliffs of eastern Cuba. Remaining genera within core Olyrinae were not resolved, and are included within the “rest of the Olyrinae” clade in Figure 1.

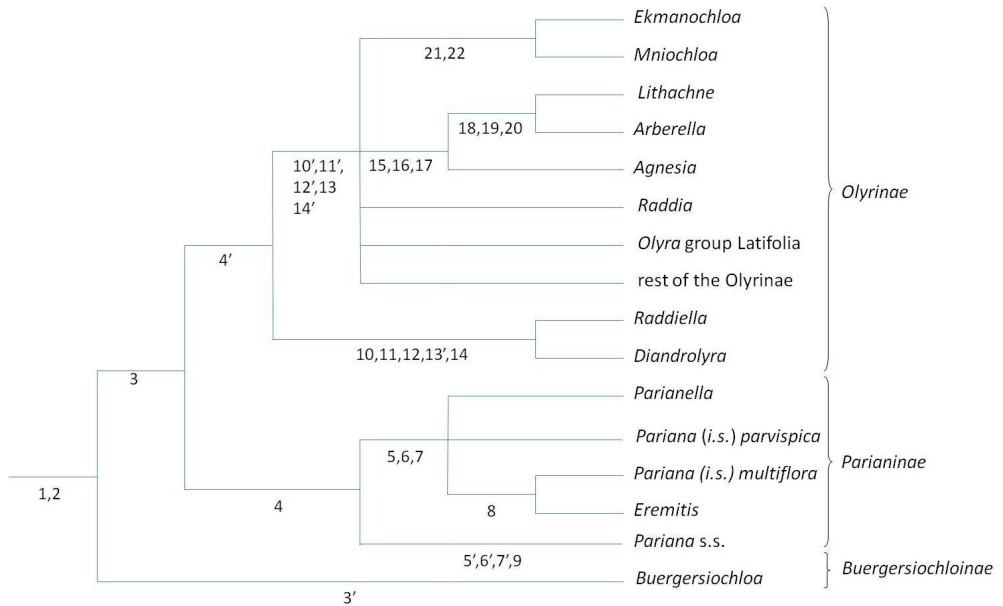


Figure 1: Maximum Synapomorphy (MS) tree showing relationships between subtribes, genera and species groups in the tribe Olyreae, based on morphological characters, and following Direct Phylogentic Argumentation (DPA); the arrow shows the core Olyrinae; numbers with apostrophes indicate alternative (derived) states of the characters; 1: Unisexual spikelets; 2: reduction of male glumes (rarely reaching a half of the total length of the spikelet); 3: male and female spikelets conjugate (3': male and female spikelets remote, forming distinct clusters); 4: spikelets in gynecandrous whorls (4': female spikelets to the top of branches, generally subtended by male spikelets); 5: male spikelets highly reduced (5': male spikelets slightly reduced); 6: male pedicels conspicuous and laminar (6': male pedicels reduced and not laminar); 7: male spikelets with just one pair of stamens (rarely three stamens; 7': stamens 6 to 40 per spikelet); 8: basal whorls strictly male; 9: lunar marks (two paired scars at the apex of sheaths); 10: female spikelets generally falling entire, with two points of disarticulation, one above and other below glumes (10': female glumes persistent [female spikelets with just one point of disarticulation, above glumes]); 11: male glumes more or less developed (11': male glumes absent); 12: female pedicels not expanded at apex (12': female pedicels expanded at apex); 13: basal callus absent (13': female spikelets with a basal callus formed by the fusion of the basal portion of the glumes); 14: basic chromosome number  $x=9,10$  or their multiples (14':  $x=11$ , exceptionally  $x=7$  [Olyra fasciculata, fide Calderón and Soderstrom 1973] or  $x=12$  [one specimen of Arberella costaricensis fide Reeder et al. 1969], or their multiples); 15: culm calluses; 16: pseudope-

tiole swellings; 17: male spikelets early deciduous; 18: anthercia with conspicuous flattened macrohairs (generally absent in *Lithachne*); 19: inflorescence type (*sensu* Soderstrom and Calderón 1979); 20: knoblike processes at both base and apex of pseudopetioles; 21: inflorescences jugate (*i.e.*, one male raceme and one female raceme arising at the apex of the peduncle; this character is shared with *Piresiella*, also a Cuban endemic); 22: abaxial epidermal cells conspicuously bilobed to two-toothed. For generic autapomorphies see the general text.

1. *Agnesia* Zuloaga & Judz., *Novon* 3(3): 306-307. 1993, *hic emend.* TYPUS: *Olyra lancifolia* Mez, Mez, *Notizbl. Bot. Gart. Berlin-Dahlem* 7: 45. 1917 ( $\equiv$  *A. lancifolia* (Mez) Zuloaga & Judz.).

Secundum circumscriptionem hic propositam, species *Agnesia* habitu herbaeo, perenni et humili, culmis haud ramificatis, inflorescentiis paniculatis spiculis femineis apicalibus, masculis basalibus, rariter unisexualibus, antherciis femineis fusiformibus pilis cilindraceis aliquantum reductis, et parvis aculeis (praesertim ad apicem) conspicue obtectis, rite distinguenda ab omnibus generibus tribus *Olyreae*. Anthercia feminea imatura membranacea, cartilaginea in maturitate. Spiculae masculae conspicue minores quam femineae, valde variabiles in speciebus.

## Etymology and distribution

The genus *Agnesia* was named “in honor of Agnes Chase (1869-1963), outstanding American agrostologist and author of a monumentally complete and useful index of published grass names (Chase & Niles, 1962)” (Zuloaga and Judziewicz 1993); an alternative version of this etymology, also referring to the eminent agrostologist Mrs. Chase is offered in Judziewicz *et al.* (1993). Including the new combinations, *Agnesia* inhabits forested ecosystems of tropical South America, excluding the Andes, from near sea level to 1200 m a.s.l. *Agnesia ciliatifolia* (Raddi) J.R. Grande is the most widespread species, generally growing in semideciduous forests life zones, including disturbed sites. Argentina, Bolivia, Brazil, Colombia, Guyana, Paraguay, Peru and Venezuela.

1a. *Agnesia amapana* (Soderstr. & Zuloaga) J.R. Grande, *comb. nov.* *Olyra amapana* Soderstr. & Zuloaga, *Smithsonian Contr. Bot.* 69: 5–8, f. 1–2, 15. 1989. TYPUS: Brazil: Amapá: Rio Aguari, vicinity Camp 13, 1°45' N, 52°W, in shadow of upland forest, 06 X 1961, J.M. Pires, W. Rodrigues & G.C. Irvine 51536 (holotypus: IAN; isotypi: K 433337!, NY 381530!, U 2307!, US 153826!, US 153827!).

1b. *Agnesia bahiensis* (R.P. Oliveira & Longhi-Wagner) J.R. Grande, *comb. nov.* *Olyra bahiensis* R.P. Oliveira & Longhi-Wagner, *Revista Brasil. Bot.* 28(4): 835-836, f. 1. 2005. TYPUS: Brazil: Bahia: Una, km 15.6 da rodovia São José/Una, 10 km SE até São José, 21 II 1986, T.S. dos Santos & E.J. Judziewicz 4113 (holotypus: CEPEC, isotypus: US).

1c. *Agnesia ciliatifolia* (Raddi) J.R. Grande, *comb. nov. Olyra ciliatifolia* Raddi, *Agrostr.* Bras. 19-20 (Atti R. Accad. Lucchese Sei, Lett., ed. Arti 2: 345). 1823. LECTOTYPUS (designated by Judziewicz, E.J., 2000, *Contr. U.S. Natl. Herb.* 39: 83, as “HT”, but correctable to “lectotype” according to Artt. 7.10 and 9.9). Brazil: Rio de Janeiro: “Invenitur in saltibus montosis, et sepibus prope Rio-Janeiro, nec non in Montibus estrell.” [as in the protologue], *G. Raddi s.n.* (PI (photo in US 132859!); isolectotypi: BAA 2281! (fragm. ex FI), FI 4593!, G 99443!, US 132859 (=US-2879005!, fragm. ex PI [erroneously published as “FI” in Judziewicz (2000)]).

For technical details on the lectotypification process of this species, the reader is referred to part VI of the series (Grande, in prep.).

1d. *Agnesia jubata* (J.R. Grande) J.R. Grande, *comb. nov. Olyra jubata* J.R. Grande, *Novon* 24(1): 16, f. 1. 2015. TYPUS: Peru: Loreto: Prov. Maynas, Yanomono, Explorama Tourist Camp, betw. Indiana & mouth of Rio Napo, non-inundated forest on lateritic soil, 3° 28' S, 72° 48' W, 130 m a.s.l., 18 II 1981, A.Gentry, K.Young, R. Vásquez, S.Libenson, M. Olson & N. Jaramillo 31405 (holotypus, VEN-276963!; isotypi: F, MO-3334157, US-3125868, USM, AMAZ).

1e. *Agnesia juruana* (Mez) J.R. Grande, *comb. nov. Olyra juruana* Mez, *Notizbl. Bot. Gart. Berlin-Dahlem* 7(63): 45. 1917. TYPUS: Brazil: Amazonas: ad flumen Jurua prope Minas Geraes, 25 IV 1901, E. Ule 5469 (holotypus: B 10 0249098!; isotypus: US 132874! (fragm. ex B)).

1f. *Agnesia lorentensis* (Mez) J.R. Grande, *comb. nov. Olyra lorentensis* Mez, *Notizbl. Bot. Gart. Berlin-Dahlem* 7(63): 47. 1917. TYPUS: Peru: Loreto: prope Leticia in silvis, VI 1902, E. Ule 6224 (holotypus: B 10 0249091!; isotypi: G 99439!, K 433345!, MG 6095!, US 132876! (fragm. ex B)).

When describing *Agnesia*, Zuloaga and Judziewicz (1993) considered this genus as realted (but distinct) to *Arberella* by the inflorescences with a single (rarely several) solitary female spikelets over clavate pedicels and densely silky-hairy female anthercia, and similar to some species of *Olyra* group *Ciliatifolia* (viz. *Olyra amapana* Soderstr. & Zuloaga and *O. juruana* Mez) by the presence of 1-10 inflorescences at the uppermost nodes, subequal female glumes and, once again, silky-hairy female anthercia, especially *O. amapana*, with which *Agnesia lanicfolia* (Mez) Zuloaga & Judz. (then the only species in the genus), shares inflorescences with solitary (rarely 2-4 [-6 *fide* Grande 2009]) terminal female spikelets. *Arberella*, however, can be easily differentiated from *Agnesia* by the anthercia with conspicuous flattened macrohairs, inflorescence type and the knoblike processes at both base and apex of pseudopetioles (Figure 1). The only consistent characters that differentiate *Agnesia s.s.* from *Olyra* group *Ciliatifolia* are the relatively narrow leaf blades, and glumes of the female spikelets with a relatively reduced number of veins (five veins plus an additional pair toward the apex in the lower glume, three veins in the upper glume); additional characters cited by Zuloaga and Judziewicz (1993), viz. the more or less strongly asymmetrical leaf blade bases and awnless

female florets, are either associated to morphological constraints (blades in fact are also asymmetrical, but in the bases they are too narrow to clearly show this character) or are rather variable (cf. subgroups of *O.* group *Ciliatifolia* in Grande 2009 and 2015, based on the presence/absence of awns). Within *Agnesia* s.l. (i.e., including *Agnesia* s.s. and *Olyra* group *Ciliatifolia*), *A. lorentensis* is the most divergent species, with bladeless flowering culms, and pseudopetioles with adaxial as well abaxial swellings.

Species of *Agnesia* are characterized, as circumscribed in the present revision, by the herbaceous perennial habit, no ramified shoots, short size of the plants, and presence of fusiform female anthercia, conspicuously covered by cylindrical macrohairs, some of them reduced to small aculei, especially toward the apex. Female anthercia of *Agnesia* are membranous in immature spikelets, turning cartilaginous when the caryopsis is fully developed. Male spikelets are considerably smaller than in females, and quite variable between species. Species of *Agnesia* included in *Olyra* group *Ciliatifolia* in Grande (2015) shares with *Arberella* and *Lithachne* the so-called “culm calluses” of Judziewicz & Zuloaga (1992), pseudostipule’ swellings (highly variable between species), male spikelets early deciduous and (generally) unramified low habit. *Agnesia* can be differentiated, however, by the female anthercia characters cited above (vid. supra). Depending on the degree of development of the female spikelets, the anthercia could be considered as either membranous (immature; Grande 2015) or cartilaginous (fully mature; Grande 2009).

Only one additional species is known from this genus (viz. *Agnesia lancifolia*, its type species). One variant of that species, growing in Pará, shows markedly narrowed leaves, and could deserve taxonomic recognition, but additional material is needed (cf. Zuloaga and Judziewicz 1993).

2. *Arberella* Soderstr. & C.E. Calderón, *Brittonia* 31(4): 433. 1979, *hic emend.* TY-PUS: *Arberella dressleri* Soderstr. & C.E. Calderón, *Brittonia* 31(4): 433. 1979.

*Olyra* sect. *Pleurandrogynae* Döll, *Fl. Bras. (Martius)* 2(2): 326. 1877, *syn. nov.* LECTOTYPUS (*hic designatus*): *Olyra flaccida* Döll, *Fl. Bras. (Martius)* 2(2): 326. 1877.

Species generis *Arberellae* a reliquis tribus generibus distinguendae: culmis herbaceis callis rotundis ad apicem internodorum, inflorescentiis monoecis ad nodos superiores (aliquando ad nodos medios et/vel basales); glumis femineis magis minusve paucinervatis (5-7(-8-11)-nervatis in *Arberella*, (5-)7-15-nervatis in *Olyra* s.s.), antherciis femineis fusiformibus pilis complanatis secus margines donatis, basibus apicibusque lemmatis paleaeque aliquando apice absentibus (in *Olyra davidseana* Judz. & Zuloaga ad basin restrictis) dispositis, spiculis masculis femineisque subaequalibus sed conspicue dimorphicis; spiculis femineis ad apicem inflorescentiae; spiculis masculis ad basin restrictis.



## Etymology and distribution

“The generic name commemorates the eminent English plant morphologist, Agnes Arber (1879-1960), whose extensive studies of grasses, including bamboos, earn her a special place in agrostology” (Soderstrom and Calderón 1979). Not to be treated as a homonym of *Arberella* D.D. Pant & Nautiyal by a recommendation of the Spermatophyta Committee of Nomenclature (Brummitt, 2001: 568). Neotropics, from Yucatán peninsula and San Luis Potosí (Mexico) to northern Argentina (Corrientes and Misiones).

2a. *Arberella davidseana* (Judz. & Zuloaga) J.R. Grande, *comb. nov.* *Olyra davidseana* Judz. & Zuloaga, *Syst. Bot.* 17(1): 25, f. 1. 1992. *Typus*: Brazil: Pará: km 100 on Belém-Brasília highway, forest, 14 VIII 1964, G.T. Prance & N.T. Silva 58735 (holotypus: IAN; isotypi: K 433341!, MO 2230030!, MO 2780048!, NY743590!, NY 743589!, US 290907!).

2b. *Arberella glaberrima* (Raddi) J.R. Grande, *comb. nov.* *Olyra gaberrima* Raddi, *Agrostogr. Bras.* 19. 1823. *LECTOTYPUS* (designated by Baldini & Longhi Wagner, *Taxon* 55(2): 470. 2006): Brazil: “in monte Corcovado prope Rio de Janeiro locis umbrosis humidis” (as in the W’s isolectotype), G. Raddi s.n. (PI [photo in US 132870]!; isolectotypus: BAA 2282! (fragm. ex FI), FI 4620!, US 132870!, W 1904-001337!).

2c. *Arberella humilis* (Nees) J.R. Grande, *comb. nov.* *Olyra humilis* Nees, *Fl. Bras. Enum. Pl.* 2(1): 304-306. 1829. *LECTOTYPUS* (designated, as holotype, by Soderstrom & Zuloaga, *Smithsonian Contr. Bot.* 69: 24. 1989): Brazil: Habitat ad ripas Taquari fluminis, 12 IX 1823, F. Sellow s.n. (B10 0249099!; isolectotypus: US 132872! (fragm. ex B)).

2d. *Arberella maranonensis* (Swallen) J.R. Grande, *comb. nov.* *Olyra maranonensis* Swallen, *Phytologia* 14(2): 86. 1966. *Typus*: Peru: Amazonas: valley of the Río Marañón near Cascadas de Mayasi, in rainforest on ridge crest of Quebrada Chuiva, 500-550 m a.s.l., 20 IX 1962, J.J. Wurdack 1936 (holotypus: US 132844!).

Species of *Arberella*, as here defined, are characterized by presence of conspicuous and rounded calluses toward the apex of the culm internodes, several (monoecious) inflorescences at the uppermost nodes (sometimes also present at the medial nodes), female glumes more or less paucinerved (5-7(-8-11) nerved in *Arberella* vs. (5-)7-15 nerved in *Olyra* s.s.), female anthercia fusiform, with flattened hairs distributed along the margins, base and apex of the lemma and the palea (sometimes absent in the apex of the anthercium; the pubescence of *A. davidseana* (Judz. & Zuloaga) J.R. Grande restricted to the base), female and male spikelets of similar size, but markedly dimorphic (female spikelets toward the apex of the inflorescence, subtended by pedicels conspicuously thickened apically, male spikelets subtended by filiform pedicels, restricted toward the base), and hilum linear, as long as the caryopsis.



As stressed recently by Grande (2015) members of *Arberella* s.s. share with *Olyra* group *Glaberrima* a characteristic type of flattened macrohair in the female anthercium; this last group has been considered distinct from *Arberella* only for the minor habit and a tendency to produce inflorescences toward the middle of the plant (instead of only toward the apex), both characters very variable within the subtribe. In this work, the four species of such informal group are merged with *Arberella*. Results of de Oliveira et al. (2014) corroborates monophyly of *Arberella* s.l. (i.e., as here defined). The so-called “culm calluses” of Judziewicz and Zuloaga (1992) are present (but reduced) in several species of *Agnesia* and *Lithachne*, as well as in *Cryptochloa dressleri* Soderstr., *Piresia leptophylla* Soderstr. and *Olyra filiformis* Trin.; their presence in only one species of these last three genera could indicate convergence rather than homology.

Remaining species in the genus are: *Arberella bahiensis* Soderstr. & Zuloaga, *Arberella costaricensis* (Hitchc.) Soderstr. & C.E. Calderón, *Arberella dressleri* Soderstr. & C.E. Calderón, *Arberella flaccida* (Döll) Soderstr. & C.E. Calderón, *Arberella grayumii* Davidse, *Arberella lancifolia* Soderstr. & Zuloaga, and *Arberella venezuelae* Judz. & Davidse.

3. *Olyra* L., Syst. Nat. (ed. 10) 2: 1253, 1261, 1379. 1759. TYPUS: *Olyra latifolia* L., Syst. Nat. (ed. 10) 2: 1261. 1759.

*Mapira* Adans., Fam. Pl. 2: 39, 574. 1763, nom. illeg. superfl.

Diagnostic characters as for core Olyrinae (i.e., genera in subtribe Olyrinae in Judziewicz et al. 1999, except *Raddiella* and *Diandrolyra*; see Figure 1). Its members share a somewhat robust habit as well as monoecious and terminal (rarely also axillary) inflorescences (cf. Judziewicz et al. 1999), and include *Olyra latifolia*, the type of the tribe. Despite recent segregation of a part of its original members (Soderstrom and Calderón 1979; Soderstrom 1981; Soderstrom and Zuloaga 1989; Zuloaga and Judziewicz 1993), this genus is still highly polymorphic, and in need of a thorough systematic study. When completed, recognition of additional segregates is expected. Although an infrageneric subdivision would be desirable at present, traditional (and validly published) infrageneric taxa do not reflect remaining heterogeneity; the proposed sections, in fact, correspond to already described generic concepts, and two of them are here synonymized (viz., *Olyra* sect. *Heterogenicae* and *O. sect. Pleuroandrogyne*); remaining two represent either a superfluous name (*O. sect. Acrandrogyne*) or a previously synonymized name (viz., *O. sect. Lithachne* (P. Beauv.) Rchb., under *Lithachne*). Although in their protologues the term “sectio” or its abbreviation is not accompanying these names, they can be associated to sections according to Art. 37.5; that term, in fact, is directly associated to them in general text of the same volume (e.g., in p. 326). *Olyra ecaudata* Döll and *O. pineti* Wright ex Griseb. were treated by Döll (1877) as independent species.

## Etymology and distribution

According to Judziewicz *et al.* (1999) *Olyra* means [in classical greek] “a lily”, though Linnaeus did not publish its etymology when describing the genus (Linnaeus 1759); this name is also applied to a fish genus described later, in the order Siluriformes (*viz.* *Olyra* McClelland, 1842), which is also validly published (more properly “available”), because the governance of plant names is independent of that of the animals (Principle I of the preamble, and Art. 54 of McNeill *et al.* 2012). Its species distributes along the Neotropics, from Florida (not recently collected) and Mexico to northern Argentina (Salta, Corrientes and Misiones); *Olyra latifolia* L. is also present in western Paleotropics, including tropical Africa, Madagascar and Comoro Islands (just between these two landmasses). For an etymology of the sections proposed by Döll (1877), see the second paragraph of the introductory notes of the present revision.

3a. *Olyra* sect. *Acrandrogynae* Döll, Fl. Bras. (Mart.) 2(2): 315. 1877, *nom. illeg. superfl.* (Art. 52.1, because include the type of the genus and, thence, the automatically established *O. L.* sect. *Olyra*).

Included within this section were species here considered as part of *Arberella* s.l., *Cryptochloa* Swallen, *Olyra*, *Piresia* and *Raddiella* Swallen s.l. Originally included species are: *Olyra latifolia* L., *O. cordifolia* Willd. (= *O. latifolia*), *O. scabra* Nees (= *O. latifolia*), *O. capillata* Trin. (≡ *Cryptochloa capillata* (Trin.) Soderstr.), *O. ramosissima* Trin. (= *Raddiella*), *O. sarmentosa* Döll (= *Raddiella lateralis*), *O. glaberrima* Raddi (= *Arberella*), *O. semiovata* Trin. (= *A. glaberrima*), *O. humilis* Nees (= *Arberella*), *O. ciliatifolia* Raddi, *O. sympodica* Döll (≡ *Piresia sympodica* (Döll) Swallen), *O. micrantha* Kunth (= *Raddiella*), *O. fasciculata* Trin., *O. longifolia* Kunth and *O. filiformis*.

3b. *Olyra* sect. *Heterogenicae* Döll, Fl. Bras. (Mart.) 2(2): 327. 1877. LECTOTYPUS (*hic designatus*): *Olyra polypodioides* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3, 1(2-3): 117. 1834 (= *Raddia distichophylla* (Schrad. ex Ness) Chase).

This section, as defined by its author, include *Raddiella* and *Raddia*, and it is synonymized in the present revision under *Raddia* (*vid. infra*). Species included by Döll (1877) are: *Olyra polypodioides* Trin. (= *Raddia distichophylla* (Schrad. ex Nees) Chase), *O. floribunda* Raddi (= *Raddia brasiliensis* Bertol.) and *O. nana* Döll (= *Raddiella esenbeckii* (Steud.) C.E. Calderón & Soderstr.).

3c. *Olyra* sect. *Lithachne* (P. Beauv.) Rchb., Consp. Regn. Veg. 50. 1828 (≡ *Lithachne* P. Beauv.). TYPUS: *Olyra pauciflora* Sw., Prodr. (O.P. Swartz) 21. 1788 (≡ *Lithachne pauciflora* (Sw.) P. Beauv.).

A discussion in nomenclature of this section was omitted in the historical account of *Lithachne* made by Chase (1908) and recent taxonomic studies, including the last comprehensive revision of the genus *Olyra* (Soderstrom and Zuloaga

1989) and the synoptical study of *Lithachne* by Soderstrom (1980); apparently, *O.* sect. *Lithachne* was first synonymized by Ohrnberger (1999: 417), who explicitly includes this name under *Lithachne* (considered by him as a genus).

3d. *Olyra* sect. *Pleurandrogynae* Döll, Fl. Bras. (Martius) 2(2): 326. 1877. LECTOTYPUS: *O. flaccida* Döll., Fl. Bras. (Martius) 2(2): 326. 1877.

Included within this section were: *Olyra flaccida* Döll ( $\equiv$  *Arberella flaccida*) and *O. pauciflora* Sw. ( $\equiv$  *Lithachne pauciflora* (Sw.) P. Beauv.). In the present revision, *Olyra* section *Pleurandrogynae* is lectotypified, and synonymized under *Arberella* (*vid. supra*).

The genus *Olyra*, as presently circumscribed, includes 25 species in at least five informal groups (Judziewicz and Zuloaga 1992; Grande 2015). The characters traditionally employed to separate *Olyra* from similar genera, however, could be considered artificial, and either homoplastic (Judziewicz *et al.* 1999, Grande 2015) or symplesiomorphic (de Oliveira *et al.* 2014), if not typical of the entire tribe but for *Raddiella s.l.* (*i.e.*, as defined in the present revision) and *Diandrolyra*, which possess spikelets (at least partially) falling entire (*vs.* with the glumes persistent), male spikelets with glumes more or less developed, female pedicels not expanded at apex, and female spikelets with a basal callus formed by the fusion of basal portion of the glumes. This putative clade is consistent with an ancestor with female pedicels not expanded at apex and with male spikelets subtending female spikelets, like in *Parianinae*, and is supported by a recent molecular study (de Oliveira *et al.* 2014), in which two of the three published trees (corresponding to the non combined ITS and *trnD-trnT* data matrices) suggest this same relationship. This is the first time such clades are proposed based on (direct) hennigian argumentation and supported by a transformation series fully based upon non-molecular characters.

4. *Raddia* Bertol., Opusc. Sci. 3: 410. 1819, *hic emend.* TYPUS: *Raddia brasiliensis* Bertol., Opusc. Sci. 3: 410. 1819, non Mazziari, Ionios Antologia 2: 448. 1834 ( $\equiv$  *Sporobolus* sect. *Crypsis* (Aiton) P.M. Peterson [Gramineae]), nec DC. ex Miers, Trans. Linn. Soc. London 28(2): 389. 1872 ( $\equiv$  *Salacia* L. [Hippocrateaceae-Celastraceae *s.l.*]), nom. illeg. superfl. (Art. 52.1; *Raddisia* Leand., published in 1821, is cited in synonymy).

*Strepium* Schrad. ex Nees, Fl. Bras. Enum. Pl. 2(1): 298. 1829. TYPUS: *Strepium distichophyllum* Schrad. ex Nees, Fl. Bras. Enum. Pl. 2(1): 298-299. 1829 (*Raddia distichophylla* (Schrad. ex Nees) Chase).

*Olyra* sect. *Heterogenicae* Döll, Fl. Bras. 327. 1877, *syn. nov.* LECTOTYPUS: *Olyra polypodioides* Trin. ( $\equiv$  *Raddia distichophylla* (Schrad. ex Nees) Chase), designated in this work (*vid. supra*).

*Sucrea* Soderstr., Brittonia 33(2): 200. 1981, *syn. nov.* TYPUS: *Sucrea monophylla* Soderstr., Brittonia 33(2): 200, 204, f. 1-3. 1981.

Gramina radibus conspicue epigeis, valde congestis. Pedicelli spicularum masularum breves ad apicem vix turbinati (sed conspicue crassiores quam feminearum). Spiculae femineae glumis conspicue cartilaginosis secus eis margines, antheis femineis vix punctatis.

## Etymology and distribution

“Bertoloni states that the specific name will commemorate the courageous voyage to Brazil of [Giuseppe] Raddi [1770-1829] to whom the genus is dedicated” (Chase 1908, IPNI 2015). *Raddia* is also a name in the Hippocrateaceae (=Celastraceae s.l.) and Gramineae, both published later and, consequently, illegitimate homonyms (Art. 53.1). Neotropics, from Venezuela, Trinidad & Tobago, the Guianas and northeastern Amazonia to southeastern and central-western Brazil.

4a. *Raddia maculata* (Soderstr.) J.R. Grande, *comb. nov. Sucrea maculata* Soderstr., *Brittonia* 33(2): 205, 207, f. 4, 5. 1981. TYPUS: Brazil: Rio de Janeiro: Serra de Bica prope Cascadura, 1886, C.A.W. Schwacke s.n. (holotypus: R46717!).

4b. *Raddia monophylla* (Soderstr.) J.R. Grande, *comb. nov. Sucrea monophylla* Soderstr., *Brittonia* 33(2): 200, 204, f. 1-3. 1981. TYPUS: Brazil: Bahia: Município Itabuna, Ferradas, Fazenda Aberta Grande (ca. 14°47'21" S, 39°16'36" W), 16 I 1968, C.E. Calderón 2045 (holotypus: CEPEC; isotypi: B 10 0250218!, G 168441!, G 168442!, K1087!, LE, MO-2816641!, NY431659!, P642205!, RB, US 136211!, US 136212!, W 1993-0002213!).

4c. *Raddia sampaiana* (Hitchc.) J.R. Grande, *comb. nov. Olyra sampaiana* Hitchc., *J. Wash. Acad. Sci.* 17(9): 215, f. 1. 1927. *Sucrea sampaiana* (Hitchc.) Soderstr., *Brittonia* 33(2): 208, f. 6. 1981. TYPUS: Brazil: Espírito Santo: Reeve, 06 XII 1924, J. Vidal 44 (holotypus: US 132848!; isotypus: R 16000!).

As noted in previous works (e.g., Soderstrom 1981, Clayton and Renvoize 1986, de Oliveira et al. 2014, Grande 2015), members of *Raddia* s.l. (i.e., as here defined) have female spikelets with glumes conspicuously cartilaginous along margins, a character related to ballistochory (Sendulsky 1993). As stressed by Grande (2015), species of *Sucrea* Soderstr. are very similar to that of *Raddia* s.s. as previously circumscribed, the characters proposed to separate this two taxa being the sex and pattern of distribution of the inflorescences along the plant (terminal and monoecious in *Sucrea* vs. axillary female and terminal male in *Raddia* s.s.), leaf blades (with symmetrical apices and undersurfaces bluish-green in *Sucrea* vs. asymmetrically apiculate at the apices and undersurfaces green in *Raddia* s.s.), and general size and habit (generally bigger and with a more robust habit in *Sucrea*; Soderstrom 1981 and de Oliveira et al. 2008a, 2014). As could be noted in recent studies on *Raddia* s.s. (de Oliveira et al. 2008a, 2014). However, apices of leaves, undersurface coloration, habit, and even inflorescence distribution could be intermediate in some instances. As pointed out previously, in-

florescence structure is a highly complex character, as yet poorly understood (cf. Calderón and Soderstrom 1980: 4), and with many transitional forms within genera, species, and even single individuals. Perhaps the best example of this phenomenon is *Raddia soderstromii*, an endemic of the Atlantic forests of Brazil. In this species there are populations with individuals with both male and female spikelets in the terminal panicle, and depauperate individuals that bear only two leaves, as is common in *Sucrea sampaiana* (Hitchc.) Soderstr. Geographic distribution and habitats of *Raddia s.s.* and *Sucrea*, moreover, are highly similar, with major centers of diversity overlapping. In the recent study of de Oliveira *et al.* (2014) *Raddia megaphylla* R.P. Oliveira & Longhi-Wagner appears as highly nested within the *Raddia s.s.* clade, despite being very similar in vegetative characters with *Sucrea monophylla*, the type species of the genus (similarities include apical leaves with free sheaths resembling pseudopetioles); in the same study, monophyly of *Sucrea* plus *Raddia s.s.* is highly supported by the ITS sequence analysis (bootstrap value =89%), and only moderately supported by the *trnD-trnT* tree (bootstrap value =63%), the alternative hypothesis (based on the combined matrix of chloroplastic and nuclear sequences) being scarcely supported and leaving as paraphyletic both *Raddia* and *Sucrea*; this last scenario suggests further segregation, with resulting genera very poorly supported and with almost no apomorphies. Only one of the three trees published in de Oliveira *et al.* (2014; corresponding to the chloroplastic sequences), moreover, supports a monophyletic *Sucrea*, but with a relatively low bootstrap value (63%) and no consistent morphological synapomorphic characters, as discussed above. Female anthecia are finely pitted in these two genera (de Oliveira *et al.* 2014); additional synapomorphies proposed in the present revision include female pedicels short and scarcely turbinate at the apex (though conspicuously stouter than males), and radical system strongly epigeous with corresponding plant bases notably stout, similar to that found in palms (family *Arecaceae*).

The genus *Raddia* includes *Strephium* and *Hellera* Schrader ex Döll, an invalid name published by Döll (1877) as an inedit synonym of *Olyra*. That name was included by Schrader in an unpublished manuscript. Because *Hellera* is an invalid name it could not be considered as a synonym of either *Raddia* or any other genus (the code provides that for nomenclatural purposes, botanical names must be validly published (Art. 12.1)).

Remaining species in this genus are: *Raddia angustifolia* Soderstr. & Zuloaga, *Raddia brasiliensis* Bertol., *Raddia distichophylla* (Schrad. ex Nees) Chase, *Raddia guianensis* (Brongn.) Hitchc., *Raddia lancifolia* R.P. Oliveira & Longhi-Wagner, *Raddia megaphylla*, *Raddia portoi* Kuhlm., *Raddia soderstromii* R.P. Oliveira, L.G. Clark & Judz. and *Raddia stolonifera* R.P. Oliveira & Longhi-Wagner. According to Chase (1935) *Raddia sampaiana* possess underground tubercles; similar structures are extremely rare within the family, with just three additional records in *Puelia coriacea* Clayton, *Lophantherum gracile* Brongn. and *Molinia caerulea* (L.) Moench. (Clayton 1967).



5. *Raddiella* Swallen, Bull. Torrey Bot. Club 75(1): 89. 1948, *hic emend.* TYPUS: *Olyra nana* Döll, Fl. Bras. (Martius) 2(2): 329. 1877, nom. illeg. superfl. *Raddiella nana* (Döll) Swallen, Bull. Torrey Bot. Club 75(1): 89. 1948 (= *Raddiella esenbeckii* (Steud.) C.E. Calderón & Soderstr.).

*Parodiolyra* Soderstr. & Zuloaga, Smithsonian Contr. Bot. 69: 64. 1989, *syn. nov.* TYPUS: *Olyra ramosissima* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3, 1(2-3): 116. 1834.

Spiculae masculae femineaeque pedicellis filiformibus obtectae; spiculae masculae glumis reductis pulvinum mentientibus ad basin ornatae; spiculae femineae relative parvae duobus punctis partitionis praesertim infra glumas, raro supra; hilum minus longum quam caryopsis.

### Etymology and distribution

*Raddiella* should be considered a feminine diminutive of *Raddia*, perhaps due to the remarkable low habit of its type species (*R. esenbeckii*); Swallen himself, however, never published the etymology of the genus (cf. Swallen 1948). Neotropics, from Costa Rica, Panama, and northern South America (Colombia, Venezuela and Trinidad Island [Trinidad & Tobago]) to southern Brazil and Paraguay, with one species (*R. micrantha*) probably introduced in Fiji.

5a. *Raddiella aratitiyopensis* (J.R. Grande) J.R. Grande, *comb. nov.* *Parodiolyra aratitiyopensis* J.R. Grande, Novon 21(1): 40-43, f. 1. 2011. TYPUS: Venezuela: Amazonas: Dept. Río Negro, cerro Aratitiyope, ca. 70 km al SSW de Ocamo, con riachuelos afluentes al río Manipitare [erroneously cited as “Manipitiare” in the protologue], piedra ígnea, forest toward bluff, 2°10'N, 65°34'W, 990-1670 m a.s.l., 24-28 II 1984, J.A. Steyermark, P.E. Berry & F. Delascio 130118 (holotypus: VEN358959!; isotypi: VEN-195204!, MO-3247229).

5b. *Raddiella colombiensis* (Davidse & Zuloaga) J.R. Grande, *comb. nov.* *Parodiolyra colombiensis* Davidse & Zuloaga, Novon 9(4): 587, f. 1-2. 1999. TYPUS: Colombia: Caquetá: Región de Araracuara, alrededores de la pista aérea, 00°25'S, 72°30'W, 200-300 m a.s.l., 11 XI 1991, D. Restrepo & A. Matapi 467 (holotypus: COAH-17796!; isotypi: COAH-20068!, MO-5102566!).

5c. *Raddiella lateralis* (J. Presl ex Nees) J.R. Grande, *comb. nov.* *Panicum laterale* var.  $\alpha$  J. Presl ex Nees, Fl. Bras. Enum. Pl. 2(1): 213-214. 1829. *Parodiolyra lateralis* (J. Presl ex Nees) Soderstr. & Zuloaga, Smithsonian Contr. Bot. 69: 66. 1989. TYPUS: Peru: “In montibus Orinocensibus lectam” (as cited in the protologue), *Haenke s.n.* (holotypus: PR; isotypus: US148228! (fragment ex PR)). Note: the quoted locality is that of the work of Nees, who misread the label of Haenke according to Soderstrom & Zuloaga (1989); they read “huanoccenses” instead of “Orinocenses”.



5d. *Raddiella luetzelburgii* (Pilg.) J.R. Grande, *comb. nov.* *Olyra luetzelburgii* Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 10(100): 1049. 1930 (as *Olyra* “*Luetzelburgii*”). *Parodiolyra luetzelburgii* (Pilg.) Soderstr. & Zuloaga, Smithsonian Contr. Bot. 69: 70. 1989. TYPUS: Brazil: Nord-Brasilien [Roraima]: Igarapé, Caicán, auf Sand, IX 1927, von Luetzelburg 21354 (holotypus: B10 0249094!; isotypi: IAN,R 49314!, US 132877 (fragm. ex B)).

5e. *Raddiella micrantha* (Kunth) J.R. Grande, *comb. nov.* *Olyra micrantha* Kunth, Nov. Gen. Sp. (H.B.K.), quarto ed., 1: 199. 1815 [1816]. *Parodiolyra micrantha* (Kunth) Davidse & Zuloaga, Novon 9(4): 590. 1999. TYPUS: [Venezuela]: „Crescit in umbrosis, humidis ad ripam Orinoci prope cataractam Maypurensium, floret Aprili“ (as in the protologue), [1800], Humboldt & Bonpland s.n. (holotypus: P642201!; isotypus: US 132879! (fragm. ex P)).

5f. *Raddiella ramosissima* (Trin.) J.R. Grande, *comb. nov.* *Olyra ramosissima* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci Nat. 3,1(2–3): 116. 1834. *Parodiolyra ramosissima* (Trin.) Soderstr. & Zuloaga, Smithsonian Contr. Bot. 69: 73. 1989. TYPUS: Brazil: Bahia: Esperança, 1831, Riedel 161 (holotypus: LE-TRIN-1131.01; isotypi: G-99754!, GH, K433348!, LE-TRIN-1131.02, probably P 642202!, US (fragm. ex LE-TRIN)).

As noted by previous authors, both *Parodiolyra* Soderstr. & Zuloaga and *Raddiella* s.s. have male and female spikelets supported by filiform pedicels, female spikelets (and female anthesia) relatively small, generally disarticulating below glumes, glumes with a cushion-like pulviniform base (the only vestige of glumes in male spikelets), and hilum not reaching the entire length of the caryopsis (Soderstrom 1981, Soderstrom and Zuloaga 1989, Zuloaga and Judziewicz 1991, Grande 2011, 2015). Davidse and Zuloaga (1999) expanded the original circumscription of *Parodiolyra* (i.e., as published in Soderstrom and Zuloaga 1989) to include species with the following diagnostic characters: 1) female spikelets falling entire (i.e., by disarticulation below glumes), but also above glumes (specially in those with mature caryopsis), 2) filiform female pedicels, 3) a conspicuous, thickened internode between the lower and upper glume, 4) prolongation of the rachilla between the upper glume and the anthesis, and 5) hilum not reaching the entire length of the caryopsis. At least four of these five characters (characters 4 were not evaluated in the present revision) were noted to occur also in *Raddiella*, as was done formerly in Soderstrom and Zuloaga (1989), but not in Davidse and Zuloaga (1999). The only character that justifies segregation of *Parodiolyra* from *Raddiella* is, thus, partial inflorescence distribution and distribution of sexes within them. Partial inflorescence distribution varies in *Raddiella* s.l. (i.e., as considered in the present revision) from terminal and monoecious (e.g., typical *R. micrantha*) to axillary/terminal and monoecious (e.g., *R. luetzelburgii*), axillary male/female (in separate inflorescences) and terminal male (*R. esenbeckii* (Steud.) C.E. Calderón & Soderstr.), and axillary female and terminal male (the most common in the genus, with terminal inflo-

rescence reduced to only two spikelets and concealed or slightly protruding from terminal leaf sheath in *R. vanessiae*). In *Raddiella kaieteurana*, inflorescences may vary, even within type locality, between axillary female and terminal male to both axillary and terminal female (Zuloaga and Judziewicz 1991). The absence of male flowers was the character chose by Swallen (1948) to recognize *Raddiella truncata* Swallen as a distinct species (and even part of a different genus!) from *R. lateralis* (then in the genus *Olyra*; Swallen 1948); as the pedicels are not differentiated between sexes, as is typical in core Olyrinae, and material available to Swallen have an important percentage of the spikelets fallen, it is felt that with additional material the male flowers might be discovered; however, like in *R. kaieteurana* (also from central Guyana), some plants may have only female spikelets, while others both male and female.

Precedent discussion shows enough transitions between inflorescence type of *Parodiolyra* and *Raddiella s.s.* (*i.e.*, within *Raddiella s.l.*) as to consider this character of secondary importance when compared with the more conserved pedicel, anthecium and caryopsis characters. In some specimens of *Olyra micrantha* further transitions could be observed: namely, those corresponding to *O. micrantha* var. *dioeca* Döll (Döll 1877), with either male or female spikelets, and specimens with the lowermost (male) branches atrophied. Altogether, these facts exclude inflorescence structure, at least in its traditional meaning (*i.e.*, according to the distribution of sexes), as a valid character to separate *Raddiella s.s.* and *Parodiolyra*, in a similar fashion than for *Raddia s.s.* and *Sucrea*, as stated above. Based on putative shared apomorphies (discussed under *Olyra*), the most related genus is *Diandrolyra*, which can be easily differentiated by the presence of paired spikelets, the males having two (*vs.* three) stamens. Several species groupings have been suggested (Zuloaga and Davidse 1999, Grande 2009, 2011), but all exhibit the same shared characters typical of the genus *Raddiella s.l.* (*i.e.*, as defined in the present revision), and possess less synapomorphies than *Raddiella s.l.* (*i.e.*, as here defined). Thus, for example, phreatophytic species share a very low habit, upper anthecium ornamentation (anticlinal epidermic cell walls undulate and with more or less prominent siliceous phytolith(s) or “papillae”), a (generally) very reduced or punctiform hilum, and absence of fusoid cells (Zuloaga and Judziewicz 1991, Judziewicz and Sepsenwol 2007). Further studies will determine, hopefully, if they are meritorious of taxonomic recognition, probably at the subgenus level; as is understood in the present revision, recognition of the phreatophytic species as a segregate genus would lead to a paraphyletic *Raddiella s.l.* and to the recognition of poorly defined genera.

Remaining species in this genus are: *Raddiella esenbeckii* (Steud.) C.E. Calderón & Soderstr., *Raddiella kaieteurana* Soderstr., *Raddiella lunata* Zuloaga & Judz., *Raddiella malmeana* (Ekman) Swallen, *Raddiella minima* Judz. & Zuloaga, *Raddiella molliculma* (Swallen) C.E. Calderón & Soderstr., *Raddiella potaroensis* Soderstr. and *Raddiella vanessiae* Judz. *Raddiella truncata*, with a habit similar to that present in *R. aratitoyopensis* (*vs.* climbing and bambusoid in typical *R. lateralis*) could be reha-

bilited as a different species, but further study would be required. Genus *Raddiella* includes the smallest herbaceous bamboo of the world (viz. *R. vanessiae* Judz.), being only 2 cm tall at maturity (Judziewicz and Sepsenwol 2007), the smallest woody bamboo being probably *Pleioblastus pygmaeus* (Miq.) Nakai, from eastern Asia (tribe Arundinarieae, closely related to the North American genus *Arundinaria* Michx.), cultivated in some countries as lawn.

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