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Typology of Synflorescences in *Oryzeae* (*Poaceae*)

By

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With 6 Figures

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Summary

VEGETTI A. C. 2000. Typology of synflorescences in *Oryzeae* (*Poaceae*). – *Phyton* (Horn, Austria) 40 (1): 71–88, 6 figures. – English with German summary.

The paper intends to typologically characterize synflorescences in species of *Oryzeae*. In all the species the inflorescence is polytelic, with main florescence and paracladial zone. The greatest variability among the studied species can be found in the paracladial zone. All taxa have a subzone of long and short paracladia. Short paracladia are made up of a single spikelet (coflorescence). Long paracladia, comprising the flowering unit only, are termed long paracladia without trophotagma. The extension of the region of long paracladia without trophotagma is well developed in *Zizaniopsis* DOELL & ASCHERS., *Rhynchoryza* BAILLON and in some *Oryza* L. species, less in *Luziola* A. L. JUSS. and in *Leersia* SOLAND. Long paracladia with trophotagma are only found in *Luziola* and *Rhynchoryza*.

Zusammenfassung

VEGETTI A. C. 2000. Typologie der Synfloreszenzen bei *Oryzeae* (*Poaceae*). – *Phyton* (Horn, Austria) 40 (1): 71–88, 6 Abbildungen. – Englisch mit deutscher Zusammenfassung.

In vorliegender Studie werden die Synfloreszenzen von 13 Arten der *Oryzeae* typologisch charakterisiert. Alle Arten haben polytele Infloreszenzen mit Hauptfloreszenz und Parakladienzone. Die größte Variabilität zeigt sich bei den untersuchten Arten in der Parakladienzone. Alle Taxa haben eine Subzone mit Lang- und eine mit Kurzparakladien. Kurzparakladien werden aus einem einzigen Ährchen gebildet (Kofloreszenz). Langparakladien, die nur die Blüheinheit umfassen, werden

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als Langparakladien ohne Trophotagma bezeichnet; diese Region ist wohl entwickelt bei *Zizaniopsis* DOELL. & ASCHERS., *Rhynchoryza* BAILLON und bei den untersuchten *Oryza* L.-Arten, weniger bei *Luziola* A. L. JUSS. und *Leersia* SOLAND. Langparakladien mit Trophotagma (basalen Laubblättern bzw. Vorblättern) wurden nur bei *Luziola* und *Rhynchoryza* beobachtet.

Introduction

A comprehensive understanding of the great variability in *Poaceae* inflorescences is hindered by the relative paucity of comparative studies. In this family, descriptive terms pertaining to simple racemose inflorescences have often been applied, without considering that inflorescences here combine monopodial and sympodial ramification systems (VEGETTI & TIVANO 1991). The need to revise inflorescence terminology in grasses has been raised by several authors (GOULD & SHAW 1983; CLAYTON & RENVOIZE 1986). A typological analysis can be a useful tool to describe the inflorescences in *Poaceae* in a more precise way and to establish relationship among taxa.

TROLL 1969 was the first to apply this analysis to *Poaceae*. After this initial work, several studies have analyzed species or genera (VEGETTI & TIVANO 1991), a tribe (VEGETTI 1994), or the family *Poaceae* (CÁMARA HERNÁNDEZ & RÚA 1991; VEGETTI 1991; CÁMARA HERNÁNDEZ & MIANTE-ALZOGARAY 1994; VEGETTI & WEBERLING 1996).

Typical inflorescences in *Poaceae*, are terminal, either spikes, racemes or panicles (CLAYTON & RENVOIZE 1986; GOULD & SHAW 1983). In the tribe *Andropogoneae* some genera have a reduced inflorescence and a proliferation of axillary buds; this system can in some instances resemble a panicle, and is therefore termed 'false panicle'.

The tribe *Oryzaceae* is found in the Tropics and Subtropics. Members of this tribe are either annual or perennial, caespitose or rhizomatous, with either terminal or axillary and terminal panicles, which can have hermaphrodite spikelets or male and female spikelets (NÍCORÁ & RÚGOLO DE AGRASAR 1987). Inflorescence ramification systems in the species of this tribe have not been analyzed in detail. Thus, the aim of this work is to characterize synflorescences in species of *Oryzaceae* typologically.

Material and Methods

Studies were performed in the following species: *Oryza latifolia* DESV., *O. sativa* L., *O. rufipogon* GRIFFITH, *Leersia hexandra* SW., *L. ligularis* TRIN. var. *grandiflora* (DOELL) PYRAH., *Zizaniopsis bonariensis* (BALANSA & POITR.) SPEG., *Z. villanensis* QUARIN, *Luziola peruviana* GMELIN, *L. bahiensis* (STEUDEL) HITCHCOCK, *L. pittieri* LUCES, *L. doelliana* PROD., *L. gracillima* PROD. and *Rhynchoryza subulata* BAILLON.

The typology developed by TROLL 1964 and WEBERLING 1989 was applied to the interpretation of the compound inflorescence in *Oryzaceae* - species. For the specific terminology used in this work see WEBERLING 1989, WEBERLING & al. 1993 and VEGETTI & WEBERLING 1996.

Live samples, in alcohol preserved material and herbarium specimens were analyzed. Observations were organized according to the characteristics of the various zones in the inflorescence: the main inflorescence, the paracladial zone (short and long *paracladia subzones*) and each type of *paracladia*.

Dissections were performed under a stereoscopic microscope, and diagrams of the ramification systems were made. Drawings were scanned and corrected using graphics software.

Investigated specimens:

Leersia hexandra Sw.

ARGENTINA: Cartaginese 69109 (BA), Castellanos 31/899 (BA), Daguerre 235 (BA, BAA), Hunziker 948 (BA), Jorgensen 3296 (BA), L.H. 38535 (BA), Luna 29006 (BA), Nuñez 28248, 28249 (BA), Partridge 63236 (BA), Perez Moreau 29376, 65921 (BA), Venturi 771 (LP, BA), Venturi 710, 2773 (BA), Weber & Bachman 61987 (BA), Alonso-Panigatti 432 (BAA), Bettfreund 45 (BAA), Cabrera & al. 13763 (BAA), Cabrera & Fabris 19974 (BAA,CTES). Calderon 418, 375 (BAA), Castellanos 1071 (BAA), Clos 478 (BAA), Corradi 3420 (BAA), Daguerre 235 (BAA), Fabris 3837 (BAA), Grondona-Dawson 6327 (BAA), Hassler 2831 (BAA), Ibarrola 224 (BAA), Meyer 86 (BAA), Nicora 5310, 6834 (BAA), Nicora & Cámara Hernández 130, 239 (BAA), Parodi 683, 684, 995, 1237, S/N, 2653, 5537, 6197, 8822 (BAA), Parodi & Horovitz 540 (BAA), Rojas 9044 (BAA), Valencia 2323 (BAA), Villamil & Martinez 5304 (BAA), Bettfreund & al. 18, (CORD), Hatschbach 2271 (CORD), Hunziker 3372, 11968, 18594, 18687, (CORD), Hunziker & al. 10837 (CORD, BAA), Kurtz 9082, 10535, 12731, 12873, (CORD), Montes 249, (CORD), Saravia Toledo 1789 (CORD), Stuckert 12666b, 12915, 12937, 14819, 15520, 16865, 18745, 20012 (CORD), Ahumada 257, 329, 421, 476, 592, 1559, 1806, 2027, 2554, 2638, 2663, 2754, 2941, 3028, 3140, 3143 (CTES), Ahumada & al. 790 (CTES, BAA), Battu 18 (CTES), Benitez & al. 120 (CTES), Bresky & Radovancich 1 (CTES), Carnevali 4213, 4573 (CTES), Digiacomio 42, 117 (CTES), Krapovickas & al. 23843, 24574 (CTES), Krapovickas & Cristobal 12921 (CTES), Lewis 1575 (CTES), Martinez Crovetto 482 (CTES), Neiff 240, 309, 501, 710, 740 (CTES), Quarin 460, 504, 615, 2893 (CTES), Quarin 564 (CTES, BAA), Quarin & al. 2011, 2159, 2519 (CTES), Quarin & al. 524 (CTES, BAA), Quarin & Norrman 3654 (CTES), Saravia Toledo 13471 (CTES), Schinini & Ahumada 12701 (CTES), Schinini & al. 11016, 17483, 19080, 24318 (CTES), Schulz 10724, 10859, 15091, 18254 (CTES), Tressens & al. 811, 4180 (CTES), Ahumada 3023 (LIL), Saravia Toledo 6282 (LIL), LP 18387, Cabrera 1698, 9889 (LP), Cabrera & al. 26058 (LP), Maldonado 1344, (LP), Pedersen 1424, (LP), Venturi 771 (LP), Zuloaga & al. 473, (LP), Hilgert 361 (SF), Pensiero 670 (SF), Pensiero & Tivano 3034 (SF), Ragonese 2368 (SF, BAA), Ragonese 2160 (SF, BAA). – BOLIVIA: Steinbach 2180, 7453 (BA). – BRASIL: Araujo 80, 171 (BAA), Orth 9849 (BAA), Sacco 632, 800 (BAA), Tenorio 68-376 (BAA). – MEXICO: Hinton 2503 (BAA). – PARAGUAY: Jorgensen 4086 (BA), Rojas 4264, 4281, 13156 (BAA), Schinini 6300, (LP). – URUGUAY: Corn. Osten. 16315 (BA), Boelcke 8246 (BAA), Legrand 48 (BAA).

Leersia ligularis var. *grandiflora* (DOELL) PYRAH

ARGENTINA: Hauman 24/783 (BA). C. S. 1574 (BAA). Gruner 1418 (BAA), Honfi 71 (BAA CTES), Hunziker 833 (BAA). Llamas 1571 (BAA). Parodi 5494, 5600,

5605, 13008 (BAA). Cabral 1629 (CTES), Honfi 37, 97 (CTES), Martinez Crovetto G244 (CTES), Morrone & al 825 (CTES), Mroginski & al. 283 (CTES), Schinini 19875 (CTES), Schwarz 2789 (LIL). Hilgert 407, 408 (SF). – BRASIL: Dusen 13857 (BAA). – PARAGUAY: Hassler 11074 (BAA). Rojas 3274 (BAA). Woolston 71 (BAA). Pedersen 4146 (BAA). Pedersen 10134 (CTES).

Luziola peruviana GMELIN

ARGENTINA: Ahumada 419 (BAA; CTES), Arbo 472 (BAA; CTES), Benitez & al. 119, (BAA; CTES), Burkart s/n (BAA), Cusato 3427 (BAA), Hunziker 941 (BAA; CORD), 9906 (BAA), Ibarrola 166 (BAA), Krapovickas & al. 18243, 23840, 24575 (BAA), Krapovickas & Irigoyen 17847, (BAA), Legrand 1353 (BAA), Lewis y Colantes 235 (BAA), Martinez 11, (BAA), Meyer 76 (BAA; CTES), Meyer & al. 20563 (BAA), Millan 283 (BAA), Morgan 14 (BAA), Nicora 3030, 5093 (BAA), Nicora & al. 170, (BAA), Parodi 682, 1018, 1917, 2652, 3275, 6210, 6310, 6357, 6363, 6949, 6981, 7720, 9094, 13485, 15088, 15281, s/n (BAA), 6729 (BAA; CTES), Quarin 774 (BAA; CTES), Quarin & al. 525 (BAA; CTES), Ragonese 106 (BAA), Rojas 8973 (BAA), Schinini 7799 (BAA; CTES), Schulz 1057 (BAA), Spegazzini 2437 (BAA), Claren 12247 (CORD), Hackel 18746 (CORD), Hunziker 5880 (CORD), Stuckert 2432, 2451, 12666, 15819, 22404 (CORD), Ahumada 2627, 2811, 2978, 3210 (CTES), Arbo & al. 6319, 6904 (CTES), Krapovickas & al. 20323 (CTES), Neiff 852 (CTES), Pedersen 12757 (CTES), Piccinini & Hilfer 4291 (CTES), Quarin 59, 624, 686, 2153 (CTES), Quarin & al. 2153 (CTES), Quarin & Schinini 1024 (CTES), Schinini & al. 19075 (CTES), Schulz 10302, 10904 (CTES), Tressens & al. 2774, 4179, 4230, 4279 (CTES), Ragonese 2106, (LP), Zuloaga & al. 557 (LP), LP 018733. – BRASIL: Araujo N282 (BAA), Capparelli 195 (BAA), Leopoldo 1051, (BAA), Rambo 54926 (BAA), Sacco 810, 811 (BAA). – U.S.A.: Langlais 1888 (BAA). – PARAGUAY: Hassler 5534, 12473 (BAA), Jimenez 106 (BAA), Ramirez 138 (BAA), Rojas 12466, 13144 (BAA), Woolston 98 (BAA), 4084 (BAA), Jörgensen 4084 (LP). – URUGUAY: Boelcke 8245 (BAA), Leon 289 (BAA), Montoro Guarch 3240 (BAA), Rosengurt B208 (BAA).

Luziola gracillima PROD.

ARGENTINA: Del Aguila & al. 24 (BAA), Saravia Toledo 1563 (CORD; CTES), 1035 (CTES).

Luziola bahiensis (STEUD.) HITCHC.

ARGENTINA: Burkart 1104 (BAA), Cusato 3690 (BAA), Hatschbach 1884 (BAA), Krapovickas & al. 25380 (CTES), Parodi 5470, 5610, 5649 (BAA), Pedersen 6418 (BAA), Quarin 459 (CTES). – BRASIL: Davidse & al. 11063, 11505 (BAA). – PARAGUAY: Pedersen 7659 (BAA).

Luziola pittieri LUCES

VENEZUELA: Davidse 2987, 4395 (BAA).

Luziola doelliana PROD.

BRASIL: Manet 670 (BAA), Swallen 4407 (BAA).

Oryza latifolia E. DESV.

ARGENTINA: 18950, (CORD), Pedersen 5533, (CORD), Carnevali 1576 (CTES), Digiacomo 32 (CTES), Krapovickas & al. 24021, 24252 (CTES), Meyer 37 (CTES), Pedersen 5883 (CTES), Quarin 3062 (CTES), Quarin & Norrman 3655 (CTES), Schinini & Martinez Crovetto 12905 (CTES), Schulz 1795, 10990, 16514 (CTES), Spezzazzini S/N (LP), Pensiero & Tivano 3251 (SF), Ragonese 3185 (SF). – BRASIL: Hunziker 25440, (CORD). – PARAGUAY: Schinini & Borda 15192 (CTES), Jörgensen & al. 4570, (LP).

Oryza sativa L.

ARGENTINA: Agronomía 1933 (BAA), Ahumada (BAA), Arbo & al. 1033 (BAA), Bragadin 14382, 15132, 15133, 15134, 15135, 15137, 15138 (BAA), Orth 3075, 3077 (BAA), Parodi 686, 7086, 7087, 9588, 11093 (BAA), Rey 12, 13, 15 (BAA), Rojas 12590 (BAA), Schinini & Pire 8674 (BAA), Türpe 210 (BAA), 2698 (BAA), E.S.B S/N (LP), Pensiero 2814 (SF). – BRASIL: Macedo 2273 (BAA).

Oryza rufipogon GRIFFITH

ARGENTINA: Ahumada 133 (CTES), Ahumada & al. 908, 3640 (CTES), Ahumada 2542 (LIL).

Rhynchoryza subulata BAILLON

ARGENTINA: Partridge 61317 (BA), Ahumada & al. 6755 (CTES), Carnevali 2236 (CTES), Krapovickas & Irigoyen 18391 (CTES), Krapovickas & al. 24157, 27518 (CTES), Norrman & al. 179 (CTES), Quarin 1633, 2326 (CTES), Quarin & al. 2680 (CTES), Schinini & al. 6323 (CTES), Schinini & Gonzalez 9391 (CTES), Schinini & Martinez Crovetto 12913 (CTES), Schulz 11527, 1061 (CTES), Tressens & al. 1724 (LIL; CTES), Tressens & al. 3184, 3222 (CTES), Vegetti 1223 (SF), Pensiero & Tivano 3243 (SF), Pensiero & Vegetti 2680 (SF).

Zizaniopsis bonariensis (BALANSA & POITR.) SPEG.

ARGENTINA: Arbo & al. 1346 (CTES), Grondona 6495 (CTES), Irigoyen 68 (CTES), Krapovickas & al. 20229, 20251, 37530 (CTES), Quarin 3194, 3204 (CTES), Quarin 1701 (CTES, SI), Quarin & al. 2491 (CTES), Schinini 30387 (CTES), Schulz 18692 (CTES), Tressens & al. 4338 (CTES), Herbario Instituto M. Lillo 85 (LIL), Cabrera 9826, 16421 (LP), Pensiero 5244, 5290 (SF).

Zizaniopsis villanensis QUARIN

ARGENTINA: Schulz 13816, 13864 (CTES), Pedersen 1019 (SI).

Observations

The following zones can be distinguished typologically (Fig. 1):

Innovation zone (J): it is the basal zone of the plant, where axillary buds (innovations) are separated by short internodes. These can be typical intravaginal orthotropical shoots such as in *Oryza* species (Fig. 6), or

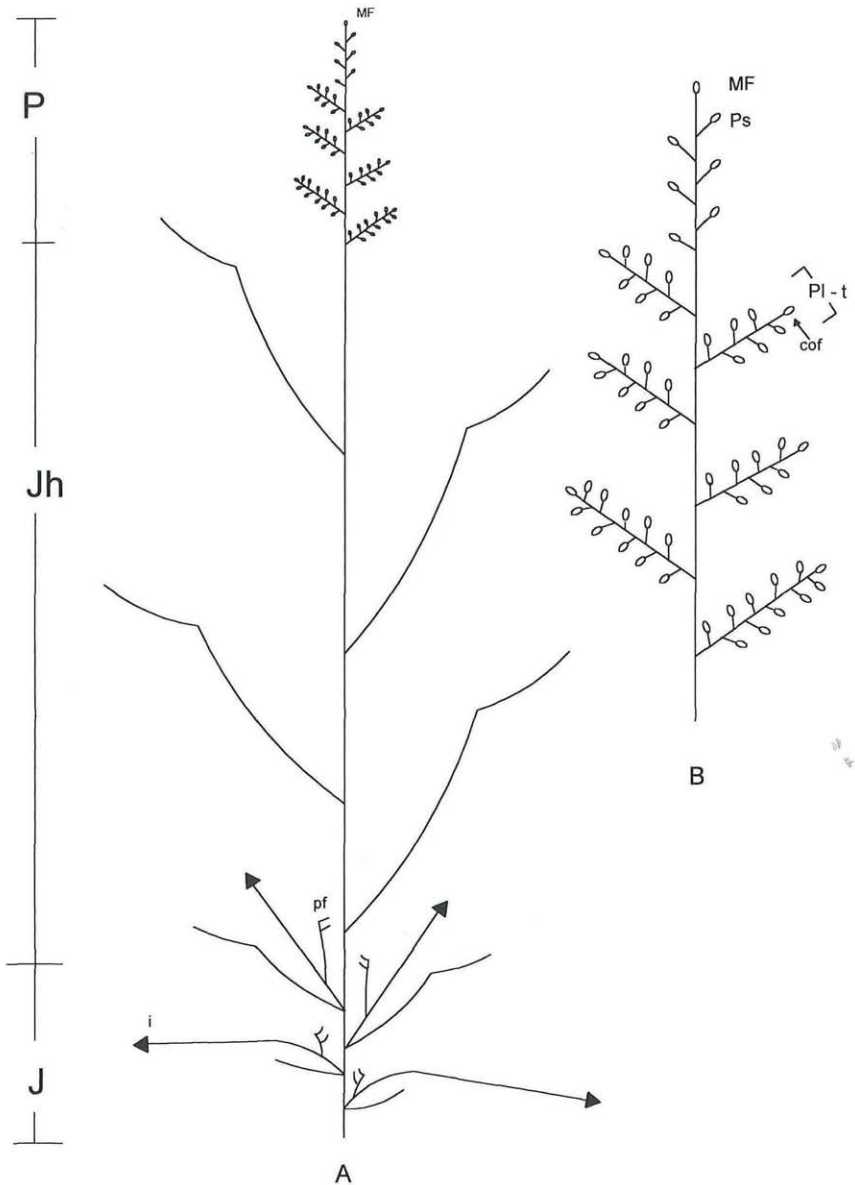


Fig. 1. - *Leersia hexandra* Sw. A, synflorescence structure; B, flowering unit. Abbreviations: MF main florescence; P paraclyadial zone; Jh inhibition zone; J innovation zone; Ps short paraclyadium; Pl-t long paraclyadium without trophotagma; cof cofillorescence; i innovation; pf prophyll.

mostly extravaginal plagiotropical shoots appearing as very short sympodial rhizomes, where the apical bud soon resumes orthotropical growth (such as in *Rhynchoryza*, Fig. 3), as somewhat longer (2–4 cm) sympodial rhizomes which resume orthotropical growth later (such as in *Zizaniopsis*, fig. 4), or as long rhizomes (or stolons) which either anchor in the soil, or are submerged or floating, and extend the plant over a large surface like in *Leersia* and *Luziola*. All these plagiotropical structures greatly increase the innovation zone of the plant.

Inhibition zone (Jh): in taxa with caespitose plants, either from the development of intravaginal innovation or from short rhizomes that soon produce orthotropical shoots, it is possible to observe, that, above the short internode zone (innovation zone) internodes elongate and there are leaves where axils do not generate buds (such as in *Zizaniopsis*, *Rhynchoryza* and *Oryza*). A different pattern is observed in *Luziola* and *Leersia*, where plagiotropic structures of long internodes can behave as an inhibition zone or else buds can develop and act as an enrichment zone.

Paracladial zone (P): The first lateral floral shoots (paracladia) appear above the inhibition zone, and gradually reduce acropetally until spikelets are observed directly on the main axis. This zone extends from the first proximal floral axis to the last distal lateral spikelet of the paracladial zone.

Main florescence (MF): Above the paracladial zone, the main axis ends in a terminal spikelet which is the main florescence.

In all the species, the paracladial zone comprises of short paracladia which are reduced to a coflorescence, and long paracladia that besides the coflorescences, show a variable degree of development of consecutive order paracladia. Long paracladia generally lack bracts and prophylls, except those that form the spikelet. Thus, they are long paracladia without trophotagma (Pl-t). The main florescence and Pl-t comprise the flowering unit. In some species, long paracladia with trophotagma (Pl+t) are formed below the flowering unit, generally ending in a flowering unit repeating the structure observed on the main axis.

In the *Leersia* species studied, the synflorescence is only a flowering unit, and long paracladia with trophotagma are not observed (Fig. 1). The subzone of short paracladia includes (1) 2–9 (–13) paracladia and the subzone of long paracladia 4–23 Pl-t. The latter generally have secondary paracladia reduced to a coflorescence. However, some specimens showed long developed paracladia, supporting tertiary paracladia reduced to a coflorescence. The florescences (spikelets) possess one perfect flower which abscise early.

In the *Luziola* species studied, a flowering unit and 2–4 long paracladia with trophotagma were found (Fig. 2). The flowering unit on the main axis bears monofloral male florescences. Each long paracladium with



Fig. 2. – Synflorescence structure in *Luziola pittieri* LUCES. Abbreviations: Ps subzone of short paracladia; Pl subzone of long paracladia; - t region of the long paracladia without trophotagma; + t region of long paracladia with trophotagma; Pl+t, Pl+t', Pl+t'' consecutive order long paracladia with trophotagma, with female spikelets only; Pl-t, Pl-t', Pl-t'' consecutive order long paracladia without trophotagma; ●— male spikelet; ◐— female spikelet; other abbreviations as in Fig. 1. Only the hypopodium, prophyll and part of the epipodium of the Pl+t' and Pl+t'' are shown.

trophotagma has a short hypopodium, a prophyll, a long epipodium and a terminal flowering unit. All florescences in the region of Pl+t are female spikelets. In *L. gracillima*, each Pl+t is richly developed, resulting in a larger number of Pl-t per node, with a greater degree of branching, to fifth order paracladia. *L. bahiensis* has a reduced region of Pl+t (1-2), while up to third order Pl+t are observed in *L. pittieri* (Fig. 2).

A flowering unit and a Pl+t of *Rhynchoryza subulata* are shown in Fig. 3. The flowering unit is made up of a main florescence, short and long paracladia. The subzone of short paracladia is made up of (3) 5–6 (9) paracladia and the long paracladia zone has 7–9 long paracladia without trophotagma. These have coflorescences and up to third order paracladia reduced to their coflorescence. Less frequently, inflorescences with tertiary Pl-t bearing fourth order paracladia reduced to their coflorescence can be observed.

A long paracladium with trophotagma is formed in the axil of the distal leaf. It consists of an hypopodium, a prophyll, a long epipodium and a terminal flowering unit similar to the one on the main axis. The axillar bud of the prophyll of this Pl+t can generate a cymose branching sequence with up to sixth order paracladia. The florescences (spikelets) possess one perfect flower.

The synflorescence in *Zizaniopsis* (Figs. 4 and 5) is formed only by a flowering unit, with a main florescence, very few short paracladia and a large number of long paracladia, which do not have trophotagma. Tertiary Pl-t can bear quaternary paracladia reduced to a coflorescence, or, less frequently, quaternary Pl-t with fifth order paracladia reduced to a coflorescence. A distinctive florescence differentiation along the synflorescence is observed. In *Z. bonariensis*, the main florescence and the coflorescences of main order paracladia are female spikelets, while coflorescences of upper order paracladia are male spikelets. In contrast, *Z. villanensis* male florescences are located in the distal part of the inflorescence, while female coflorescences dominate the basal part.

Synflorescences in the *Oryza* species we studied (Fig. 6) only had the flowering unit, and lacked Pl+t. The main florescence, short paracladia and Pl-t can be observed in the flowering unit. The short paracladia subzone is variable. In *O. latifolia* it is made up of (8) 11–20 (–27) Pl-t, generally bearing tertiary paracladia reduced to a coflorescence. In the primary long paracladia of this species, branching can be observed only at the basal third towards the apex, consequently a relatively long basal internode is observed. In *O. rufipogon* the zone of long paracladia has 7–15 Pl-t and in *O. sativa*, 9–10 Pl-t. These Pl-t bear secondary long paracladia in both species, which in turn bear tertiary paracladia reduced to a coflorescence. Branching of Pl-t is close to the basis of the paracladium.

The inflorescence in *O. latifolia* is longer than in the other two species due to the length of the internodes in the various axes, and the larger number of Pl-t.

Discussion

The terms *paniculodium*, *stachyodium* and *botryodium* have been proposed by TROLL 1969 specifically for *Poaceae*, instead of panicle, spike

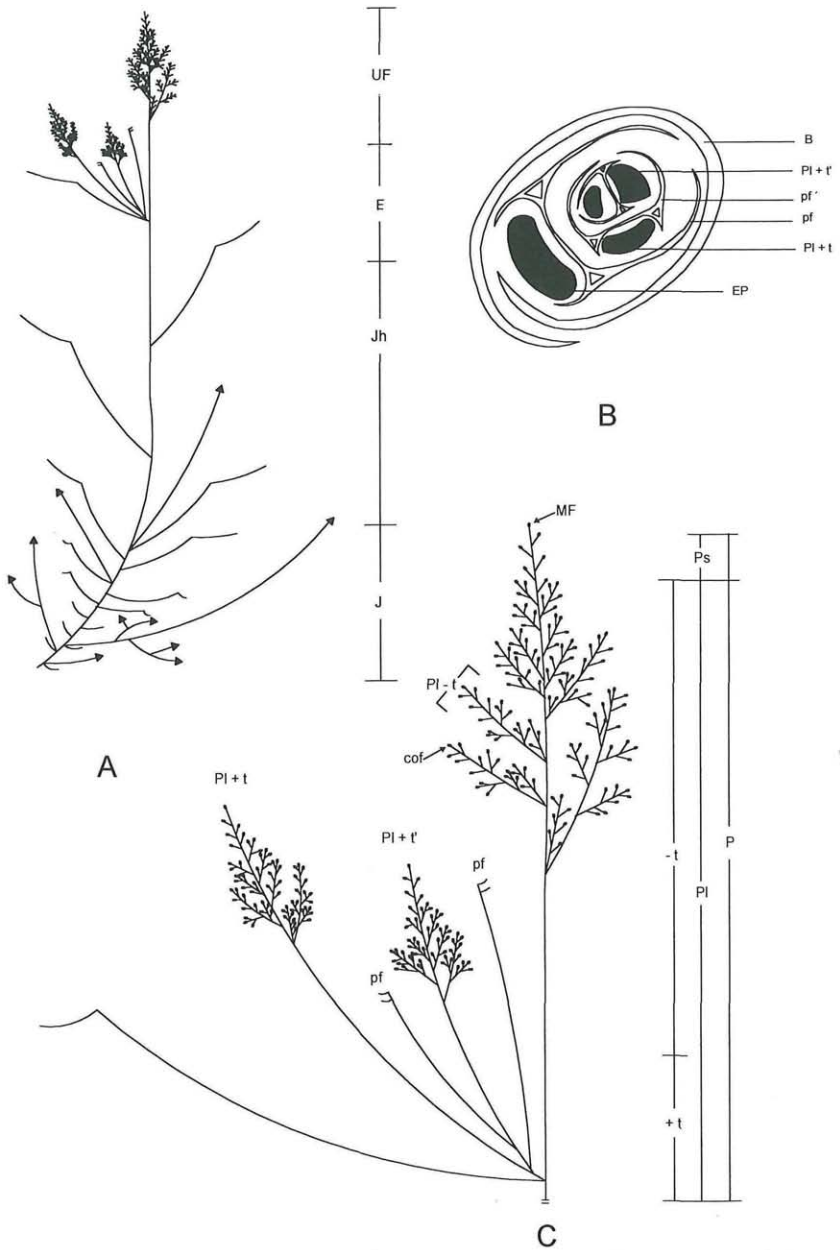


Fig. 3. – *Rhynchoryza subulata* (NEES) BAILLON. A, diagram of the structural plan of the whole plant; B, transection along the + t; C, detail of the distal part of the synflorescence. Abbreviations: UF flowering unit; E enrichment zone; Pl-t long paraclypeus without trophotagma; Pl+t, Pl+ t' consecutive order long paraclypeus with trophotagma; EP main axis; B distal leaf; pf, pf' prophylls of consecutive order; other abbreviations as in Fig. 1 and Fig. 2.

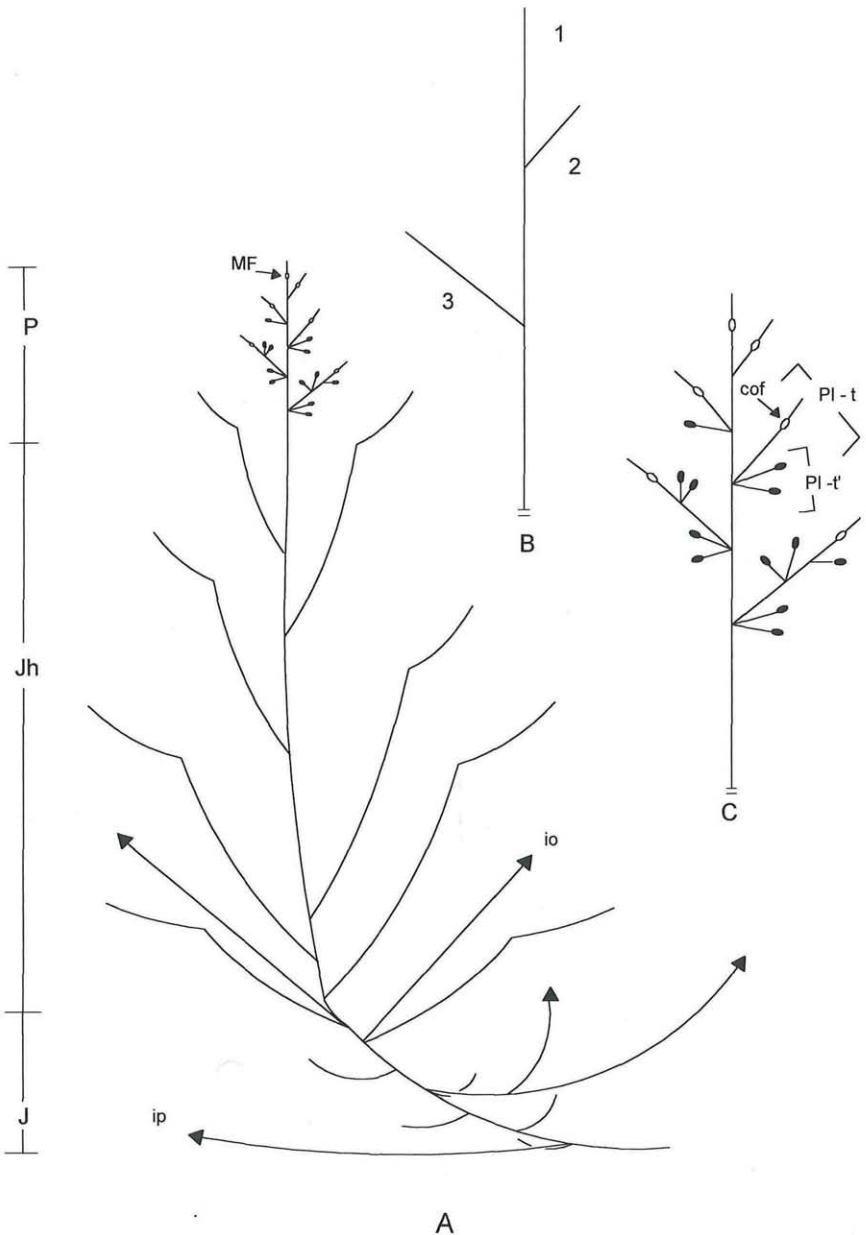


Fig. 4. – *Zizaniopsis bonariensis* (BALANSA & POITR.) SPEG. A, synflorescence structure; B, simplified diagram of the flowering unit, indicating the position of parts shown in Fig. 4 C and in Fig. 5; C, distal part indicated in B as 1. Abbreviations: io orthotropic innovation; ip plagiotropic innovation; ● male spikelet; ○ female spikelet; other abbreviations as in Fig. 1.

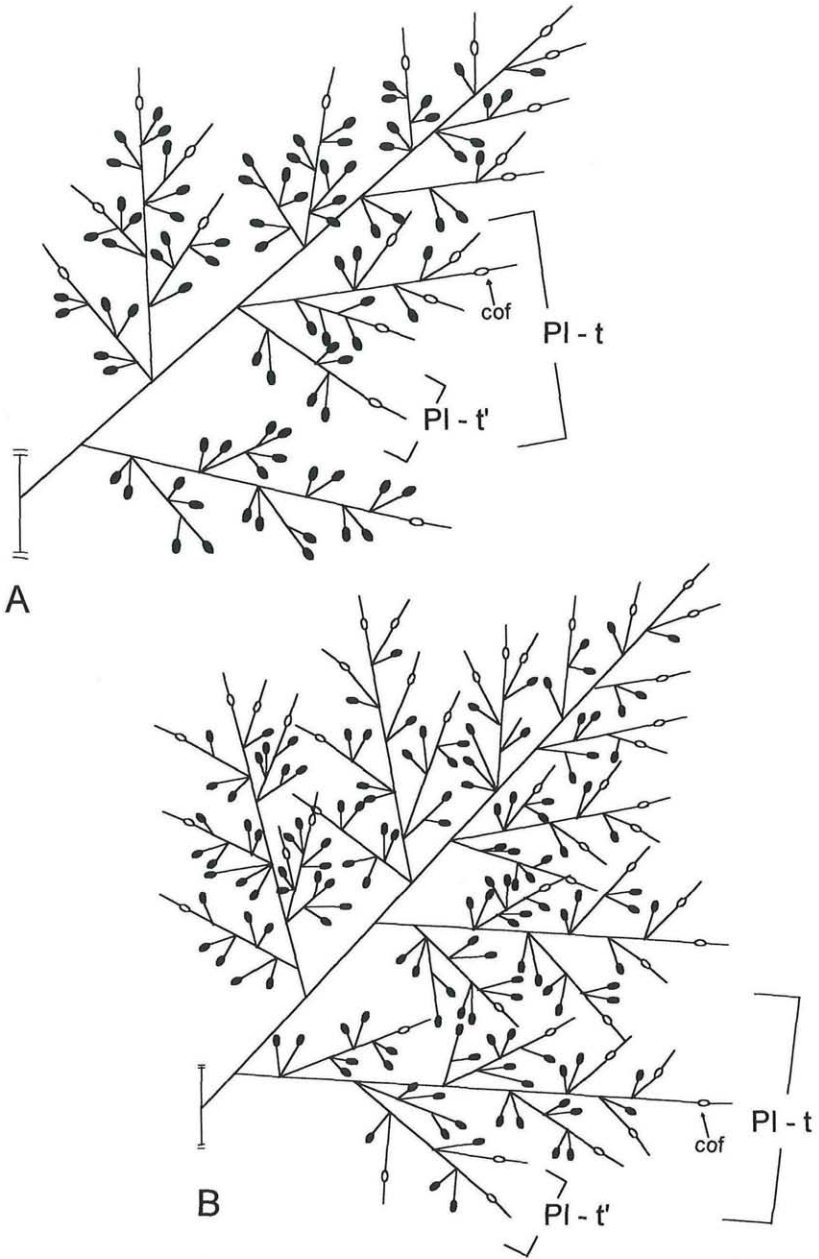


Fig. 5. - Long paracladia without trophotagma in *Zizaniopsis bonariensis* (BALANSA & POTR.) Speg. A, long paracladium in the middle section, indicated in Fig. 4 B as 2; B, basal paracladium, indicated in Fig. 4 B as 3. Abbreviations: ● - male spikelet; ○ - female spikelet; other abbreviations as in Fig. 1.

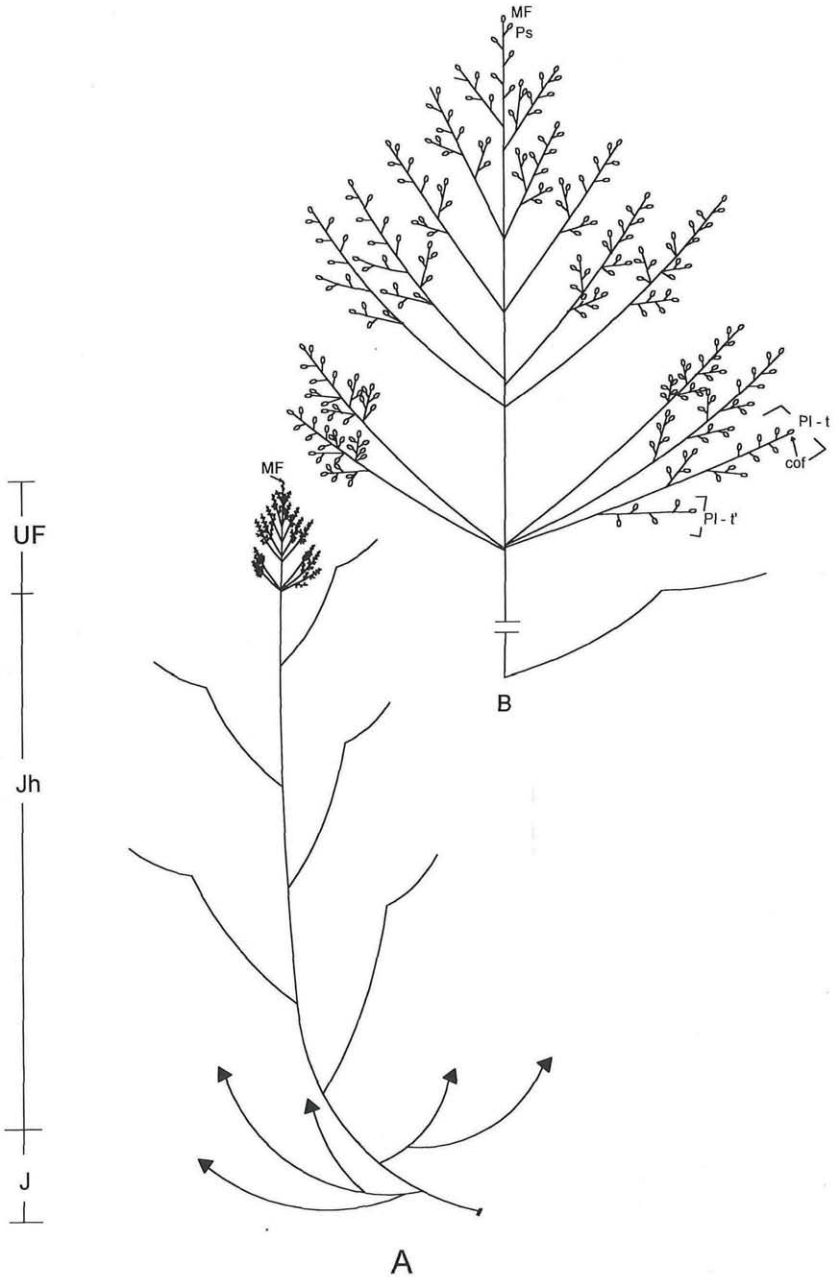


Fig. 6. - *Oryza latifolia* DESV. A, Synflorescence structure; B, flowering unit on the main axis. Abbreviations as in Fig. 1 and Fig. 3.

and raceme. These terms apply to polytelic inflorescences with racemose, spike and spikelet branching patterns that do not bear relation with the corresponding monotelic systems (WEBERLING & al. 1993). In view of the large variability in inflorescence structure present in this family, some other terms would still seem necessary to describe special inflorescences. Such is the case of *thyrsoidium* and *botryoidium*, proposed by RUA & WEBERLING 1995 for *Paspalum* – L. inflorescences. In the *Oryzaceae* species studied, the inflorescence is a *paniculodium*, with variable number of spikelets, reduced to a few in *Hygroryza* NEES (WATSON & DALLWITZ 1992).

In the tribe *Oryzaceae*, both the main axis as well as the paracladia bear a monofloral terminal spikelet with one floret, but since the spikelet represents an open system (BUTZIN 1979; CÁMARA HERNÁNDEZ & MIANTE ALZOGARAY 1994), the inflorescence is polytelic, as has been described for *Poaceae* (TROLL 1969; CÁMARA HERNÁNDEZ & RUA 1991; VEGETTI 1991; CÁMARA HERNÁNDEZ & MIANTE-ALZOGARAY 1994; VEGETTI & WEBERLING 1996). The main florescence and coflorescences are the fundamental floral groupings in these species, and are repeated throughout the whole plant. In *Poaceae*, the main florescence and each coflorescence are represented by the spikelet (CÁMARA HERNÁNDEZ & RUA 1991; VEGETTI 1991; VEGETTI & WEBERLING 1996). Other spikelets to each one of the ramifications recognized as successive order paracladia, and thus, are homologous to coflorescences (WEBERLING & al. 1993). In *Oryzaceae* the main axis as well as long paracladia bear a terminal spikelet, that is, bear main florescence and coflorescences, consequently, truncation has not taken place in this tribe (CÁMARA HERNÁNDEZ & RUA 1991; VEGETTI 1991; VEGETTI & ANTON 1995), thus, inflorescences are heterothetic and heterocladic (WEBERLING & al. 1993). Long paracladia have not been homogeneized either, a character usually associated to the truncation of the main florescence (VEGETTI & ANTON 1995).

In the genera we studied, the most developed inflorescences are initiated with profusely branched floral shoots, which gradually reduce acropetally, until distal paracladia appear, generally consisting of a single spikelet.

In order to differentiate paracladia of various complexity, the terms long and short paracladia were applied by VEGETTI & TIVANO 1991, as had been previously used for dicot families by TROLL 1965 and WEBERLING 1989. The distinction between long and short paracladia should be associated to the presence of a discontinuity in the paracladial series along the main axis of the synflorescence (WEBERLING & al. 1993). These authors point out that short paracladia must be homogeneous and must appear regularly as structural subunits of long paracladia. In the *Oryzaceae* species studied, paracladia gradually reduce acropetally, and consequently, there is no evident paracladial discontinuity along the main synflorescence axis.

Yet in this work the term short paracladium is used to describe paracladia reduced to a coflorescence, and to distinguish them from long branched paracladia, that bear both a coflorescence and higher order paracladia. In all these inflorescences it is possible to distinguish the region where paracladia are reduced to a coflorescence (short paracladia subzone) from the region where long, branched paracladia are found (subzone of long paracladia).

The synflorescence, in the sense of CÁMARA HERNÁNDEZ & RUA 1991 and VEGETTI – 1991 is formed by an innovation zone and in some cases an enrichment zone (region with Pl+t), and the flowering unit. The first two zones form the trophotagma; the flowering unit is the anthotagma (RUA & WEBERLING 1995).

In agreement with SELL 1969, 1976 the flowering unit has a main florescence and long paracladia without trophotagma.

Some buds can develop in the distal part of the trophotagma, and thus the zone becomes an enrichment zone. Buds generate long paracladia bearing a proximal trophotagma, which are then termed long paracladia with trophotagma (VEGETTI 1994, VEGETTI & WEBERLING 1996) or second order paracladia (RUA & WEBERLING 1995).

A common structural pattern is exhibited by florescences represented by spikelets (both main and coflorescences), and variations are due to bract characteristics and flower gender. In this respect, one flowered florescences are perfect in *Rhynchoryza*, *Leersia*, *Oryza*, *Prospychochloa* SCHWEICKERDT, *Porteresia* TATEOKA, *Chikusichloa* KOIDZ., *Hygroryza* and *Maltebrunia* KUNTH; and are male and female in the other genera (WATSON & DALLWITZ 1992). In *Luziola* male florescences are on the main axis flowering unit, and female florescences in the flowering unit of Pl+t. In *Zizaniopsis* and *Zizania* L. male and female florescences are in different positions along the main axis flowering unit. In *Potamophila* R. BR. perfect, male and female florescences are found along the main axis flowering unit (WATSON & DALLWITS 1992).

The greatest variability among the species studied can be found in paracladia. All taxa have a subzone of long and short paracladia in the flowering unit. Short paracladia are made up of a single spikelet (coflorescence) as originally defined by TROLL 1965. In other genera of *Poaceae*, short paracladia have more spikelets (CÁMARA HERNÁNDEZ & RUA 1991; RUA & WEBERLING 1995; VEGETTI 1997a, 1997b). The *Zizaniopsis* – species which we studied, had the least developed short paracladial zone.

Long paracladia comprising the flowering unit are termed long paracladia without trophotagma (Pl-t) (VEGETTI & WEBERLING 1996). The extension of the Pl-t zone is well developed in *Zizaniopsis*, *Rhynchoryza* and in some *Oryza* species, less in *Luziola* and in *Leersia*.

Long paracladia with trophotagma are found in *Luziola* and *Rhynchoryza*. The inflorescence of *Luziola* has 3–4 primary paracladia of this type, which are generally not branched from the axillar bud of their prophyll, except in *L. pittieri* where up to the third order long paracladia with trophotagma can be observed. In *Luziola* the region of Pl+t is separated from the Pl-t by a sterile bract (Fig. 2) with developed sheath and lamina, as has been described for some inflorescences in *Andropogoneae* (VEGETTI & WEBERLING 1996; VEGETTI 1997a, 1997b).

In *Rhynchoryza*, a single primary Pl+t is observed in the last distal leaf axil, and there is no sterile bract between the two zones of long paracladia (Fig. 3). This single Pl+t is branched at the axillar bud, and up to sixth the order paracladia can be observed in some inflorescences.

Pl+t are open structures which can potentially develop new paracladia from axillar buds of bracts and prophylls (VEGETTI 1994).

Primary paracladia are set along the main axis in an alternate form or in pseudoverticils. GRAM 1961 attributes this last phenomenon to two processes. One process is derived from the assumption that in some primary paracladia the basal internode remain undeveloped, thus causing the branches to appear to have a common origin. The other process is the abbreviation of the internodes of the inflorescence axis, leading to the formation of a pseudoverticil of primary paracladia. The former process is probably responsible for the constitution of *Oryzaceae* inflorescences with several paracladia per node.

It is quite frequent to observe in *Oryzaceae* species a variable degree of peduncle growth, determining the appearance of inflorescences either exerting from, or partially included in the respective sheath.

Axillary buds in the distal trophotagma zone in *Prospyrtochloa*, develop into shoots that can eventually flower (WATSON & DALLWITZ 1992), which would therefore be Pl+t. This does not happen in *Maltebrunia*, *Chikusichloa*, *Hygroryza*, *Zizania* and *Potamophilia* (WATSON & DALLWITZ 1992).

In conclusion, the main variations in typology in *Oryzaceae* inflorescences are related to the flowering unit and the presence or absence of Pl+t.

Variability among species in flowering units refers to the gender of florescences, the extension of the short paracladial subzone and the zone of long paracladia without trophotagma, in the number and degree of branching of the paracladia. Pl+t, if present, can vary in number, position and branching degree.

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Recensio

HESS Hans Ernst, LANDOLT Elias, HIRZEL Rosemarie & BALTISBERGER Mathias 1998. Bestimmungsschlüssel zur Flora der Schweiz und angrenzender Gebiete. 8°, 7 + 659 Seiten, zahlr. Strichzeichnungen; geb. – 4., überarbeitete Aufl. – Birkhäuser Verlag, Basel, Boston, Berlin. – sFr. 48,-. – ISBN 3-7643-5831-9.

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Seite 42: *Anthoxanthum odoratum* und *A. alpinum* sind gewiß nicht nach Länge und Farbe des Blütenstandes zu unterscheiden, zumal die strohgelbe Farbe erst den Fruchtstand nach der Vollreife kennzeichnet. – Seite 110: In der Schweiz kommen nicht zwei, sondern ganz sicher drei *Nigritella*-Arten vor. – Seite 259: Die Blühspresse von *Geum montanum* werden häufig bis ca. 25 cm hoch und sind nicht immer einblütig. – Seite 390: Man kann es drehen und wenden wie man will, *Onosma taurica* WILLD. (von Bulgarien und Griechenland an ostwärts) und *O. stellulata* W.K. (im Index p. 597; NW-Balkanhalbinsel) kommen in der Schweiz absolut sicher nicht vor; es handelt sich um *O. helvetica* BOISS., die mit den beiden vorgenannten gar nicht näher verwandt ist.

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