KEW BULLETIN VOL. 63: 525–563 (2008)

An integrative approach to species delimitation in *Echinodorus* (*Alismataceae*) and the description of two new species

Samuli Lehtonen[1]

Summary. Taxonomy of the genus *Echinodorus* is partially revisited in the light of current understanding of the phylogenetic relationships of the genus. As a result of new taxonomy, the species status of some previously synonymised taxa are restored, other names are synonymised, and some nomenclatural problems unnoticed by previous authors are resolved. Two new species, *Echinodorus reptilis* and *E. emersus* are described. The subgeneric divisions of the genus are not accepted, and all subspecific taxa are either rejected or established as species. As a result, 28 species based on a phylogenetic species concept are now recognised in *Echinodorus* and an identification key to these species is provided.

Key Words. *Alismataceae*, cladistics, *Echinodorus*, Neotropics, new species, phylogeny, taxonomy.

Introduction

Practical species delimitation and identification are essential objectives of taxonomy, and failure in that task might lead to ambiguous biodiversity information (see Alroy 2002; Dayrat 2005). An example of a taxonomically challenging plant group is the genus *Echinodorus* Rich. ex Engelm. (*Alismataceae*). It consists of aquatic and semi-aquatic herbs naturally distributed in the Americas from USA to Argentina, but used worldwide as ornamentals in aquaria (Haynes & Holm-Nielsen 1994). Great phenotypic plasticity, together with sparse botanical collections in the Neotropics, lack of phylogenetic information and varying taxonomic practices have confused the taxonomy of the genus, resulting in highly contradictory species delimitations and ambiguous generic classification.

Micheli (1881) was the first author to monograph *Echinodorus* after the formal description of the genus by Engelmann (1848). Micheli (1881) recognised 17 species, including four species that have later been transferred to *Baldellia* Parl., *Helanthium* (Benth. & Hook.) Britton or *Ranalisma* Stapf. Britton (1905) separated *Helanthium* from *Echinodorus*. Pichon (1946) accepted this, and also considered *Albidella* as a separate genus. Afterwards Fassett (1955) considered *Helanthium* as a subgenus of *Echinodorus* and later workers (Rataj 1975; Haynes & Holm-Nielsen 1994; Lot & Novelo 1994) have followed this classification. In recent phylogenetic analyses (Lehtonen 2006; Lehtonen & Myllys 2008) *Echinodorus sensu lato* was found to be polyphyletic, and in order to obtain a monophyletic circumscription of the genus the classification proposed by Pichon was followed by transferring *E. nymphaeifolius* into *Albidella*, and *E. bolivianus*, *E. tenellus* and *E. zombiensis* into *Helanthium* (Lehtonen & Myllys 2008).

The circumscription and number of accepted species in the genus have varied even more than generic boundaries depending on the authors. Rataj has been the most productive researcher in the taxonomy of *Echinodorus* by publishing two revisions of the genus (Rataj 1975, 2004). The older revision recognised 47 species, 19 of which Rataj described. Many species descriptions were based on cultivated and sometimes sterile material of unknown origin. This work was criticised for accepting too many species, accepting species based on insufficient material, and making serious errors in typification (Cook 1978; Haynes & Holm-Nielsen 1986, 1994). This criticism did not prevent Rataj from describing many new species and finally accepting 62 species in his new revision (Rataj 2004). Haynes & Holm-Nielsen (1986, 1994) accepted the same circumscription of the genus as Rataj (1975), but rejected his sectional division and many of his species thus reducing the number of species to 26. In the course of their revision Haynes & Holm-Nielsen (1986, 1994) made a monumental work in correcting typification errors and designating lectotypes. Both Rataj (1975, 2004) and Haynes & Holm-Nielsen (1986, 1994) included *Helanthium* and

Accepted for publication September 2008.

[1] Department of Biology, Section of Biodiversity and Environmental Science, University of Turku, 20014 Turku, Finland. e-mail: samile@utu.fi

Albidella in their circumscription of the genus. When these genera are excluded, the numbers of species they included in *Echinodorus sensu stricto* were 52 (Rataj 2004) and 23 (Haynes & Holm-Nielsen 1994), respectively. Later, Haynes & Burkhalter (1998) described one more species. None of these studies were based on phylogenetic analysis or included any molecular characters.

In order to achieve robust and reliable phylogenetic taxonomy an integrative approach to species delimitation has been proposed (Dayrat 2005). The integrative approach studies species boundaries from various perspectives at the same time: morphological, molecular, ecological and other biological evidence are used synthetically (Dayrat 2005). With the intention of reducing the creation of further synonyms taxonomists should avoid introducing new names on the basis of single specimens and without knowledge of infraspecific variation (Dayrat 2005).

Recent advances in *Echinodorus* phylogenetics have revealed several unnatural species and subspecies level rankings thus resulting in the need for a partial revision of the genus (Lehtonen 2006; Lehtonen & Myllys 2008). In the present study, I examine further the results of the combined analysis of molecular and morphological data by Lehtonen & Myllys (2008) in order to achieve a more reliable, phylogeny-based species delimitation in *Echinodorus*. As a result, I describe two new species and propose 20 new synonyms. I also summarise the available taxonomic, ecological and biogeographical information on each species, and provide an identification key. Variable taxonomic practices and the quality of the plant material used have resulted in a varying level of confidence in the described species. Accordingly, the species names are treated here as 1) accepted as reliable indicators of phylogenetic relationships, 2) accepted, but considered less reliable due to insufficient material, and 3) doubtful names that have been validly published but are not applicable in practice, because neither type material nor species descriptions allow unambiguous identification.

Materials and Methods

Material Studied and Phylogenetic Background

The species delimitation proposed here is based on studies of c. 3000 herbarium specimens deposited in AAU, AMAZ, BA, BM, BR, C, CAR, CTES, FCQ, H, K, LPB, M, MEXU, MVFA, MVFQ, MVJB, MVM, MY, MYF, PR, PY, Q, QCA, QCNE, QPA, S, SI, TUR, U, UC, UNA, VEN, and W, (herbarium codes according to Holmgren & Holmgren 1998) studies on digital images of selected herbarium sheets deposited in B, BH, F, G, G-DC, GOET, MOR, NY, P, PH, RB, SP, UB, and US, intensive field studies in different parts of the range of the genus (113 populations studied), and on phylogenetic studies of both morphological characters and *matK*, *ITS1;2*, *LEAFY*, and *5S-NTS* sequences (Lehtonen 2006; Lehtonen & Myllys 2008). Morphological, plastid DNA, and nuclear DNA data sets were interpreted to be congruent on the basis of tree-similarity measurements, which were obtained by calculating the minimum number of SPR moves required to transform a tree obtained from one data set into the tree obtained from another data set (Goloboff *et al.* 2003; Lehtonen & Myllys 2008). The total evidence approach (Kluge 1989; Fitzhugh 2006) was therefore applied and all the data were analysed simultaneously.

In the combined phylogenetic study 43 individuals from different populations were sequenced and each population separately coded in a morphological data matrix, and ten additional populations were coded for morphological data only (Lehtonen & Myllys 2008). Thus, in total the analysis was based on 53 terminal populations, including all the species accepted in the present paper. The DNA sampling was emphasised on taxonomically challenging groups, and geographically distant populations were sampled whenever sufficient material was available. By coding each studied population separately for the analysis it was possible to avoid the problem of pre-defined species boundaries which could have affected the analysis if variation between populations had been coded as polymorphism (Lehtonen & Myllys 2008). Hence, the analysis was free from *a priori* classification, and the most severe possible test for the species hypotheses was implemented. Confidence of the obtained classification was evaluated *a posteriori* by jackknifing (Farris *et al.* 1996) implied alignments and morphological data of combined analysis with 1000 TBR branch-swapping replicates by TNT (Goloboff *et al.* 2003).

Species Concept and Delimitation

The main purpose of taxonomy is to reflect phylogeny, i.e. evolutionary history of the studied organism group. As shown already by Farris (e.g. 1979, 1982) the most informative classification, and also the one that best serves the needs of other fields of biology, is achieved by the one based on phylogeny. Therefore my species concept is phylogenetic.

Methods recently suggested for delimiting species boundaries often rely on sequence data (see Sites & Marshall 2003 and 2004 for a review) and hence require DNA sampling of a large number of individuals, which reduces the practicality of these methods. Furthermore, these methods are prone to incomplete lineage sorting and other similar problems, and may be misleading if based on poorly selected DNA-regions (Brower *et al.* 1996; Nichols 2001; Álvarez & Wendel 2003). Therefore species trees should be estimated on the basis of all possible data available (Wahlberg *et al.* 2003; Stace 2005). Consequently species are here

recognised through an analysis of total available evidence. Here, "analysis" refers to a cladistic analysis and "evidence" equals observed features (=characters) of the specimens, either morphological or molecular. Unambiguous character state changes are used as a guideline in recognising smallest monophyletic groupings of populations which are diagnosable by a unique combination of character states (partly following Nixon & Wheeler 1990). In the phylogenetic analysis 43 morphologically distinct populations were sequenced and their phylogeny resolved (Lehtonen & Myllys 2008). In the present study, the amount of morphological and molecular character state changes along lineages are investigated (Fig. 1) and relative length differences of sister lineages are considered as an indication of an existing species boundary. If the corresponding lineage length based on another data set supports or does not contradict the assumption of species boundary, the lineage is considered to represent a phylogenetic species. In ambiguous situations ecological and biogeographical evidence is also considered.

Results and Discussion

Phylogeny and Species Delimitation in *Echinodorus*

In the combined analysis of morphological and molecular data, the type species of the genus (*E. berteroi*), was resolved as a sister lineage to other *Echinodorus* (Fig. 1) (Lehtonen & Myllys 2008). However, this position was found to be somewhat ambiguous, since the nuclear genome suggested independent origins for *E. berteroi* and the main bulk of *Echinodorus*. The lineage leading to *E. berteroi* is relatively long and thus potentially erroneously resolved (Bergsten 2005), and the sister lineage relationship to other *Echinodorus* is considered the best supported hypothesis on the basis of morphology, plastid DNA, and the combined analysis. Otherwise the topology within *Echinodorus* did not vary much between analyses of different data sets (Lehtonen & Myllys 2008), and the recognised clades are discussed below.

Clade A. *Echinodorus berteroi* is resolved as a sister to the rest of *Echinodorus*.

Clade B. This clade can be recognised by sepals that surround the mature fruiting aggregate. This group has been recognised previously, but with the inclusion of *Echinodorus glandulosus* that in the phylogenetic analyses was resolved to clade F (Rataj 1969b; Haynes & Holm-Nielsen 1989; Fig. 1).

Clade C. This clade mainly corresponds with Rataj's (1975) section *Palaefolii* Rataj. The species of the clade share a common flower morphology by having 12 stamens and relatively small non-overlapping petals. However, these character states are not unique to this clade, but can be found in *Echinodorus. trialatus* (in clade F) as well.

Clade D. This clade is composed of the amphibious and highly polymorphic species *Echinodorus grisebachii* and *E. heikobleheri*. Species of this clade share a unique flower morphology of small flowers with 9 stamens.

Clade E. *Echinodorus lanceolatus* forms a lineage of its own, but the species is based on the type specimen only, and therefore its phylogenetic position and species status are not fully certain. No molecular data were available for the species.

Clade F. This clade is an unexpected group if morphological evidence alone is considered (Lehtonen 2006). *Echinodorus glandulosus* is resolved as a member of this clade, although usually it is considered to be related to the species in the clade B (Rataj 1969b; Haynes & Holm-Nielsen 1989). However, only two specimens of *E. glandulosus* are known, and as no molecular data were available its phylogenetic position is based on morphological data only. No morphological synapomorphies are known for the entire clade, but its monophyly is supported by molecular evidence.

Clade G. *Echinodorus macrophyllus* and *E. bracteatus* form a small clade. However, no molecular evidence was available from the former species, and its position therefore lacks molecular support.

Clade H. The species in this clade, *Echinodorus glaucus* and *E. cylindricus*, are unique in having a bluish wax cover and large flowers with 24 – 30 stamens.

Clade I. This large clade was found to have almost no variation in the DNA segments that were sequenced, although the species are both ecologically and morphologically clearly distinct from each other.

Haynes & Holm-Nielsen (1994) rejected Rataj's (1975) sectional division of the genus, because many characters that supposedly separate the sections actually overlap among different sections. This conclusion was further supported by phylogenetic evidence: even though well supported clades can be recognised in *Echinodorus*, high phenotypic plasticity combined with wide morphological variation within clades does not support subgeneric splitting. Consequently, I reject all proposed subgeneric divisions (Lehtonen & Myllys 2008).

Based on the phylogenetic evidence I recognise 28 phylogenetic species in *Echinodorus* (Fig. 1). Two species have remained undescribed, while others have been named, but in some cases with ambiguous delimitation and description. The accepted species are circumscribed and discussed below with comments on species delimitation in the cases where circumscription differs from Haynes & Holm-Nielsen (1994).

Previously proposed subspecific taxa are either rejected or established as species when it seems that they are of polyphyletic origin. Subspecific rankings

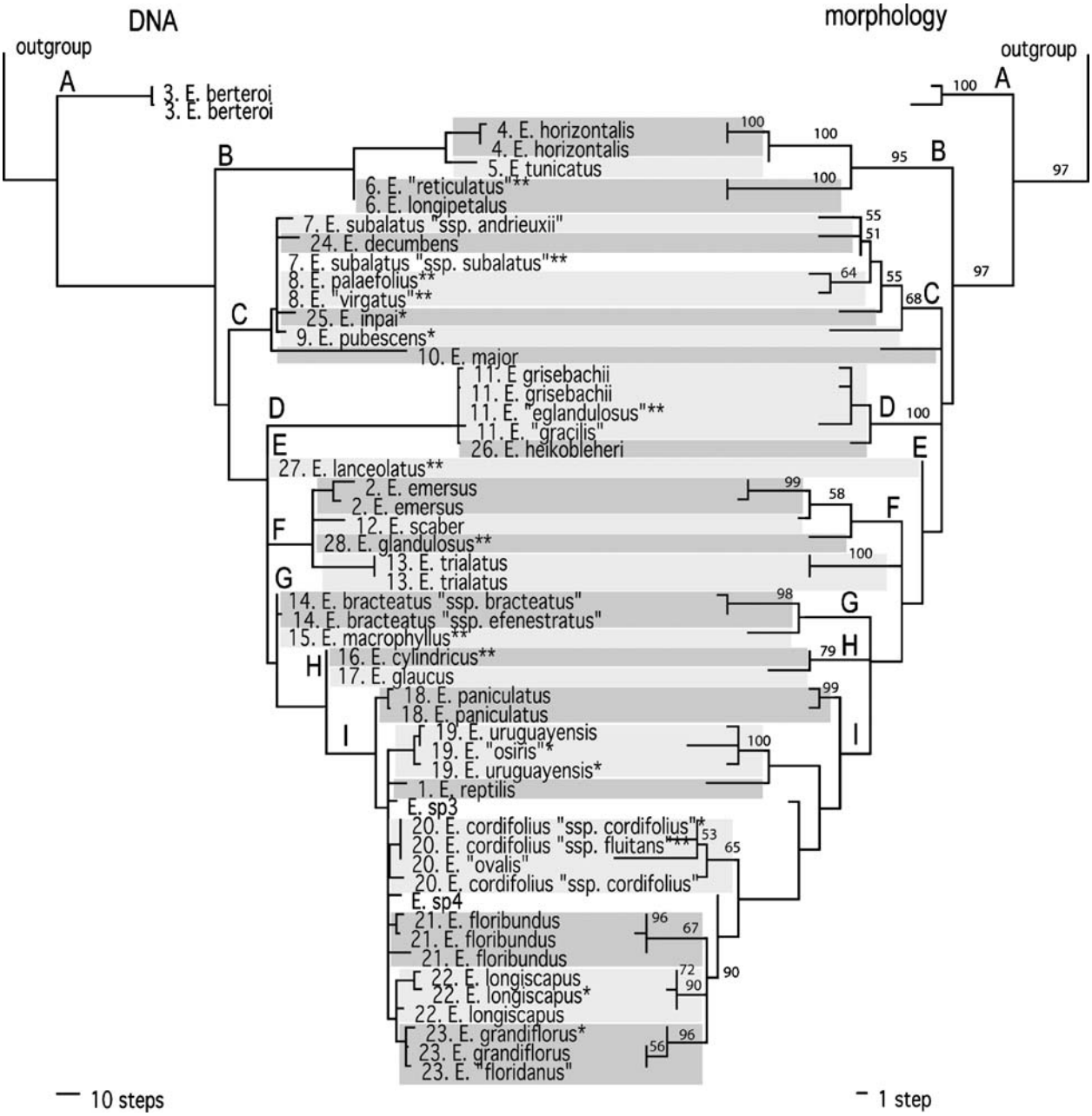


Fig. 1. Species delimitation in *Echinodorus* on the basis of molecular and morphological evidence. *Shaded boxes* represent species as they are delimited here. Jackknife support values are shown on the right side, but are calculated for combined analysis of molecular and morphological data. Topology is based on the total-evidence analysis of Lehtonen and Myllys (2008) with branch lengths corresponding to unambiguous character changes (studied with MacClade, Maddison & Maddison 2005). Terminals that lack some molecular data are marked with *asterisk* (*), terminals that lack all molecular data are marked with *two asterisks*. Names that are not accepted here are written in *quotation marks*.

have been widely used in the taxonomy of *Echinodorus*, but the justification for these rankings has frequently remained vague. In phylogenetic taxonomy, subspecific rankings are often denied (e.g. Hennig 1966), but as there is no clear demarcation line between tokogeny and phylogeny, reticulate patterns may exist above species level and phylogenetic patterns may exist below species level (Mishler & Theriot 2000). In such cases, it may be justified to rank some taxa in a subspecific category. However, detailed understanding of the population-level biology, phylogeny, genetics, and variation would be needed to justify such a decision, and in the case of *Echinodorus*, such understanding does not exist.

Key to the species of *Echinodorus*

1a. Leaf base cordate. 2
1b. Leaf base attenuate to truncate. 19
2a. Pellucid markings present 3
2b. Pellucid markings absent 12
3a. Pellucid markings present as a reticulate network 4
3b. Pellucid markings present as separate lines and/or dots 6
4a. Sepals not surrounding fruit aggregate, inflorescence paniculate, rachis alate . . . . . **28. E. glandulosus**
4b. Sepals surrounding fruit aggregate, inflorescence racemose, rachis not alate 5
5a. Inflorescence decumbent, overtopping the leaves, the whorls with 3 – 4 flowers . . . . . **2. E. horizontalis**
5b. Inflorescence erect, shorter than leaves, the whorls with 7 – 50 flowers . . . . . **3. E. tunicatus**
6a. Pellucid markings present as lines only 7
6b. Pellucid markings present as lines and dots, or dots only 8
7a. Inflorescence rachis alate . . . . . **6. E. palaefolius**
7b. Inflorescence rachis not alate . . . . . **1. E. berteroi**
8a. Inflorescence rachis alate . . . . . **13. E. bracteatus**
8b. Inflorescence rachis not alate 9
9a. Inflorescence decumbent . . . . . **20. E. cordifolius**
9b. Inflorescence erect 10
10a. Pellucid markings present as dots only, leaves with 7 – 21 veins . . . . . **21. E. floribundus**
10b. Pellucid markings present as lines and dots, leaves with 5 – 11 veins 11
11a. Inflorescence < 1 m tall, usually not branching, leaf blade 5 – 20 cm long . . . . . **22. E. longiscapus**
11b. Inflorescence usually > 1 m tall, branching, leaf blade 15 – 30 cm long . . . . . **23. E. grandiflorus**
12a. Inflorescence rachis alate 13
12b. Inflorescence rachis not alate 14
13a. Sepals erect, covering the base of fruit aggregate, with 13 – 20 veins, stamens 15 – 20 . . . . . **13. E. bracteatus**
13b. Sepals not covering the base of fruit aggregate, with 10 – 13 veins, stamens 12 . . . . . **6. E. palaefolius**
14a. Inflorescence decumbent, pedicels 3 – 10 cm long . . . . . **20. E. cordifolius**
14b. Inflorescence erect, pedicels 0.5 – 3 cm long 15
15a. Inflorescence and petioles glabrous 16
15b. Inflorescence and petioles scabrous 17
16a. Leaves and stems covered with bluish wax, sepals with 18 – 30 veins . . . . . **16. E. glaucus**
16b. Leaves and stems without wax cover, sepals with 11 – 19 veins . . . . . **14. E. macrophyllus**
17a. Leaves with 9 – 21 veins, blades almost as wide as long, apex round to retuse, fruit with 2 – 3 elongate glands and beak < 5 mm long . . . . . **21. E. floribundus**
17b. Leaves with 5 – 11 veins, blades clearly longer than wide, apex acute to round, fruit with 0 – 2 circular glands and beak > 5 mm long 18
18a. Pedicels < 1 cm long, fruit without glands, inflorescence racemose or branching at the lowest whorl . . . . . **10. E. emersus**
18b. Pedicels 0.5 – 2.5 cm long, fruit with 0 – 2 glands, inflorescence usually branching, often also at the second whorl . . . . . **11. E. scaber**
19a. Pellucid markings present 20
19b. Pellucid markings absent 32
20a. Pellucid markings present as a reticulate network . . . . . **4. E. longipetalus**
20b. Pellucid markings present as separate lines and/or dots 21
21a. Inflorescence decumbent 22
21b. Inflorescence erect 25
22a. Inflorescence umbelliform, or racemose of 2 whorls . . . . . **19. E. reptilis**
22b. Inflorescence racemose or paniculate, 3 or more whorls 23
23a. Pedicels longer than 3 cm, flower diam. > 2 cm, stamens 15 – 28 . . . . . **20. E. cordifolius**
23b. Pedicels < 2 cm long, flower diam. < 2 cm, stamens 9 – 12 24
24a. Fruit with 1 large gland and beak > 5 mm, petioles channelled . . . . . **24. E. decumbens**
24b. Fruit with several small glands and beak < 5 mm, petioles triangular in cross-section, not channelled . . . . . **9. E. grisebachii**
25a. Pellucid markings present as short lines and dots 26

25b. Pellucid markings present as lines only 27
26a. Inflorescence < 1 m tall, usually not branching, leaf blade 5 – 15 cm long . . . . . **22. E. longiscapus**
26b. Inflorescence usually > 1 m tall, branching, leaf blade 15 – 30 cm long . . . . . **23. E. grandiflorus**
27a. Rachis alate 28
27b. Rachis not alate 29
28a. Base of the blade truncate, blade < twice as long as wide . . . . . **6. E. palaefolius**
28b. Base of the blade attenuate, blade usually > twice as long as wide . . . . . **5. E. subalatus**
29a. Pedicels recurved in fruit . . . . . **9. E. grisebachii**
29b. Pedicels spreading in fruit 30
30a. Pedicels < 1 cm long . . . . . **25. E. inpai**
30b. Pedicels > 1 cm long 31
31a. Fruit with beak > 1 mm long, with 0 – 2 large glands, flower diameter < 1.5 cm, petals with claws . . . . . **1. E. berteroi**
31b. Fruit with beak < 1 mm long, with several small glands, flower diameter > 2 cm, petals without claws . . . . . **18. E. uruguayensis**
32a. Fruit without glands 33
32b. Fruit with glands 34
33a. Pedicels < 1 cm long, flower diam. < 1.5 cm, 12 stamens, rachis usually alate, inflorescence racemose . . . . . **12. E. trialatus**
33b. Pedicels usually longer than 1 cm, flower diam. > 2 cm, 18 – 24 stamens, rachis not alate, inflorescence often paniculate . . . . . **17. E. paniculatus**
34a. Inflorescence decumbent 35
34b. Inflorescence erect 36
35a. Pedicels longer than 3 cm, flower diameter > 2 cm, stamens 15 – 28 . . . . . **20. E. cordifolius**
35b. Pedicels shorter than 1.5 cm, flower diameter < 2 cm, stamens 9 – 12 . . . . . **26. E. heikobleheri**
36a. Inflorescence rachis alate, petiole channelled 37
36b. Inflorescence rachis not alate, petiole not channelled 38
37a. Base of the blade truncate, blade < twice as long as wide . . . . . **6. E. palaefolius**
37b. Base of the blade attenuate, blade usually > twice as long as wide . . . . . **5. E. subalatus**
38a. Inflorescence, pedicels and sepals pubescent, hairs simple . . . . . **7. E. pubescens**
38b. Inflorescence, pedicels and sepals glabrous 39
39a. Bracts almost as wide as long, with 18 – 30 veins, leaves and stems covered with bluish wax . . . . . **15. E. cylindricus**
39b. Bracts much longer than wide, with < 15 veins, leaves and stems without wax cover 40
40a. Inflorescence paniculate . . . . . **27. E. lanceolatus**
40b. Inflorescence racemose 41
41a. Leaf blade with attenuate base, stamens 15 – 20, flower diameter > 2 cm. . . . . **18. E. uruguayensis**
41b. Leaf blade with truncate base, stamens 12, flower diameter < 1.5 cm . . . . . **8. E. major**

Accepted Species

1. Echinodorus berteroi (*Spreng.*) Fassett (1955: 139 – 140); Rataj (1970c: 21; 1975: 23); Haynes (1984: 6); Holm-Nielsen & Haynes (1986: 13); Haynes & Holm-Nielsen (1994: 39); Lot & Novelo (1994: 4); Haynes & Hellquist (2000: 9); Rataj (2004: 26). Type: based on the type of *Alisma berteroi*.

Alisma berteroi Spreng. (1825: 163). Type: Guadeloupe, *Bertero* s.n. (holotype GOET?).

Alisma berteroanum Balb. ex Schult. & Schult. f. (1830: 1605). (*nomen superfluum*, name based on the type of *Alisma berteroi*).

Alisma rostrata Nutt. (1835: 159). Type: USA, Arkansas (Oklahoma), *Nuttall* s.n. (holotype PH; isotype BM).

Echinodorus rostratus (Nutt.) Engelm. (1848: 460); Micheli (1881: 56), Buchenau (1903: 31). Type: based on the type of *Alisma rostrata*.

Echinodorus rostratus (Nutt.) Engelm. var. *lanceolatus* Engelm. (1890: 556). Type: USA, *Engelmann* s.n. (holotype MO; isotype GH).

Echinodorus cordifolius (L.) Griseb. f. *lanceolatus* (Engelm.) Fernald (1936: 73). Type: based on the type of *Echinodorus rostratus* var. *lanceolatus*.

Echinodorus rostratus (Nutt.) Engelm. f. *lanceolatus* (Engelm.) Fernald (1947: 108). Type: based on the type of *Echinodorus rostratus* var. *lanceolatus*.

Echinodorus berteroi (Spreng.) Fassett var. *lanceolatus* (Engelm.) Fassett (1955: 144). Type: based on the type of *Echinodorus rostratus* var. *lanceolatus*.

Echinodorus patagonicus Speg. (1902: 174); Hauman (1915: 316). Type: Argentina, Neuquen, Fuerte Roca, *Spegazzini* s.n. (holotype BAB [photograph in QCA!]).
Echinodorus berteroi (Spreng.) Fassett subsp. *patagonicus* (Speg.) Rataj (1969e: 29; 2004: 30).
Echinodorus longilineatus Rataj (2004: 32). Type: Ecuador, Azuay, *MacBryde* 445 (holotype US; isotypes AAU!, QCA!). **synon. nov.**

Annual, glabrous, to 110 cm. *Leaves* emersed or submersed, emersed blades elliptic-lanceolate, 3 – 11-veined, 3 – 15 cm long, 1 – 19 cm wide, the pellucid markings present as lines, the apex acute to round, the base truncate to cordate, petioles terete to triangular in cross-section, angled, 3 – 55 cm long, 5 mm diam., the base with a sheath to 7 cm long, submersed blades linear, with 1 – 3 veins, c. 15 cm long, 1 – 1.5 cm wide, the pellucid markings absent or present as lines, the apex acute, the base attenuate, petioles triangular in cross-section, to 4 cm long, 1 mm diam., the base with a sheath to 3 cm long. *Inflorescence* racemose or paniculate, of 1 – 9 whorls, each 3 – 18-flowered, erect, overtopping leaves, not proliferating, to 50 cm long, to 25 cm wide, rachis triangular in cross-section, peduncles terete, angled, 7 – 60 cm long, 5 mm diam., bracts free, lanceolate, 0.5 – 3.5 cm long, 2 – 7 mm wide, 5 – 10-veined, apex acute, pedicels spreading in flower and fruit, terete, 1 – 3 cm long, 0.3 mm diam. *Flowers* 1 – 1.5 cm diam., sepals and petals spreading, sepals 10 – 13-veined, c. 5 mm long, c. 3 mm wide, veins without papillae, petals white, clawed, not overlapping, c. 7 mm long, c. 6 mm wide, stamens 13 – 15, the anthers versatile, c. 0.5 mm long, the filaments c. 2 mm long, carpels numerous. *Fruit* oblanceoloid, 4 – 6-ribbed, 2-keeled, glandular, 1.5 – 3 mm long, 0.5 – 1 mm wide, glands 1 – 2, separated by ribs, elliptic, beak terminal, erect, 0.9 – 1.8 mm.

DISTRIBUTION AND ECOLOGY. USA, the Caribbean Islands, Mexico, Pacific coast of Ecuador and Peru, Argentinian and Paraguayn Chaco, and Patagonia (Map 2). Temporal pools and mud flats. Flowering and fruiting year round in South America, from April to October in USA. From sea level to 1500 m.
SELECTED COLLECTIONS. ANTIGUA AND BARBUDA. *Box* 1380 (UC!), *Box* 702 (BM!). **ARGENTINA.** *Flossdorf* s.n. (BA!), *Flossdorf* 94 (SI!). **BARBADOS.** *Goodwip* 32 (BM!). **DOMINICAN REPUBLIC.** *Zanoni & Mejia* 17992 (UNA!), *Fuertes* 1132 (BM!, UC!). **ECUADOR.** *MacBryde* 445 (AAU!, QCA!), *Madsen* 63654 (AAU!, QCA!, QCNE!). **GUADELOUPE.** *Duss* 3652 (F!), *Stehle* 1555 (UC!), *Christenhusz* 4081 (TUR!). **HAITI.** *Ekman* 3347 (C!). **JAMAICA.** *Stearn* 302 (BM!), *Adams* 10728 (M!). **MEXICO.** *Carter* 4320 (BM!, MEXU!, UC!), *Pringle* 8484 (BM!, C!, MEXU!, PR!, UC!), *Lehtonen & Ramírez-García* 412 (TUR!, MEXU!). **PARAGUAY.** *Mereles* 707 (CTES!), *Mereles* 708 (FCQ!). **PERU.** *Santos Lltas* 491 (UNA!). **PUERTO RICO.** *Sintenis* 3844 (BR!, C!, UC!), *Ricksecker* 275 (UC!). **USA.** *Davidse et al.* 101 (UNA!), *McGregor* 166 (S!), *Miller & Horn* 430 (UNA!), *Lindheimer* 1233 (BR!, UC!, K!, MEXU!), *Palmer* 10174 (S!). **VENEZUELA.** *Ruizz* 657 (VEN!), *Agostini & Agostini* 1001 (VEN!). **VIRGIN ISLANDS.** *Raunkiaer* 506 (C!).
NOTES. This species is resolved as sister to the rest of the genus in morphology-based (Lehtonen 2006), DNA-based, and total-evidence analysis (Lehtonen & Myllys 2008), but nuclear DNA suggested a drastically different phylogenetic position for the species. Since *Echinodorus berteroi* is the type species of the genus, its phylogenetic position determines the generic name of the other species treated here. If more comprehensive studies in the future place *E. berteroi* in a non-monophyletic position in relation to the other species treated here, a new genus should be established for the rest of the species. South American populations of *E. berteroi* are morphologically similar with those from North America, and proposed species (*E. patagonicus*, Spegazzini 1902; *E. longilineatus*, Rataj 2004) or subspecific (*E. berteroi* subsp. *patagonicus*, Rataj 2004) rankings for South American populations are not warranted.

2. Echinodorus horizontalis *Rataj* (1969b: 335); Holm-Nielsen & Haynes (1986: 12); Haynes & Holm-Nielsen (1994: 29); Rataj (2004: 88). Type: Peru, Loreto: Gamitanacocha, Río Mazán, *Schunke* 279 (holotype US [digital image!]; isotypes GH, F, NY [digital image!], UC!)
Echinodorus interruptus Rataj (2004: 111). Type: Brazil, Acre, Tarauacá, *Prance et al.* 7475 (holotype US; isotype K!). **synon. nov.**

Perennial, from erect rhizomes, glabrous, to 100 cm, rhizomes to 10 cm long, 1 cm diam. *Leaves* emersed, blades ovate, 7 – 9-veined, 11 – 30 cm long, 6 – 17 cm wide, pellucid markings present as a reticulate network, apex acuminate, base cordate, petioles terete, 17 – 50 cm long, 4 mm diam., base with a sheath to 15 cm long. *Inflorescence* racemose, of 2 – 5 whorls, each 2 – 5-flowered, decumbent, overtopping leaves, proliferating, to 70 cm long, 5 cm wide, rachis terete in cross-section, peduncles terete, to 60 cm long, 2 mm diam., bracts deciduous, free, lanceolate, coarse, 1 – 2.5 cm long, 4 – 8 mm wide, c. 12 – 16-veined, apex acuminate, pedicels spreading in flower and recurved in fruit, terete, 1 – 3 cm long, 1 mm diam. *Flowers* open for only a few hours in the morning, 1.5 – 1.8 cm diam., sepals erect, 19 – 24-veined, c. 10 mm long, c. 10 mm wide, veins without papillae, petals spreading, white, not clawed, not overlapping, c. 10 mm long, c.

8 mm wide, stamens 19 – 24, anthers versatile, c. 1 mm long, filaments c. 2 mm long, carpels numerous. *Fruit* clavate, 3 – 4-ribbed, glandular, 1.8 – 2.8 mm long, 1 mm wide, glands 5 – 6, circular, beak terminal, horizontal, c. 0.3 – 0.5 mm.

DISTRIBUTION AND ECOLOGY. Amazonia. Growing in palm swamps, inundated forests along black water rivers, and small creeks in tierra firme. Flowering and fruiting year round. From sea level to 450 m.
SELECTED COLLECTIONS. BRAZIL. *Prance et al.* 7475 (K!), *Cid* 4147 (UNA!). **COLOMBIA.** *Sanchez et al.* 308 (AAU!), *Sanchez et al.* 1483 (AAU!). **ECUADOR.** *Cerón* 272 (QCA!, QCNE!, QPA!), *Cerón* 2043 (AAU!, QCA!, QCNE!, UNA!), *Jaramillo & Coello* 4226 (AAU!, QCA!), *Bennet & Alarcón* 4347 (QCNE!, UNA!), *Lehtonen & Quester* 512 (TUR!, QCA!). **GUYANA.** *van Andel et al.* 1107 (U!). **PERU.** *Diaz et al.* 585 (AAU!), *Ayala* 1751 (AMAZ!, UNA!), *Schunke* 279 (UC!), *Grández & Ruiz* 1160 (UNA!), *Rimachi* 4209 (UNA!), *Lehtonen & Arévalo* 54 (TUR!), *Lehtonen & Arévalo* 99 (TUR!). **VENEZUELA.** *Steyermark et al.* 114788 (AAU!, UNA!, VEN!).
NOTES. Rataj (2004) re-described the species as *Echinodorus interruptus*. According to Rataj (2004) *E. interruptus* lack pellucid markings, but the isotype has all the typical characters of *E. horizontalis*, including pellucid network.

3. Echinodorus tunicatus *Small* (1909: 48); Fassett (1955: 181); Rataj (1969b: 332; 1975: 46); Holm-Nielsen & Haynes (1986: 9); Haynes & Holm-Nielsen (1994: 31); Lot & Novelo (1994: 6); Rataj (2004: 86). Type: Panama, Marraganti and vicinity, *Williams* 991 (lectotype NY [digital image!]; isolectotype NY [digital image!], selected by Haynes & Holm-Nielsen 1994).

Perennial, from short erect rhizomes, glabrous, to 100 cm, rhizomes to 7 cm long, 1.5 cm diam. *Leaves* emersed, blades ovate, 7 – 13-veined, 14 – 40 cm long, 6 – 24 cm wide, pellucid markings present as a reticulate network, the apex acuminate, the base cordate, petioles terete, 20 – 80 cm long, 10 mm diam., base with a sheath to 20 cm long. *Inflorescence* racemes, of 1 – 6 whorls, each 7 – 50-flowered, erect, shorter than leaves, occasionally proliferating, to 30 cm long, 6 cm wide, rachis triangular in cross-section, peduncles terete, to 30 cm long, 1.3 cm diam., bracts deciduous, free, lanceolate, coarse, 3 – 6 cm long, 8 mm wide, c. 20-veined, apex acuminate, pedicels spreading in flower and recurved in fruit, terete, 2 – 4 cm long, 0.5 mm diam. *Flowers* open for only a few hours in the morning, 1.6 – 1.8 cm diam., sepals erect, 20 – 26-veined, c. 10 mm long, c. 10 mm wide, veins without papillae, petals spreading, white, not clawed, not overlapping, c. 10 mm long, c. 6 mm wide, stamens 19 – 24, anthers versatile, c. 1 mm long, filaments c. 2 mm long, the carpels numerous. *Fruit* clavate, 4 – 6-ribbed, glandular, 2.6 – 4.3 mm long, 1 mm wide, glands 3 – 4, circular, beak terminal, horizontal, c. 0.4 – 1 mm.

DISTRIBUTION AND ECOLOGY. Western Amazonia, Central America. Growing on the floor of inundated forests. Flowering and fruiting year round. From sea level to 500 m.
SELECTED COLLECTIONS. COLOMBIA. *Callejas et al.* 9716 (UNA!). **COSTA RICA.** *Khan et al.* 1225 (BM!), *Robles* 1885 (MEXU!), *Grayum & Flores* 9120 (UNA!). **ECUADOR.** *Quester* 307 (M!), *Zaruma et al.* 147 (QCNE!, UNA!), *Luteyn et al.* 8677 (AAU!, QCA!), *Holm-Nielsen et al.* 21495 (AAU!, QCA!), *Lehtonen & Quester* 516 (TUR!, QCA!). **PANAMA.** *Knapp & Mallet* 3979 (MEXU!). **PERU.** *Gentry et al.* 29837 (AMAZ!), *Huashikat* 124 (MEXU!), *Vasquez et al.* 2269 (UNA!), *Lehtonen* 133 (TUR!, AMAZ!).

4. Echinodorus longipetalus *Micheli* (1881: 60); Rataj (1969b: 332; 1970c: 27; 1975: 45); Haynes & Holm-Nielsen (1994: 26); Rataj (2004: 84). Type: Paraguay, Cordillera de Peribebuy, Patiño Cué, *Balansa* 570 (lectotype K [digital image!]; isolectotype K [digital image!], selected by Rataj 1969b).
Sagittaria brevipedicellata Kuntze (1898: 327). Type: Brazil, Minas Gerais, Caldas, *Widgren* s.n. (lectotype S; isolectotypes S, BR!, K [digital image!], M, selected by Haynes & Holm-Nielsen 1994).
Echinodorus brevipedicellatus (Kuntze) Buchenau (1903: 29). Type: Based on the type of *Sagittaria brevipedicellata*.
Echinodorus reticulatus R. R. Haynes & Holm-Niels. (1986: 327; 1994: 26). Type: Surinam, Sipaliwini savanna area on Brazilian frontier, *Oldenburger et al.* ON292 (holotype NY [digital image!]; isotypes NY [digital image!], U [digital image!]).

Perennial, from rhizomes, glabrous, to 300 cm, rhizomes to 15 cm long, 3 cm diam. *Leaves* emersed, blades elliptic to oblanceolate, 5 – 7 pseudopinnate veins, 30 – 80 cm long, 4 – 12 cm wide, pellucid markings present as reticulate network, apex acute, base attenuate, petioles triangular in cross section, to 50 cm long, 1.3 cm diam., base with a sheath to 13 cm long. *Inflorescence* racemes, of 3 – 11 whorls, each 4 – 18-flowered, erect, overtopping the leaves, not proliferating, 25 – 70 cm long, 7 cm wide, rachis triangular in cross-section, peduncles terete, to 200 cm long, 2.5 cm diam., bracts free, lanceolate, coarse, to 3 cm long, 8 mm wide, 11 – 16-veined, apex acute, pedicels spreading in flower, recurved in fruit, terete, 0.3 – 4.5 cm long, 1 mm diam. *Flowers* 4 – 7 cm diam., sepals

erect, 18 – 35-veined, c. 15 mm long, c. 10 mm wide, veins without papillae, petals spreading, white, not clawed, overlapping, c. 35 mm long, c. 33 mm wide, stamens c. 40, anthers versatile, c. 3 mm long, filaments c. 3 mm long, carpels numerous. *Fruit* clavate, 3 – 4-ribbed, slightly winged, without glands, 3 – 4 mm long, 1.5 mm wide, beak terminal, horizontal, c. 0.5 mm.

DISTRIBUTION AND ECOLOGY. Paraguay, central Brazil and southern Surinam. Flowering and fruiting from November to May. At elevations of 150 – 1000 m.

SELECTED COLLECTIONS. ARGENTINA. *Hauman* s.n. (BA!). **BRAZIL.** *Lima* 7384 (SP!), *Philcox & Fereira* 3865 (K!), *da Silva & de Lucca* 2475 (CTES!), *Eiten* 1555 (SP!, K!), *Gardner* 5191 (BM!), *Glaziou* 22293 (BR!, C!), *Irwin et al.* 24206 (AAU!, UNA!). **PARAGUAY.** *Zardini & Velázquez* 24628 (UNA!), *Hassler* s.n. (BM!, C!), *Hassler* 5255 (UC!), *Jiménez & Marín* 1966BJ (BM!, PY!), *Ortiz* 861 (FCQ!), *Schinini* 4154 (SI!), *Schinini* 8067 (CTES!), *Sparre & Vervoorst* 2050 (BR!), *Lehtonen & Burguez* 271 (TUR!, FCQ!). **SURINAM.** *Oldenburger et al.* ON292 (NY!, U!), *Rombouts* 447 (U!).

NOTES. Haynes & Holm-Nielsen (1986) described a new species, *Echinodorus reticulatus*, differing from *E. longipetalus* by its acuminate anther apices, longer pedicels and greater number of flowers per whorl. *E. longipetalus* has great variation in pedicel length and the number of flowers. Although pedicels are usually short (< 1 cm), they may reach a length of over 3 cm. The number of flowers per whorl varies from 3 to 15. *E. reticulatus* is said to have up to 4.5 cm long pedicels, and 10 – 18 flowers per whorl (Haynes & Holm-Nielsen 1986). There is an isotype of *E. reticulatus* deposited in U, and one older collection from Surinam as well (*Rombouts* 447). Both of these specimens have pedicels of c. 1.5 cm long, a typical length for *E. longipetalus*. Thus, these taxa seem to differ only by a few continuous and widely overlapping characters, if at all. The only known population of *E. reticulatus* is in Surinam, c. 1500 km north from the closest known *E. longipetalus* population. Based on the definition of subspecies by Haynes & Holm-Nielsen (1986), these taxa could have a subspecific rank (Lehtonen 2006), but in this treatment they are simply considered to be conspecific.

5. Echinodorus subalatus (*Mart.*) *Griseb.* (1866); Micheli (1881: 53); Buchenau (1903: 29); Rataj (1971: 15; 1975: 41), Haynes & Holm-Nielsen (1986: 326; 1994: 33); Lot & Novelo (1994: 5); Rataj (2004: 60). Type: Based on the type of *Alisma subalatum*.

Alisma subalatum Mart. (1830: 1609 – 1610). Type: Brazil. *Martius* 150 (lectotype M, selected by Rataj 1971).

Alisma intermedium Mart. (1830: 1609); Seubert (1847: 106). Type: Brazil. *Martius* 1547, the plant on the left (lectotype M [digital image!], selected by Somogyi 2006).

Echinodorus intermedius (Mart.) Griseb. (1866: 218); Haynes & Holm-Nielsen (1986: 326); Somogyi (2006: 382). Type: Based on the type of *Alisma intermedium*.

Echinodorus martii Micheli (1881: 49) (*nomen superfluum*, name based on the type of *Alisma intermedium*); Buchenau (1903: 30), Somogyi (2006: 381).

Alisma andrieuxii Hook. & Arn. (1838: 311). Type: Mexico, Tepic, *Beechey* s.n. (lectotype K (digital image!), selected by Fassett 1955) **synon. nov.**

Echinodorus ellipticus (Mart.) Micheli γ *ovata* Micheli (1881: 52). Type: Based on the type of *Alisma andrieuxii*.

Echinodorus andrieuxii (Hook. & Arn.) Small (1909: 46); Fassett (1955: 175); Rataj (1971: 13; 1975: 36); Haynes (1984: 3); Lot & Novelo (1994: 3); Rataj (2004: 58). Type: Based on the type of *Alisma andrieuxii* **synon. nov.**

Echinodorus subalatus (Mart.) Griseb. subsp. *andrieuxii* (Hook. & Arn.) R. R. Haynes & Holm-Niels. (1986: 327; 1994: 37). Type: Based on the type of *Alisma andrieuxii* **synon. nov.**

Echinodorus longistylis Buchenau (1903: 34). Type: Brazil, Rio de Janeiro, *Glaziou* 12248 (lectotype W [photograph in AAU!]; isolectotypes C!, P [digital image!], selected by Haynes & Holm-Nielsen 1986).

Echinodorus andrieuxii (Hook & Arn.) Small var. *longistylis* (Buchenau) Rataj (1971: 14; 1975: 37). Type: Based on the type of *Echinodorus longistylis*.

Perennial, from rhizomes, petioles and peduncles glabrous to scabrous, to 120 cm, rhizomes to 8 cm long, 4 cm diam. *Leaves* mostly emersed, blades elliptic to oval, 5 – 9-veined, 15 – 40 cm long, 4 – 17 cm wide, pellucid markings absent or present as lines, apex acute, base attenuate, petioles channelled, ridged, to 50 cm long, 0.5 – 2 cm diam., base with a sheath to 15 cm long, submersed blades linear-elliptic, entire, 3 – 5-veined, 7 – 15 cm long, 0.5 – 1 cm wide, apex acute, base attenuate, pellucid markings absent, petioles channelled, ridged, to 5 cm long, c. 0.3 mm diam., base with a sheath to 1.5 cm long. *Inflorescence* racemose or rarely paniculate, of 5 – 15 whorls, each 3 – 18-flowered, erect, shorter than or slightly overtopping leaves, occasionally proliferating, to 40 cm long, 2 – 8 cm wide, rachis triangular in cross-section, alate, peduncles ridged, to 50 cm long, bracts connate, lanceolate, much longer than pedicels subtended, 1.5 – 6 cm long, 2 – 9 mm wide, 11 – 19-veined, apex long acuminate, pedicels spreading in flower and fruit, 0.2 – 1.5 cm long, c. 0.5 mm diam. *Flowers* 1.5 – 3 cm diam., sepals and petals spreading, sepals 9 – 15-veined,

c. 5 mm long, c. 4 mm wide, veins without papillae, petals not clawed, not overlapping, c. 9 mm long, c. 6 mm wide, stamens 12, anthers versatile, c. 1.2 mm long, filaments c. 1.8 mm long, carpels numerous. *Fruit* oblanceoloid, 3 – 6-ribbed, glandular, 1.5 – 2.3 mm long, 1 mm wide, glands 1 (– 3), circular, separated by ribs, beak terminal, erect, 0.5 – 1.5 mm.

DISTRIBUTION AND ECOLOGY. From Mexico to Bolivia and South Brazil. Temporal ponds and wet depressions on inundated savannas, flood plains. Flowering and fruiting year round. From sea level to 1500 m.

SELECTED COLLECTIONS. BELIZE. *Gentle* 8344 (CTES!). **BOLIVIA.** *Lewis* 37570 (CTES!, SI!, UNA!, LPB!), *Saldias et al.* 3250 (UNA!), *Moraes et al.* 1414 (LPB!), *Moraes et al.* 1726 (LPB!), *Ritter et al.* 3538 (UNA!), *Ritter & Foster* 2385 (MEXU!). **BRAZIL.** *Hunt & Ramos* 5878 (K!), *Rocha* 50 (SP!), *Drouet* 2289 (UC!), *Hatschbach et al.* 56498 (MEXU!, UNA!), *Hatschbach* 40123 (C!, UNA!), *Hatschbach* 39822 (UC!), *Melo et al.* 2754 (CTES!), *Harley* 17446 (K!), *Thomas et al.* 3834 (UNA!). **COSTA RICA.** *Chavarría* 889 (BM!, UNA!), *Sousa et al.* 12697 (BM!), *Herrera et al.* 3868 (K!), *Garwood et al.* 633 (MEXU!). **EL SALVADOR.** *Linares & Martínez* 3733 (MEXU!), *Fassett* 28281 (MEXU!). **GUATEMALA.** *Contresas* 7521 (CTES!). **GUAYANA.** *Jansen-Jacobs et al.* 2058 (K!), *Horn & Wiersema* 11072 (UNA!), *Jansen-Jacobs et al.* 5084 (UNA!), *Jansen-Jacobs et al.* 31 (AAU!), *Maas & Westra* 4072 (K!). **HONDURAS.** *Davidse & Pilz* 31686 (BM!, MEXU!). **MEXICO.** *Novelo et al.* 659 (BM!, MEXU!), *Andrieux* 91 (M!, W!), *Lot & Novelo* 1013 (AAU!), *Pringle* 8256 (BM!, BR!, M!, MEXU!), *Darwin* 2449 (S!), *Hinton* 15336 (UC!), *Mexia* 1065 (BM!, UC!). **NICARAGUA.** *Atwood* 2556 (UNA!, UC!), *Stevens & Krukoff* 22646 (BM!, MEXU!, UNA!). **VENEZUELA.** *Steyermark et al.* 121246 (UNA!), *Cumana* 743 (MEXU!), *Ferrari* 1385 (MY!), *Trujillo* 14090 (MY!), *Delascio* 4000 (VEN!), *Gamez* 792 (VEN!), *Liesner et al.* 8460 (VEN!), *Lehtonen & Pacheco* 472 (TUR!, VEN!).

NOTES. *Echinodorus subalatus*, as circumscribed here, was treated as two separate species (*E. subalatus* and *E. andrieuxii*) by Rataj (1971, 1975, 2004) and Lot & Novelo (1994), and as one species with two subspecies by Haynes & Holm-Nielsen (1986, 1994). According to Rataj (1971) these species could be separated by pellucid lines, usually paniculate inflorescence and fruits with beak about one-third of fruit body in *E. subalatus*, in contrast to absence of pellucid lines, racemose or paniculate inflorescence, and fruits with beak c. 1.5 × the body in *E. andrieuxii*. He also mentioned that some specimens have mixed character states because of hybridisation between these two species (Rataj 1971). Later Rataj (2004) added that pellucid markings are actually present in both species, but sometimes visible only after leaves have been boiled in alcohol. Thus, no fixed character state differences seem to exist between *E. subalatus* and *E. andrieuxii*. These species were said to have allopatric distributions and therefore worthy of subspecific ranking by Haynes & Holm-Nielsen (1986, 1994). However, specimens with all possible sets of the aforementioned character states can be found throughout the whole range of the species. In phylogenetic analyses (Lehtonen & Myllys 2008) these taxa were not resolved as sisters, however, but *E. decumbens* was placed between them. Unfortunately the analysis (Lehtonen & Myllys 2008) did not include molecular data from *E. subalatus* subsp. *subalatus* (*sensu* Haynes & Holm-Nielsen 1986), and its position is determined only by variable morphological characters. Therefore I consider *E. andrieuxii* and *E. subalatus* to be conspecific, and *E. decumbens* as a separate species (see further discussion under *E. decumbens*) contrary to the result of the analysis (Lehtonen & Myllys 2008).

6. Echinodorus palaefolius (*Nees & Mart.*) *J. F. Macbr.* (1931: 4); Rataj (1971: 11; 1975: 39); Haynes & Holm-Nielsen (1994: 51), Rataj (2004: 62). Type: Based on the type of *Sagittaria palaefolia*.

Sagittaria palaefolia Nees & Mart. (1823: 21). Type: Brazil, Minas Gerais, Felisberto Caldeira, *Prinz Max Videnses* s.n. (holotype BR!).

Alisma palaefolium (Nees & Mart.) Kunth (1841: 152). Type: Based on the type of *Sagittaria palaefolia*.

Alisma ellipticum Mart. (1830: 1607). Type: Brazil, *Martius* s.n. (holotype M; isotype M).

Alisma ellipticum Mart. β *minus* Seub. (1847: 107). Type: Brazil, "Crescit in stagnis prope Rio St. Francisci", *Martius* s.n. (lectotype M; isolectotype M!, selected by Rataj 1971).

Echinodorus ellipticus (Mart.) Micheli δ *minor* (Seub.) Micheli (1881: 52). Type: Based on the type of *Alisma ellipticum* β *minus*.

Echinodorus palaefolius (Nees & Mart.) J. F. Macbr. var. *minus* (Seub.) Rataj (1971: 12; 1975: 40). Type: Based on the type of *Alisma ellipticum* β *minus*.

Echinodorus ellipticus (Mart.) Micheli α *latifolia* Micheli (1881: 52). Type: Brazil, Piauhy, *Gardner* 2739 (holotype K [digital image!]; isotype K [digital image!]).

Echinodorus palaefolius (Nees & Mart.) J. F. Macbr. var. *latifolius* (Micheli) Rataj (1971: 11 – 12; 1975: 40; 2004: 64). Type: Based on the type of *Echinodorus ellipticus* α *latifolia*.

Alisma virgata Hook. & Arn. (1838: 311). Type: Mexico, Tepic, *Beechey* s.n. (holotype K [digital image!]) **synon. nov.**

Echinodorus virgatus (Hook. & Arn.) Micheli (1881: 54); Buchenau (1903: 32); Small (1909: 47); Fassett (1955: 137); Rataj (1975: 54); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 94). Type: Based on the type of *Alisma virgata* **synon. nov.**

Echinodorus piauhyensis Kasselm. (2001: 139). Type: Brazil, Piauhy, 51 km S of Teresina, *Kasselmann* 207 (holotype INPA; isotype B [digital image!]).

Perennial, from rhizomes, petioles and peduncles glabrous to pubescent of simple hairs, to 110 cm. *Leaves* emersed, blades lanceolate to elliptic, 7 – 11-veined, 8 – 25 cm long, 5.5 – 20 cm wide, pellucid markings absent or present as lines, apex round, base truncate to cordate, petioles channelled, ridged, to 20 – 47 cm long, 5 – 20 mm diam., base with a sheath to 7 cm long. *Inflorescence* racemose or paniculate, of 8 – 18 whorls, each 7 – 25-flowered, erect, overtopping leaves, not proliferating, 30 – 60 cm long, to 15 cm wide, rachis triangular in cross-section, broadly alate, peduncles ridged, to 50 cm long, c. 12 mm diam., bracts slightly connate at the base, lanceolate, longer than pedicels subtended, to 1.5 – 3.5 cm long, c. 6 mm wide, 12 – 17-veined, apex long acuminate, pedicels spreading in flower and fruit, 0.1 – 1.5 cm long, c. 0.5 mm diam. *Flowers* c. 2 cm diam., sepals and petals spreading, sepals 10 – 13-veined, c. 5 mm long, c. 4 mm wide, veins without papillae, petals not clawed, not overlapping, c. 12 mm long, c. 10 mm wide, stamens 12, anthers versatile, c. 1.5 mm long, filaments c. 1.5 mm long, carpels numerous. *Fruit* oblanceoloid, 5 – 6-ribbed, glandular, 1.8 – 2.5 mm long, 1 mm wide, glands 1 – 3, circular, separated by ribs, beak terminal, erect, 0.4 – 1 mm.

DISTRIBUTION AND ECOLOGY. Eastern Brazil. Flowering and fruiting from January to June. At the elevations of 200 – 800 m.

SELECTED COLLECTIONS. BRAZIL. *Belén* 1231 (U!), *Videnses* s.n. (BR!), *Martius* s.n. (M!), *Eiten & Eiten* 4105 (SP!), *Zenaide* 91 (SP!), *Anderson* 10174 (UNA!), *Mori & Boom* 14243 (UNA!), *Kasselmann* 207 (B!), *Blanchet* 3518 (G-DC!). **MEXICO.** *Beechy* s.n. (K!).

NOTES. *Echinodorus virgatus* was described based on a single collection presumably from Tepic in the state of Nayarit, Mexico (Hooker & Arnott 1838). There are no later collections, and the taxon is presumed to be extinct (Lot *et al.* 1999). According to Haynes & Holm-Nielsen (1994) this taxon is distinct from the other species, especially from other Mexican species. The distinguishing characters are pellucid lines, winged rachis and round glands in the fruits (Haynes & Holm-Nielsen 1994). These characters are typical for *E. palaefolius*, and the phylogenetic analysis resolved *E. virgatus* as a sister to it with only few morphological differences in continuous characters (Lehtonen & Myllys 2008). There is also one intermediate specimen between *E. virgatus* and *E. subalatus* (*Alava & Cook* 1527, UC!) collected from the state of Nayarit. This specimen has ovate, unlobed leaves with clearly visible pellucid lines (pellucid lines are often absent in Mexican populations of *E. subalatus*), inflorescence with one branch and alate rachis, and immature fruits with short beak and three rounded glands. Otherwise, only *E. subalatus* is known from the state of Nayarit (Dominguez Licona 2001). Therefore, one could assume the holotype of *E. virgatus* to be an odd growth form of *E. subalatus*. At this time, however, *E. virgatus* is considered to be conspecific with the morphologically similar *E. palaefolius* on the basis of phylogenetic evidence. This conclusion might sound unreasonable from the biogeographical point of view, since the distribution of *E. palaefolius* covers East Brazil and there is only one specimen from Mexico. However, many *Echinodorus* species (*E. berteroi*, *E. cordifolius*, *E. grandiflorus*, *E. horizontalis*, *E. longipetalus*) show a similar distribution pattern of outlying populations far away from the recorded main distribution area.

7. Echinodorus pubescens (*Mart.*) *Seub.* (1872: 113); Rataj (1971: 12; 1975: 35); Haynes & Holm-Nielsen (1994: 55); Rataj (2004: 54). Type: Based on the type of *Alisma pubescens*.

Alisma pubescens Mart. (1830: 1608); Seub. (1847: 107). Type: Brazil. *Martius* 143 (holotype M!).

Echinodorus ellipticus β *pubescens* (Mart.) Micheli (1881: 51 – 52); Buchenau (1903: 34). Type: Based on the type of *Alisma pubescens*.

Echinodorus macrocarpus Rataj (1975: 69; 2004: 128). Type: Brazil, Ceará, Serra de Baturité, *Eugenio* 227 (holotype RB [digital image!]) **synon. nov.**

Perennial, from rhizomes, petioles and peduncles pubescent with simple hairs, to 120 cm, rhizomes 3 cm diam. *Leaves* emersed, blades ovate to elliptic, 5 – 9-veined, 10 – 24 cm long, 3 – 11 cm wide, pellucid markings absent or present as lines, apex round to acute, base attenuate to cordate, petioles terete, 3 – 35 cm long, c. 5 mm diam., base with a sheath to 10 cm long. *Inflorescence* racemose or paniculate, of 6 – 18 whorls, each 9 – 15-flowered, erect, overtopping leaves, not proliferating, 20 – 70 cm long, 15 cm wide, rachis triangular in cross-section, peduncles terete, to 55 cm long, c. 5 mm diam., bracts connate at the base, lanceolate, coarse with membranous margin, to 2 cm long, 5 mm wide, 11 – 16-veined, apex acute, pedicels spreading in flower and fruit, terete, 0.5 – 1 cm long, 0.5 mm diam. *Flowers* 1.5 – 2 cm diam., sepals erect, 16 – 21-veined, c. 5 mm long, c. 4 mm wide, the veins pubescent, petals spreading, white, not clawed, not overlapping, c. 15 mm long, c. 14 mm wide, stamens 12, anthers versatile, c. 1.5 mm long, filaments c. 1.5 mm long, carpels numerous. *Fruit* oblanceoloid, c. 7-ribbed, glandular, 2.5 – 3.5 mm long, 1.6 mm wide, glands 1 – 3, often transected by the ribs, elliptic, beak terminal, erect, c. 1 mm.

DISTRIBUTION AND ECOLOGY. East Brazil. Flowering and fruiting from January to July. From sea level to 500 m.
SELECTED COLLECTIONS. BRAZIL. *Harley et al.* 20019 (AAU!, F!, K!), *Kasselmann* 206 (M!), *Luetzelburg* 375 (M!), *Martius* 143 (M!), *Hatschbach* 39378 (UC!, UNA!), *Eugenio* 227 (RB!), *Blanchet* 3153 (G!).
NOTES. *Echinodorus macrocarpus* was synonymised with *E. paniculatus* by Haynes & Holm-Nielsen (1994). However, the type specimen (*Eugenio* 227 RB!) has none of the typical characters of *E. paniculatus*. Instead, *E. macrocarpus* is here considered conspecific with *E. pubescens* because of a set of typical characters of *E. pubescens*: ovate leaves without pellucid markings, large densely ribbed achenes with 2 – 3 glands, and stems covered by simple hairs.

8. Echinodorus major (*Micheli*) *Rataj* (1967: 616; 1975: 29), Somogyi (2006: 382). Type: Based on the type of *Echinodorus martii* β *major*.
Echinodorus martii Micheli β *major* Micheli (1881: 49). Type: Brazil, Goiás, *St-Hilaire, Catal. C*[1] n. 824 (lectotype P [digital image!]; isolectotype P [digital image!]).

Perennial, from rhizomes, glabrous, to 50 cm. *Leaves* submersed, blades obovate, undulating, 3 – 5 pseudopinnate veins, to 30 cm long, 6 cm wide, pellucid markings absent, apex round, base truncate, petioles triangular in cross-section, to 15 cm long, 4 mm diam., base with a sheath to 3 cm long. *Inflorescence* racemes, of 6 – 7 whorls, each 7 – 9-flowered, erect, overtopping leaves, proliferating, to 25 cm long, 4 cm wide, rachis triangular in cross-section, peduncles terete, c. 30 cm long, 5 mm diam., bracts free, lanceolate, c. 2 cm long, 8 mm wide, c. 13-veined, apex acuminate, pedicels spreading in flower and fruit, terete, 1 cm long, 0.5 mm diam. *Flowers* 1.5 cm diam., sepals and petals spreading, sepals c. 11-veined, c. 3 mm long, c. 2 mm wide, veins without papillae, petals white, not clawed, not overlapping, c. 6 mm long, c. 4 mm wide, stamens 12, anthers versatile, c. 1 mm long, filaments c. 1.5 mm long, carpels numerous. *Fruit* obovoid, 4-ribbed, glandular, c. 2 mm long, 0.5 mm wide, glands c. 9, separated by ribs, circular, beak terminal, erect, c. 0.2 mm.

DISTRIBUTION AND ECOLOGY. Central Brazil. Growing submersed in shallow streams. At elevation of c. 500 m.
SELECTED COLLECTIONS. BRAZIL. *St-Hilaire* 824 (P!), *Irwin et al.* 16684 (U!).
NOTES. *Echinodorus major* is an extremely rarely collected species, but a common aquarium plant. For this reason natural populations were not available for sequencing, and a cultivated plant was used in the phylogenetic analysis (Lehtonen & Myllys 2008). Hybrids have largely replaced native species in the aquarium trade (Kasselmann 2003), and therefore cultivated populations should be avoided in phylogenetic studies. However, no evidence was found that the specimen used in the analysis was of hybrid origin (Lehtonen & Myllys 2008).

The history of the name of this taxon is quite complicated. Martius (1830) described a new taxon *Alisma intermedium* with one specimen mentioned in the protologue, that was Martius' collection from Brazil. Seubert (1847) listed one additional specimen collected by Pohl under the name *A. intermedium*. Grisebach (1866) transferred the taxon to the genus *Echinodorus*, but unfortunately mixed it with another taxon (later described as *E. grisebachii*). This error was noticed but not corrected by Micheli (1881). Instead, he proposed an illegitimate name *E. martii* with a clear reference to the name and original description of *A. intermedium*, and listed three specimens, including the Martius' and Pohl's collections. In addition Micheli (1881) described a new variety *E. martii* β *major* with a reference to one specimen, *St-Hilaire Catal. C*[1] n. 824. The situation was further confused by Rataj (1967), who selected Pohl's specimen as the lectotype of *A. intermedium*, although this specimen was not mentioned in the original description. However, Rataj (1967) noticed that the specimen *St-Hilaire Catal. C*[1] n. 824 represents another taxon, and made a new combination *E. major* (although he misspelled the name as "E. maior"). Haynes & Holm-Nielsen (1986) realised that Rataj's (1967) lectotypification of the name *A. intermedium* was incorrect, since the Pohl's collection was not mentioned in the original description, but they did not realise that the name *E. martii* was superfluous and thus illegitimate. Therefore they considered *E. martii* to be a valid name and selected Pohl's specimen as the lectotype of that name (Haynes & Holm-Nielsen 1994). They also believed that *E. martii* and *E. martii* β *major* were conspecific and correspondingly treated Rataj's combination *E. major* as a synonym of *E. martii*. This complex nomenclatural puzzle was discussed by Somogyi (2006), but he could not solve all the pieces. Somogyi (2006) correctly recognised Martius' specimen (M 0086252) to be the lectotype of *A. intermedium*, and *St-Hilaire Catal. C*[1] n. 824 (P 00512049) to be the lectotype of *E. martii* β *major*. However, he incorrectly treated *E. martii* as a valid name and believed that Pohl's specimen (BR 841048) is the type of the name. This specimen is not the type specimen of any taxon, despite the fact that Rataj (1967) treated it as the lectotype of *A. intermedium*, and Haynes & Holm-Nielsen (1994) treated it as the lectotype of *E. martii*. I agree with Rataj (1967), Haynes & Holm-Nielsen (1994) and Somogyi (2006) that the specimens *Martius* s.n. and *St-Hilaire Catal. C*[1] n. 824 represent two distinct taxa. Furthermore, I

agree with Rataj (1967) and Haynes & Holm-Nielsen (1994) that the Martius' specimen is conspecific with *E. subalatus*. The correct name for the taxon typified by the specimen *St-Hilaire Catal. C*[1] n. 824 is *E. major*.

9. Echinodorus grisebachii Small (1909: 46); Fassett (1955: 180); Rataj (1967: 614; 1975: 30); Holm-Nielsen & Haynes (1986: 8); Haynes & Holm-Nielsen (1994: 19); Lot & Novelo (1994: 4); Rataj (2004: 42). Type: Cuba, *Wright* 3198 (lectotype US [digital image!]; isolectotypes BM!, G [digital image!], GH, K [digital image!], NY [digital image!], P [digital image!], S [photograph in AAU!], MO [digital image!], W, GOET, LE, selected by Rataj 1967).

Echinodorus amphibius Rataj (1967: 618; 1975: 31; 2004: 44). Type: Brazil, Pará, in vicinibus Santarem, *Spruce* s.n. (holotype M!; isotypes K [digital image!], NY [digital image!], P [digital image!], B [digital image!], G [digital image!]).

Echinodorus gracilis Rataj (1967: 617; 1975: 32; 2004: 46). Type: Brazil, Amapá, Rio Oiapoque, *Froes* 26723 (holotype UB [digital image!]; isotypes IAN [photograph in AAU!]).

Echinodorus parviflorus Rataj (1970b: 266; 1975: 33; 2004: 48). Type: Cult. In Bot. Inst. Sumperk-Temenice, *Rataj* s.n. (holotype PR [photograph in AAU!]).

Echinodorus amazonicus Rataj (1970b: 264 – 265; 1975: 33; 2004: 50). Type: Brazil, Rondonia, Rio Jamari – Cachoeira de Sta. Cruz, *Pires & Martin* 9972 (holotype UB [digital image!]; isotypes NY, K!).

Echinodorus bleherae Rataj (1970b: 265; 1975: 34; 2004: 52); Somogyi (2006: 381). Type: Cult. In Cornell University, *Moore* 7120 (holotype BH [digital image!]) (as 'bleheri', for discussion see Somogyi 2006).

Echinodorus eglandulosus Holm-Niels. & R. R. Haynes (1985: 17; 1986: 9), Haynes & Holm-Nielsen (1994: 18). Type: Ecuador, Napo, Río Yasuní, Jatuncocha, *Holm-Nielsen et al.* 19996 (holotype AAU!; isotypes K [digital image!], NY [digital image!], UNA!) **synon. nov.**

Echinodorus grisebachii Small var. *minor* Kasselm. (2001: 103). Type: Ecuador, Río Yuturi, *Kasselmann* 600 (holotype B [digital image!]) **synon. nov.**

Perennial, from rhizomes, glabrous, to 110 cm. *Leaves* emersed and submersed, emersed blades elliptic, undulating, 3 – 7 pseudopinnate veins, 5 – 14 cm long, 1 – 6 cm wide, pellucid markings present as lines, apex acute to acuminate, base attenuate to truncate, petioles triangular in cross-section, 2 – 25 cm long, 2 – 4 mm diam., base with a sheath to 5 cm long, submersed blades linear to elliptic, entire, margins undulate, 1 – 5 pseudopinnate veins, 6 – 25 cm long, 0.7 – 2.5 cm wide, pellucid markings absent or present as lines, apex acute, base attenuate, petioles triangular in cross-section, to 12 cm long, 2 mm diam., base with a sheath to 2 cm long. *Inflorescence* racemose or paniculate, of 3 – 12 whorls, each 3 – 9-flowered, erect to decumbent, overtopping leaves, often proliferating, 13 – 70 cm long, 1 – 5 cm wide, rachis triangular to slightly alate, peduncles triangular in cross-section, 10 – 35 cm long, 3 mm wide, bracts slightly connate at the base, lanceolate, delicate, shorter than to longer than pedicels subtended, 0.3 – 2.5 cm long, 1 – 3 mm wide, 5 – 9-veined, apex acuminate, pedicels spreading in flower, recurved in fruit, terete, 0.2 – 1 cm long, 0.2 mm diam. *Flowers* c. 1 cm diam., sepals and petals spreading, sepals 6 – 10-veined, c. 2 mm long, c. 1 mm wide, veins without papillae, petals white, not clawed, not overlapping, c. 5 mm long, c. 3 mm wide, stamens 9 – 12, anthers versatile, c. 0.5 mm long, filaments c. 1 mm long, carpels numerous. *Fruit* obovoid, 3 – 4-ribbed, glandular, 1.5 – 2.2 mm long, c. 0.5 mm wide, glands 2 – 5, separated by ribs, circular, beak terminal, erect, 0.2 – 0.5 mm.

DISTRIBUTION AND ECOLOGY. From South Brazil to Central America and Cuba. Floodplains, palm swamps, rivers and creeks with varying water level. Flowering and fruiting year round. From sea level to 280 m.

SELECTED COLLECTIONS. BOLIVIA. *Steinbach* 456 (H!), *Guillén* 1677 (CTES!, MEXU!, SI!, UNA!), *Guillén & Choré* 1771 (CTES!, MEXU!, SI!, UNA!), *Beck* 5624 (LPB!, UNA!), *Ritter* 1617 (LPB!), *Lehtonen* 151 (TUR!, LPB!). **BRAZIL.** *Kasselmann* 116 (M!), *Spruce* 617 (M!), *Windisch* 717 (AAU!), *Pirani* 1279 (UNA!), *Ratter et al.* 1604 (K!), *Pires & Martin* 9972 (K!, UB!), *Prance et al.* 14438 (M!, U!), *Black & Foster* 48–3346 (UC!), *Spruce* s.n. (BM!, C!, W!). **COLOMBIA.** *Schmidt-Mumm* 1027 (UNA!). **COSTA RICA.** *Stevens et al.* 24741 (BM!, MEXU!), *Aguilar* 5018 (K!), *Stevens & Montiel* 24741 (UNA!). **CUBA.** *Wright* 3198 (BM!, W!). **ECUADOR.** *Holm-Nielsen et al.* 19996 (AAU!, UNA!), *Holm-Nielsen et al.* 19844 (AAU!, QCA!), *Kasselmann* 601 (M!), *Jaramillo & Grijalva* 11531 (QCA!). **FRENCH GUIANA.** *Irwin et al.* 48618 (VEN!), *Veth* 202 (U!). **NICARAGUA.** *Haynes* 8387 (AAU!, UNA!), *Stevens & Krukoff* 8281 (BM!), *Pipoly* 4131 (MEXU!, UNA!), *Stevens & Krukoff* 8281 (MEXU!, UNA!). **PERU.** *Gentry & Ayala* 43209 (AMAZ!), *Ayala* 302 (AMAZ!), *Lehtonen & Arévalo* 74 (TUR!). **SURINAM.** *Geijskes* 191 (U!), *Jonker* 918 (U!). **VENEZUELA.** *Guies* 2452 (CAR!), *Trujillo* 13424 (MY!), *Aymard & Stergios* 3256 (UNA!), *Bunting & Alfonzo* 13255 (VEN!), *Bailey* 120 (VEN!).

NOTES. *Echinodorus grisebachii* is a highly polymorphic and phenotypically plastic species. Rataj (1975) split this taxon into several distinct species, which were synonymised by Haynes & Holm-Nielsen (1994).

Before that Holm-Nielsen & Haynes (1985) described *E. eglandulosus*, while they were still following Rataj's (1975) classification and circumscription of the group. The species was said to be distinguished by its fruits that are not glandular (Holm-Nielsen & Haynes 1985). I have studied the holotype, one isotype, and most of the paratypes without finding mature fruits. Instead, all this material has immature fruits lacking glands, which is generally typical for the immature fruits of *Echinodorus*. Since the only diagnostic character is not present in the type specimens, the status of this species is highly questionable even under a very narrow species concept. In the phylogenetic analyses (Lehtonen & Myllys 2008) *E. eglandulosus* was nested within *E. grisebachii*. The analyses (Lehtonen & Myllys 2008) also included one cultivated population matching Rataj's (1967) description of *E. gracilis*. According to DNA evidence it was placed within *E. grisebachii*, but total-evidence analysis resolved it as a sister to the rest of *E. grisebachii* and *E. eglandulosus* (Lehtonen & Myllys 2008).

Kasselmann (2001) described a small-sized variant of this species. However, *Echinodorus grisebachii* is a morphologically highly variable species, and the type specimen of var. *minor* falls within the normal size variation of the species. Therefore there is no need for taxonomic recognition of this growth form.

10. Echinodorus emersus *Lehtonen* **sp. nov.** *Echinodori scabro* Rataj similis sed differt inflorescentiis pauciramificati, floribus subsessilis, petalibus dispersis normalis (nec recurvatis), et frutibus eglandulosis. Typus. Peru: Loreto, Alto Amazonas, Río Pastaza, Sungachicocha, 03°42′27.1″S, 79°28′05.7″W, elev. 170 m, 29 July 2003, *Lehtonen* 139 (holotypus AMAZ!; isotypus TUR!).

Perennial, from rhizomes, petioles and peduncles scabrous, to 220 cm, rhizomes 2 cm diam. *Leaves* emersed, blades ovate, 9 – 13-veined, 12 – 25 cm long, 7 – 18 cm wide, without pellucid markings, apex round-acute, base cordate, petioles terete, ridged, stellate pubescent, longer than blade, 16 – 110 cm long, 3 – 8 mm diam., base with a sheath to 10 cm long. *Inflorescence* racemose or paniculate, of 8 – 21 whorls, each 3 – 12-flowered, erect, overtopping leaves, occasionally proliferating, to 90 cm long, to 20 cm wide, rachis terete, stellate pubescent, peduncles terete and ridged, 60 – 130 cm long, 0.6 – 1 cm diam., bracts free, lanceolate, coarse, 0.6 – 1 cm long, 0.4 – 0.8 cm wide, c. 15 – 22-veined, apex acute, pedicels spreading in flower and fruit, 0.5 – 1 cm long, 0.7 mm diam. *Flowers* c. 3 cm diam., sepals erect, 15 – 20-veined, 5 mm long, 5 mm wide, veins without papillae, petals spreading, white, without claws, overlapping, c. 15 mm long, c. 17 mm wide, stamens 14 – 22, anthers versatile, 1.2 mm long, filaments c. 1.5 mm long, carpels numerous. *Fruits* oblanceoloid, 3 – 6-ribbed, keeled, without glands, 2 – 3 mm long, 1 mm wide, beak terminal, erect, 0.3 – 1 mm. Fig. 2.

DISTRIBUTION AND ECOLOGY. Peruvian and Ecuadorian Amazonia, Bolivia (Map 1). Growing on inundated savannas, lake shores, and on mats of floating vegetation along lake shores both in black and white water communities. Flowering and fruiting year round. At the elevations of 170 – 280 m.

ADDITIONAL SPECIMENS EXAMINED. BOLIVIA. Beni: Laguna San Ignacio de Moxos, 14°59′26.9″S, 65°39′24.1″W, *Lehtonen* 181 (TUR!, LPB!); *Lehtonen* 182 (TUR!, LPB!); near Laguna Normandia, 14°51′45.4″S, 66°20′30.4″W, *Lehtonen* 190 (TUR!, LPB!); *Lehtonen* 191 (TUR!, LPB!); near biological station, 14°51′25.0″S, 66°18′07.1″W, *Lehtonen* 200 (TUR!, LPB!). **ECUADOR.** Orellana: Coca, *Palacios et al.* 317 (AAU!, QCNE!, UNA!); Coca, 00°27′47.8″S, 76°59′25.7″W, *Lehtonen* 497 (QCA!, TUR!), *Lehtonen* 498 (QCA!, TUR!). **PERU.** Madre deDios: Tambopata wildlife Reserve, Coco Cocha, *Stratton & Stratton* 300, (UNA!). Loreto: Alto Amazonas, Capahuari, *Aronson & Rodriges* 824, (UNA!); Río Pastaza, Sungachicocha, 03°42′27.1″S, 79°28′05.7″W, *Lehtonen* 135 (AMAZ!, TUR!), *Lehtonen* 136 (AMAZ!, TUR!), *Lehtonen* 137 (AMAZ!, TUR!), *Lehtonen* 138 (AMAZ!, TUR!), *Lehtonen* 139 (holotype AMAZ!; isotypes TUR!), *Lehtonen* 140 (AMAZ!, TUR!), *Lehtonen* 141 (AMAZ!, TUR!), *Lehtonen* 142 (AMAZ!, TUR!).

CONSERVATION STATUS. Least concern (LC), the species is widely distributed in western Amazonia (IUCN 2001).

ETYMOLOGY. The epithet is derived from the Latin *emergere*, meaning to appear, or becoming visible, which is chosen for the tall, erect inflorescences.

NOTES. This species was referred to as *Echinodorus* sp. 2 in Lehtonen & Myllys (2008). *E. emersus* is closely related to *E. scaber* but it can be easily recognised by its large and showy flowers, which contrast with the peculiar flowers of *E. scaber* that have tiny petals bending backwards. The distribution of *E. emersus* covers the western side of South America, while *E. scaber* is found on the northern and central parts of the continent.

11. Echinodorus scaber *Rataj* (1969c: 438 – 440; 1975: 62; 2004: 116). Type: British Guiana, Canje R., *Jenman* 4310 (holotype K [digital image!]; isotype BRG).

Echinodorus scaber Rataj var. *proliferatus* Rataj (1969c: 441; 1975: 63). Type: Colombia, Antioquia, Puerto Berrio, *Pennel & Rusby* 57 (holotype NY [digital image!]).

Echinodorus macrophyllus (Kunth) Micheli subsp. *scaber* (Rataj) R. R. Haynes & Holm-Niels. (1986: 331; 1994: 58). Type: Based on the type of *Echinodorus scaber*.

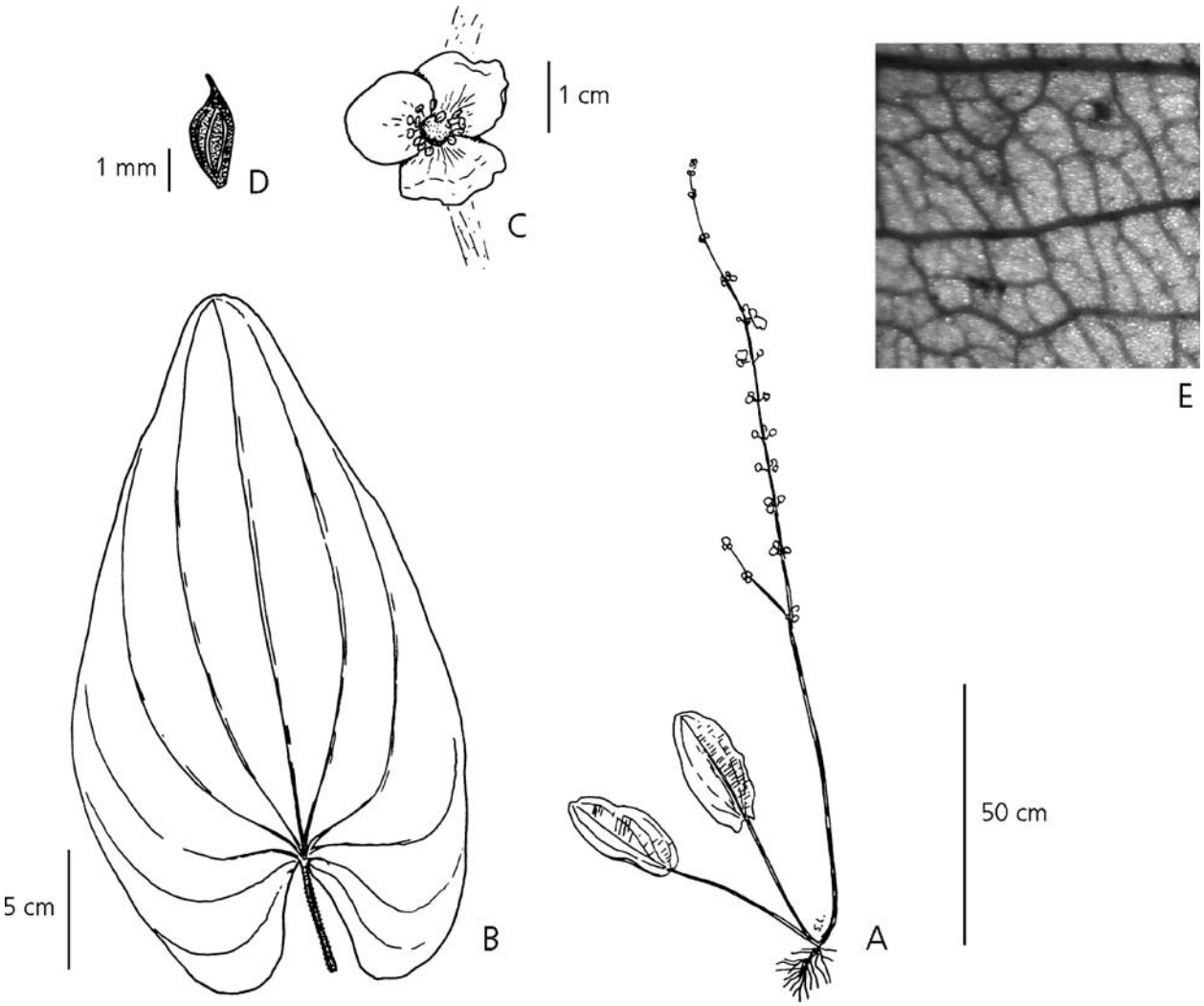


Fig. 2. *Echinodorus emersus* (*Lehtonen* 140, TUR!). A habit; B leaf; C flower; D fruit; E enlargement of leaf illustrating absence of pellucid markings. DRAWN BY SAMULI LEHTONEN.

Perennial, from rhizomes, petioles and peduncles scabrous, to 300 cm, rhizomes 3 cm diam. *Leaves* emersed, blades ovate, 5 – 9-veined, 9 – 30 cm long, 5 – 15 cm wide, without pellucid markings, apex retuse to round-acute, base cordate, petioles terete, ridged, scabrous, longer than blade, 30 – 100 cm long, 5 – 10 mm diam., base with a sheath to 7 cm long. *Inflorescence* paniculate, of 5 – 21 whorls, each 3 – 6-flowered, erect, overtopping leaves, occasionally proliferating, to 75 cm long, to 50 cm wide, rachis terete, stellate pubescent, peduncles terete and ridged, 30 – 150 cm long, 0.8 – 1 cm diam., bracts free, lanceolate, coarse, 1 – 2 cm long, c. 5 mm wide, 11 – 16-veined, apex acute, pedicels spreading in flower and fruit, 0.5 – 2.5 cm long, 0.7 – 1 mm diam. *Flowers* 1 – 1.5 cm diam., sepals erect, 10 – 20-veined, 5 mm long, 4 mm wide, veins without papillae, petals reflexed, without claws, not overlapping, c. 4 mm long, c. 3 mm wide, stamens 13 – 18, anthers versatile, 1 mm long, filament 2 mm long, carpels numerous. *Fruit* oblanceoloid, 5 – 6-ribbed, keeled, glandular, 2.3 – 3.3 mm long, 1 mm wide, glands 0 – 2, glands circular, between ribs, beak terminal, erect, 0.6 – 1 mm. Fig. 3.

DISTRIBUTION AND ECOLOGY. Nicaragua, Colombia, Venezuela, Guyana, Brazil (Map 3). Growing in wet depressions on inundated savannas. Flowering and fruiting year round. At elevations of 50 – 400 m.

SELECTED COLLECTIONS. BRAZIL. *Scremin-Dias et al.* 236 (UNA!), *Rabelo* 1038 (UNA!), *Silva* 2598 (UNA!), *Schessl* 3327 (UNA!), *Pott & Tavares* 4580 (UNA!), *Pott & Pott* 4756 (UNA!), *Burchell* 9054 (BR!), *Harley* 18210 (K!), *Hatschbach* 22741 (AAU!), *Hatschbach et al.* 34100 (UNA!), *Hatschbach et al.* 52606 (UNA!). **COLOMBIA.** *Pennell & Rusby* 57 (NY!). **GUYANA.** *Stoffers et al.* 425 (AAU!), *Jenman* 4310 (K!), *Jansen-Jacobs et al.* 5037

Map 1. Distribution of *Echinodorus reptilis* (*black dots*), *E. emersus* (*grey dots*) and *E. decumbens* (*star*), based on georeferenced herbarium material.

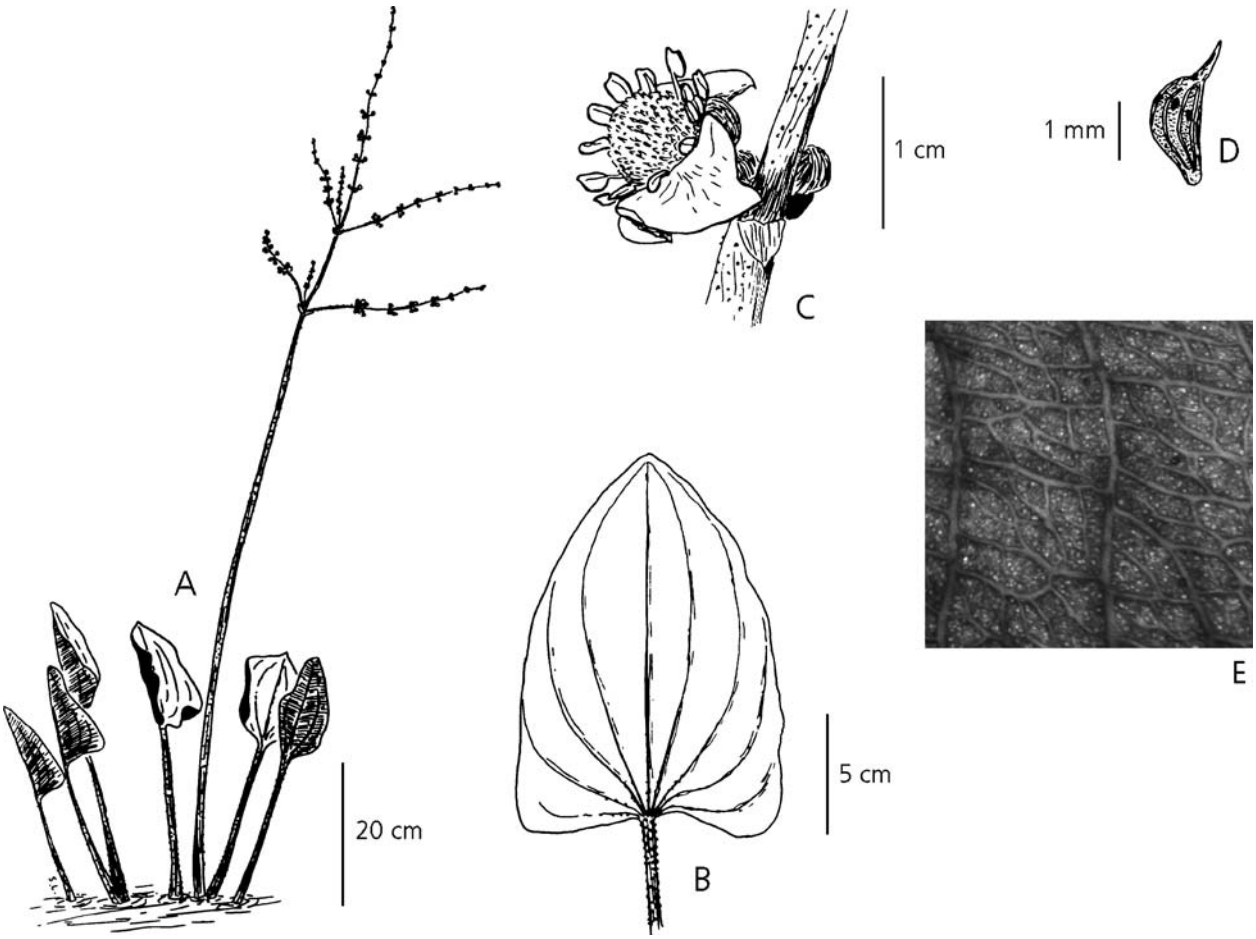


Fig. 3. *Echinodorus scaber* (*Lehtonen & Pacheco* 497, TUR!). **A** habit; **B** leaf; **C** flower illustrating small petals reflexed; **D** fruit; **E** enlargement of leaf illustrating absence of pellucid markings. DRAWN BY SAMULI LEHTONEN.

(UNA!), *Wiersema & Horn* 10103 (UNA!). **NICARAGUA.** *Haynes* 8589 (UNA!). **SURINAM.** *Oldenburger et al.* 389 (U!). **VENEZUELA.** *Lehtonen & Pacheco* 440 (TUR!, VEN!), *Lehtonen & Pacheco* 497 (TUR!, VEN!), *González & Wiersema* 2209 (UNA!), *Alston* 6308 (BM!), *Haynes* 7622 (UNA!), *Trujillo* 8583 (MY!), *Liesner & González* s.n. (VEN!).

NOTES. According to Rataj's (1969c) original description the species has small flowers with 14 – 18 stamens. Later Rataj changed his description, and in his new revision of the genus (Rataj 2004) the species is said to have 24 stamens, and his Fig. 3 on page 116 shows a large flower with overlapping petals that clearly represents a different species. *Echinodorus scaber* is readily distinguishable from other species by its flowers with peculiar tiny petals that are bent backwards, and 13 – 18 stamens. Herbarium material can be distinguished by the usually paniculate inflorescence with many branches from *E. emersus*, which has racemose, or sometimes paniculate inflorescences with only a few branches from the lowest whorl. Further, *E. scaber* usually has glandular achenes, while *E. emersus* lacks any glands. Haynes & Holm-Nielsen (1986) ranked this taxon as a subspecies of *E. macrophyllus*, but based on phylogenetic evidence (Lehtonen & Myllys 2008) it is here considered a separate species.

12. Echinodorus trialatus *Fassett* (1955: 179); Rataj (1975: 65); Haynes & Holm-Nielsen (1994: 58); Lot & Novelo (1994: 6); Rataj (2004: 120). Type: Colombia, Río Casanare, Barranco de Atahuarpa, *Cuatrecasas* 4283 (holotype US [digital image!]; isotypes US, F).

Perennial, from rhizomes, glabrous, to 80 cm. *Leaves* emersed, and submersed, blades linear-lanceolate, 3 – 7 pseudopinnate veins, 9 – 26 cm long, 1 – 7 cm wide, pellucid markings absent, apex acute, base attenuate, petioles triangular in cross-section, 5 – 35 cm long, 3 mm diam., base with a sheath to 10 cm long. *Inflorescence* racemose or paniculate, of 4 – 15 whorls, each 3 – 7-flowered, erect, overtopping leaves, not proliferating, to 30 cm long, 10 cm wide, rachis

triangular in cross-section, often broadly alate, peduncles terete, 10 – 50 cm long, 4 mm diam., bracts free, lanceolate, 1 – 2.5 cm long, 2 – 5 mm wide, 10 – 15-veined, apex long acuminate, pedicels spreading in flower, recurved in fruit, terete, 2 – 7 mm long, 0.2 mm diam. *Flowers* c. 1.2 cm diam., sepals and petals spreading, sepals 15 – 18-veined, c. 3 mm long, c. 2 mm wide, veins without papillae, petals white, not clawed, not overlapping, c. 8 mm long, c. 6 mm wide, stamens 12, anthers versatile, c. 1 mm long, filaments c. 1 mm long, carpels numerous. *Fruit* obovoid, 4-ribbed, eglandular, 1.5 – 2 mm long, 0.9 mm wide, beak terminal, erect, 0.5 mm.

DISTRIBUTION AND ECOLOGY. Panama, Colombia, Venezuela and northern Brazil. Growing along streams under forest. Flowering and fruiting from October to April. At the elevations of 50 – 250 m.

SELECTED COLLECTIONS. BRAZIL. *Milliken et al.* 756 (K!). **COLOMBIA.** *Cuatrecasas* 7391 (F!), *Schmidt-Mumm* 1016 (UNA!). **VENEZUELA.** *Trujillo* 14102 (MY!), *Trujillo et al.* 14687 (MY!), *Ramírez et al.* 342 (MYF!), *Delascio et al.* 11343 (UNA!), *Boom & Eisenberg* 6040 (K!, UNA!, VEN!), *Aristeguieta & Farinas* 6491 (VEN!), *Aristeguieta* 7335 (VEN!), *Lehtonen & Pacheco* 441 (TUR!, VEN!), *Lehtonen & Pacheco* 444 (TUR!, VEN!), *Lehtonen & Pacheco* 454 (TUR!, VEN!).

13. Echinodorus bracteatus *Micheli* (1881: 59); Buchenau (1903: 34); Small (1909: 46); Fassett (1955: 155); Rataj (1975: 53), Holm-Nielsen & Haynes (1986: 16); Haynes & Holm-Nielsen (1994: 50); Lot & Novelo (1994: 4); Rataj (2004: 90). Type: Panama, Chagres, *Fendler* 435 (lectotype K [digital image!], selected by Rataj 1975).

Echinodorus bracteatus Micheli var. *efenestratus* Fassett (1955: 174); Holm-Nielsen & Haynes (1986: 17). Type: Ecuador. *Rimbach* 90 (holotype F [digital image!]).

Echinodorus bracteatus Micheli subsp. *efenestratus* (Fasset) R. R. Haynes & Holm-Niels. (1986: 330; 1994: 51). Type: Based on the type of *Echinodorus bracteatus* var. *efenestratus*.

Perennial, from rhizomes, petioles and peduncles glabrous to scabrous, to 210 cm, rhizomes to 8 cm long, 3 cm diam. *Leaves* emersed, blades broadly ovate, 9 – 11-veined, undulating, 10 – 36 cm long, 7 – 30 cm wide, pellucid markings absent or present as dots and short lines, apex round to acute, base cordate, petioles terete, ridged, to 75 cm long, 0.5 – 1 cm diam., base with a sheath to 13 cm long. *Inflorescence* paniculate, of 8 – 21 whorls, each 5 – 25-flowered, erect, overtopping leaves, proliferating, to 150 cm long, to 45 cm wide, rachis triangular in cross-section, broadly alate, peduncles ridged, to 90 cm long, 1.5 cm diam., bracts free, lanceolate, longer than pedicels subtended, to 6.5 cm long, 0.4 – 1 cm wide, 17 – 30-veined, apex long acuminate, pedicels spreading in flower, reflexed in fruit, 0.2 – 1 cm long, c. 0.5 mm diam. *Flowers* 1.5 – 3.5 cm diam., sepals erect, 13 – 20-veined, c. 4 mm long, c. 4 mm wide, veins without papillae, petals spreading, white, not clawed, overlapping, c. 18 mm long, c. 15 mm wide, stamens 15 – 18, anthers versatile, c. 1.5 mm long, filaments c. 2 mm long, carpels numerous. *Fruit* oblanceoloid, 3 – 5-ribbed, slightly keeled, glandular, 1.6 – 2.7 mm long, 1 mm wide, glands 0 – 2, circular, separated by ribs, beak terminal, erect, 0.2 – 0.5 mm.

DISTRIBUTION AND ECOLOGY. Central America and coastal plains of Ecuador. Growing in shallow, standing water in swampy habitats. Flowering and fruiting year round. From sea level to 300 m.

SELECTED COLLECTIONS. COSTA RICA. *Burger et al.* 11803 (AAU!), *Döbbeler* 2249 (M!). **ECUADOR.** *Dodson & Dodson* 11327 (Q!), *Holm-Nielsen & Jeppesen* 25 (UNA!, AAU!, C!, QCA!), *Holm-Nielsen et al.* 7194 (AAU!, UNA!, K!, QCA!), *Lehtonen & Navarrete* 491 (TUR!, QCA!), *Lehtonen & Navarrete* 494 (TUR!, QCA!). **NICARAGUA.** *Haynes* 8391 (UNA!), *Sandino* 1774 (UNA!). **PANAMA.** *Hayes* 432 (MEXU!).

NOTES. Fassett (1955), Rataj (1975, but not in 2004) and Haynes & Holm-Nielsen (1986, 1994) divided this taxon into two subspecific taxa. This distinction was based on the presence or absence of pubescence and pellucid markings. However, individuals with characteristics of both types and a mixed set of characters can be found from the same populations. There was no significant molecular difference between the proposed subspecies either (Lehtonen & Myllys 2008), and thus no subspecies are recognised here.

14. Echinodorus macrophyllus (*Kunth*) *Micheli* (1881: 50); Buchenau (1903: 32); Rataj (1969c: 436; 1970c: 27; 1975: 64), Haynes & Holm-Nielsen (1986: 331; 1994: 55); Rataj (2004: 118). Type: Based on the type of *Alisma macrophyllum*.

Alisma macrophyllum Kunth (1841: 151 – 152). Type: Brazil, Rio de Janeiro, Porto d'Estrella. *Sellow* s.n. (lectotype BM, selected by Haynes & Holm-Nielsen 1986).

Perennial, from rhizomes, petioles and peduncles glabrous to scabrous, to 110 (– probably more) cm. *Leaves* emersed, blades ovate, 7 – 11-veined, 8 – 25 cm long, 7 – 26 cm wide, without pellucid markings, apex acute to acuminate, base deeply cordate, petioles terete, ridged, glabrous to stellate pubescent, 20 – 45 cm long, 5 mm diam., base with a sheath to 7 cm long. *Inflorescence* racemose or paniculate, of 6 – 9 whorls, each 5 – 13-flowered, erect, overtopping leaves, occasionally proliferating, to 25 – 40 cm long, and to 20 cm wide, rachis terete, glabrous to stellate-pubescent, peduncles terete,

27 – 70 cm long, 5 mm diam., bracts free, lanceolate, coarse, shorter than pedicels subtended, 1 – 2 cm long, 0.4 – 0.7 mm wide, 11 – 19-veined, apex acute to acuminate, pedicels spreading in flower and fruit, 1.5 – 2.5 cm long, 0.6 mm diam. *Flowers* 1.5 – 2.5 cm diam., sepals and petals spreading, sepals 14 – 17-veined, 6 mm long and 4 mm wide, veins without papillae, petals without claws, overlapping, c. 8 mm long and c. 6 mm wide, stamens 20 – 24, anthers versatile, 1 mm long, filament c. 1.5 mm long, carpels numerous. *Fruit* oblanceoloid, c. 4-ribbed, keeled, glandular, c. 2.5 mm long, 1 mm wide, glands c. 4, glands circular, between ribs, beak terminal, erect, c. 1 mm. Fig. 4.

DISTRIBUTION AND ECOLOGY. South Brazil (Map 3). Flowering and fruiting from October to December.

SELECTED COLLECTIONS. BRAZIL. *Miers* s.n. (BM!), *Sellow* 194 (BM!), *Bowie & Cunningham* s.n. (BM!), *Gardner* 700 (BM!, W!), *Harley et al.* 18210 (AAU!, K!), *Luetzelberg* 222 (M!).

NOTES. Haynes & Holm-Nielsen (1986, 1994) treated this species as conspecific with *Echinodorus scaber*, and ranked these taxa as subspecies. In the phylogenetic analysis (Lehtonen & Myllys 2008) this taxon was resolved as a sister to *E. bracteatus*, while *E. scaber* was resolved as sister to *E. emersus*, and more closely related to *E. trialatus* than *E. bracteatus*. However, no molecular data of *E. macrophyllus* were available for the study (Lehtonen & Myllys 2008), and its position is therefore somewhat ambiguous.

15. Echinodorus cylindricus *Rataj* (1975: 66). Type: Brazil, Rondônia, Pôrto Velho, *Oliveira & Côelho* 13646 (holotype INPA; isotype NY [digital image!]).

Perennial, from rhizomes, glabrous, to 130 cm, rhizomes to 7 cm long, 3 cm diam. *Leaves* emersed, with bluish-green wax cover, blades lanceolate to elliptic, 5 – 7-veined, 15 – 35 cm long, 4 – 10 cm wide, pellucid

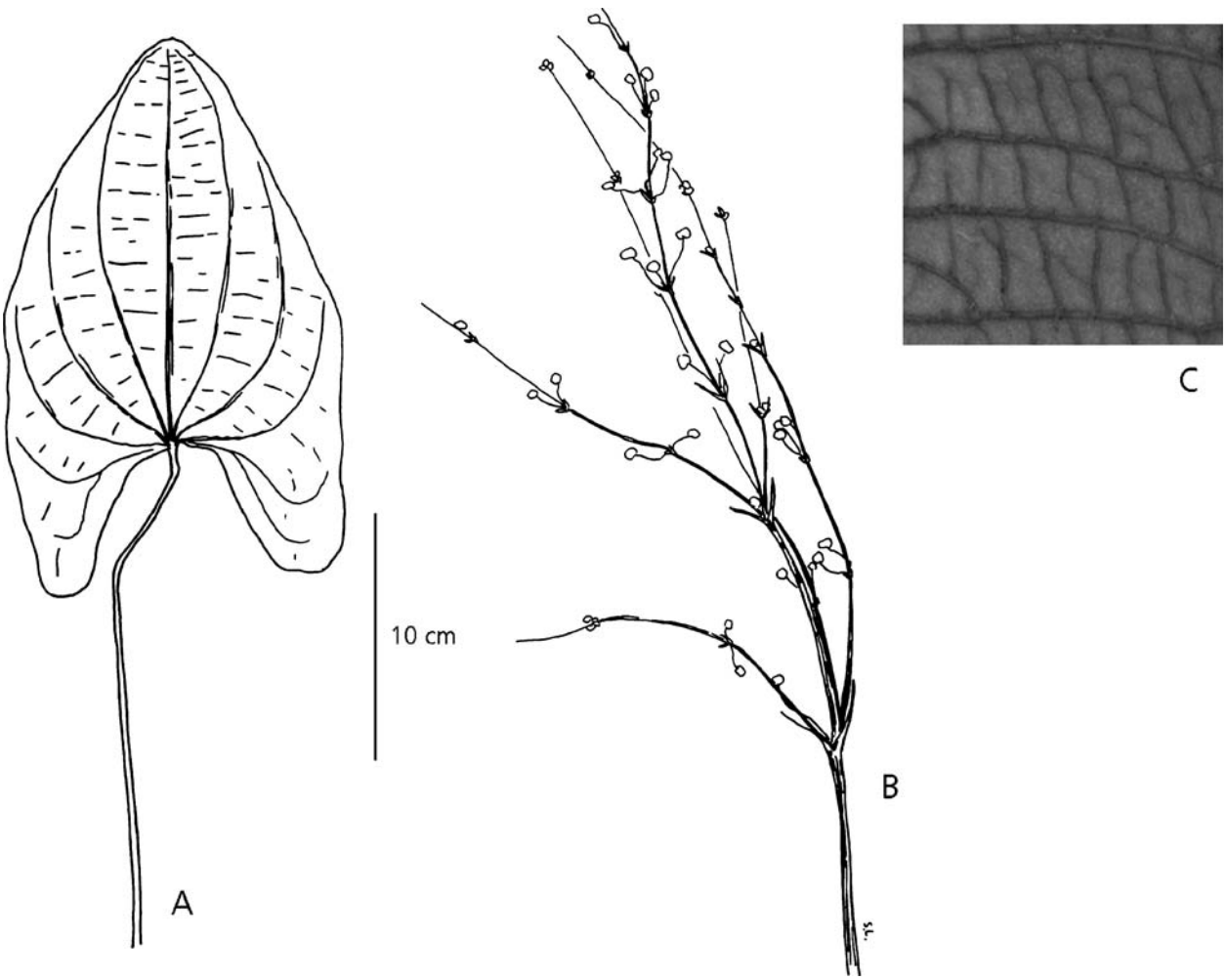


Fig. 4. *Echinodorus macrophyllus*. **A** leaf (*Sellow* 194, BM!); **B** inflorescence (*Sellow* 194, BM!); **C** enlargement of leaf illustrating absence of pellucid markings (*Harley et al.* 18210, AAU!). DRAWN BY SAMULI LEHTONEN.

markings absent, apex acute, base attenuate, petiole terete, 14 – 40 cm long, c. 5 mm wide, base with a sheath to 14 cm long. *Inflorescence* racemes or rarely branching in the lowest whorl, of 4 – 13 whorls, each 6 – 9-flowered, erect, overtopping leaves, not proliferating, to 40 cm long, c. 4 cm wide, rachis terete, peduncles terete, to 80 cm long, 7 mm diam., bracts free, coarse, deltoid, 0.9 – 1.9 cm long and 5 – 8 mm wide, 18 – 30-veined, apex acute, pedicels spreading in flower and fruit, 0.8 – 1 cm long, 1 mm diam. *Flowers* c. 3.5 cm diam., sepals erect, 25 – 30-veined, c. 6 mm long and c. 4 mm wide, veins without papillae, petals spreading, not clawed, overlapping, c. 25 mm long and c. 18 mm wide, stamens 24 – 30, anthers versatile, c. 2 mm long, filaments c. 2.5 mm long, carpels numerous. *Fruit* oblanceoloid, 5-ribbed, keeled, glandular, 3 mm long and 1 mm wide, glands 2, separated by ribs, beak terminal, erect, c. 0.7 mm. Fig. 5.

DISTRIBUTION AND ECOLOGY. States of Mato Grosso do Sul and Rondônia in Brazil (Map 2). Growing in backswamps of rivers (Wanke 1999). Flowering and fruiting from November to April. At elevation of c. 100 m.

SELECTED COLLECTIONS. BRAZIL. *Joly* s.n. (TUR!), *Pott et al* 406 (UNA!), *Pott* 2147 (CTES!, UNA!), *Pott et al.* 402 (UNA!), *Pott et al.* 3925 (UNA!), *Oliveira & Côelho* s.n. (NY!).

NOTES. Rataj (1975) described this species, but later (Rataj 2004) made it conspecific with *Echinodorus glaucus*. However, constant differences in the morphology of leaves and inflorescences are considered sufficient to accept two species, although no molecular data for this taxon was available for Lehtonen & Myllys (2008) and the molecular level differences between *E. glaucus* and *E. cylindricus* are not known.

16. Echinodorus glaucus *Rataj* (1975: 69; 2004: 122). Type: Brazil, Mato Grosso, Coxipo da Ponte, Cuiaba, *Hoehne* 4599 (holotype R).

Echinodorus teretoscapus R. R. Haynes & Holm-Niels. (1994: 63). Type: Brazil, Mato Grosso: Mt Cáceres, Rio Paraguai, (braço do Taiamã), Estação Ecológica

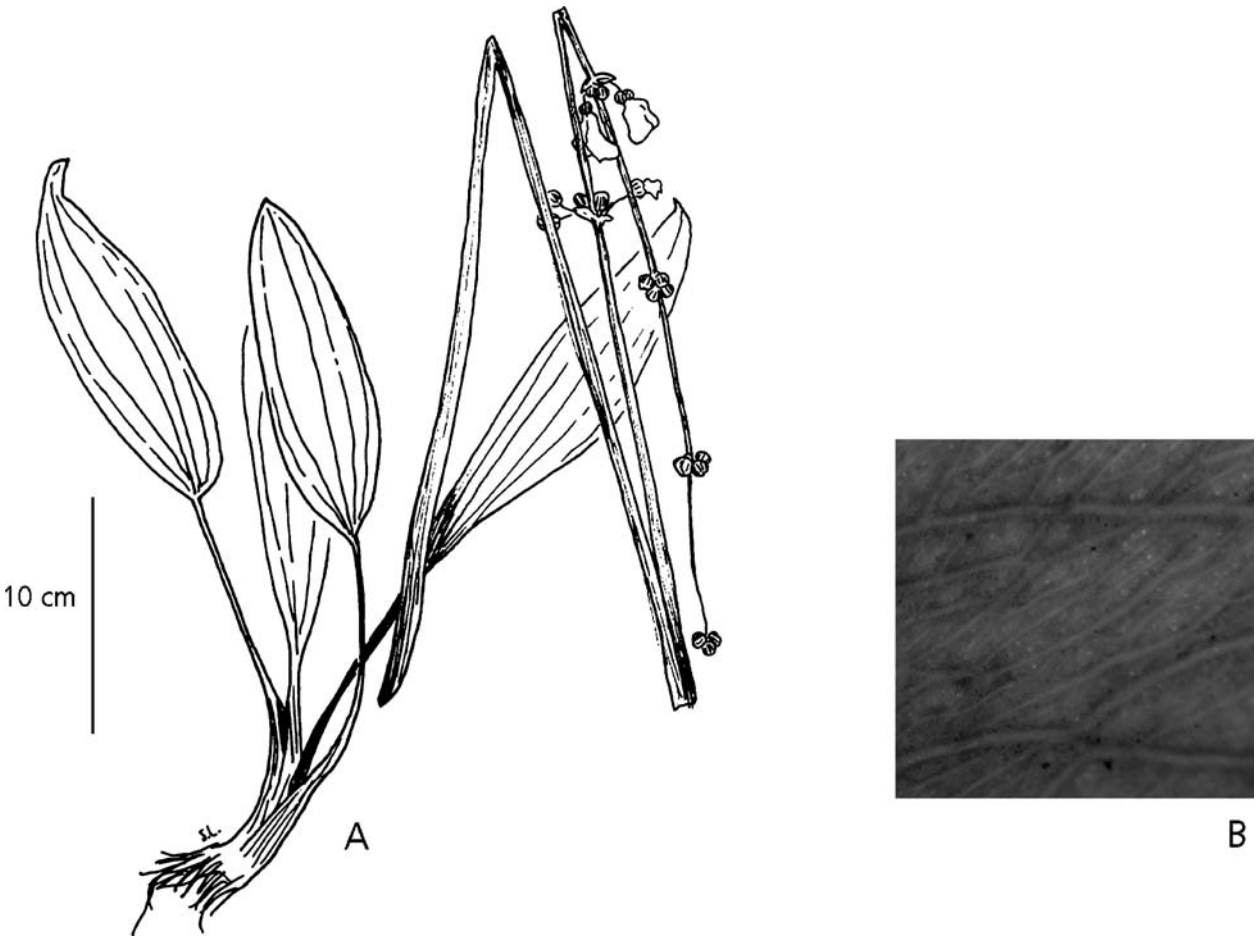
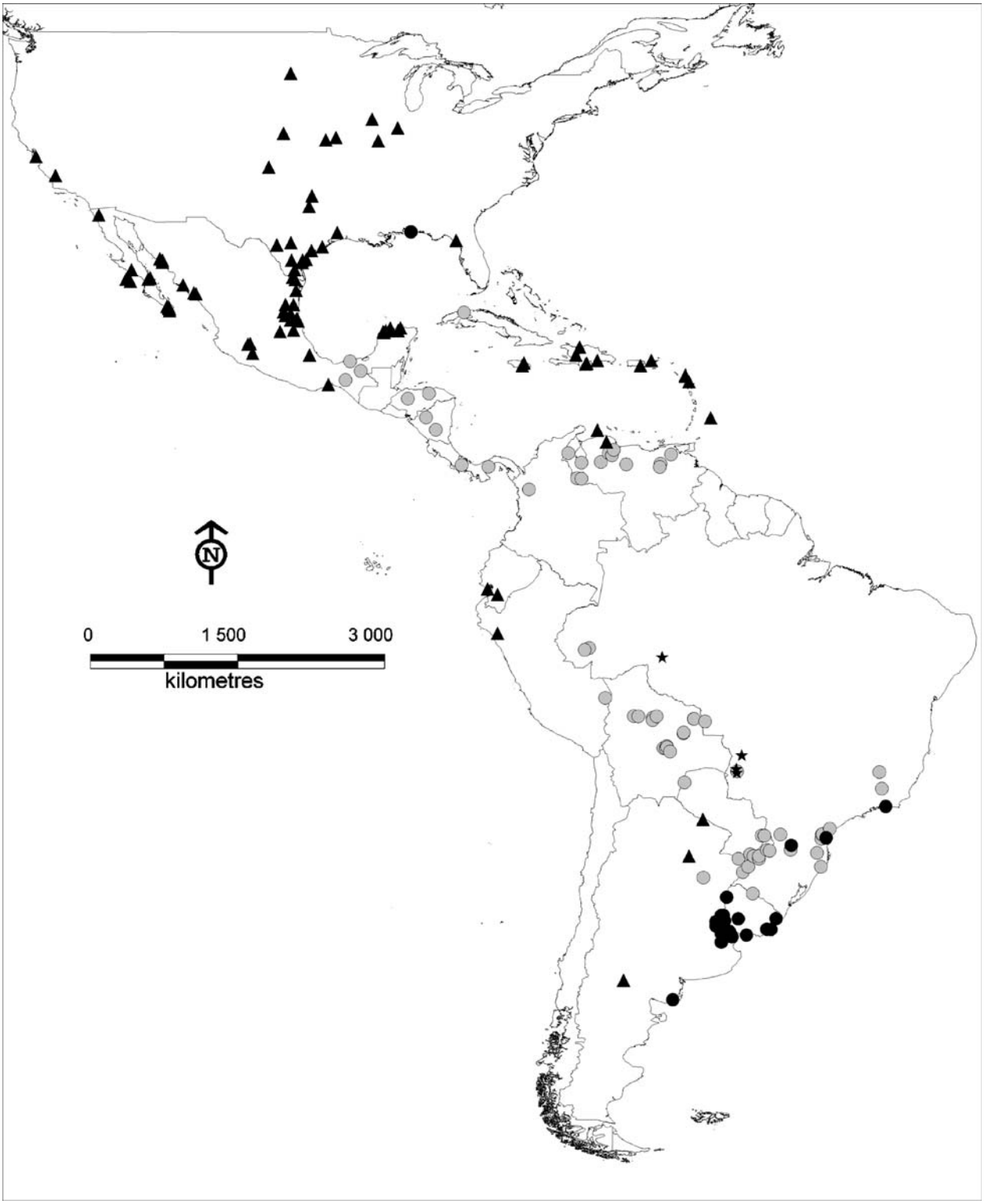


Fig. 5. *Echinodorus cylindricus* (*Pott et al.* 406, UNA!). A habit; B enlargement of leaf illustrating absence of pellucid markings. DRAWN BY SAMULI LEHTONEN.



Map 2. Distribution of *Echinodorus berteroi* (*triangles*), *E. floribundus* (*grey dots*), *E. grandiflorus* (*black dots*), and *E. cylindricus* (*star*), based on georeferenced herbarium material.

do Taiamã, *da Silva* 411 (holotype SP [digital image!]).

Perennial, from rhizomes, glabrous, to 250 cm. *Leaves* emersed, with bluish-green wax cover, blades ovate to lanceolate, 7 – 14-veined, 17 – 35 cm long, 7 – 18 cm wide, pellucid markings absent, apex round-acute, base cordate, petiole terete, 30 – 100 cm long, 0.5 – 1 cm diam., base with a sheath to 8 cm long. *Inflorescence* paniculate or racemose, of 6 – 14 whorls, each 6 – 17-flowered, erect, overtopping leaves, not proliferating, to 60 cm long, to 30 cm wide, rachis terete, peduncles terete, to 95 cm long, 7 mm diam., bracts free, coarse, deltoid, 0.6 – 1.8 cm long, 4 – 7 mm wide, 18 – 27-veined, apex acute, pedicels spreading in flower and fruit, 1 – 1.8 cm long, 1 mm diam. *Flowers* 3 – 6 cm diam., sepals erect, 15 – 32 veined, c. 5 mm long and c. 4 mm wide, veins without papillae, petals spreading, not clawed, overlapping, c. 23 mm long, c. 12 mm wide, stamens 24 – 30, anthers versatile, c. 2 mm long, filaments c. 2 mm long, carpels numerous. *Fruit* oblanceoloid, 4 – 5-ribbed, keeled, glandular, 2.2 – 3 mm long, 1 mm wide, glands 2 – 3, separated by ribs, circular, beak terminal, erect, c. 0.5 mm. Fig. 6.

DISTRIBUTION AND ECOLOGY. Pantanal wetland area in Brazil and eastern Bolivia. Flowering and fruiting from October to April. At elevation of c. 100 m.

SELECTED COLLECTIONS. BOLIVIA. *Kasselmann* s.n. (M!), *Ritter et al.* 4457 (UNA!). **BRAZIL.** *Bogner* 1258 (M!), *Pott et al.* 739 (UNA!), *Schessl* 270992–189/1–1 (UNA!), *Thomas et al.* 4557 (UNA!, K!), *Pott et al.* 2600 (UNA!), *Hatschbach et al.* 63994 (UNA!), *da Silva* 411 (SP!).

NOTES. Haynes & Holm-Nielsen (1994) synonymised *Echinodorus glaucus* with *E. paniculatus*, but re-described the taxon as *E. teretoscapus*. *Echinodorus glaucus* and *E. cylindicus* are covered by bluish wax, which is usually not preserved in herbarium material, thus making identification more difficult. Both of these species have large flowers with up to 30 stamens. These species can be distinguished by the broader and

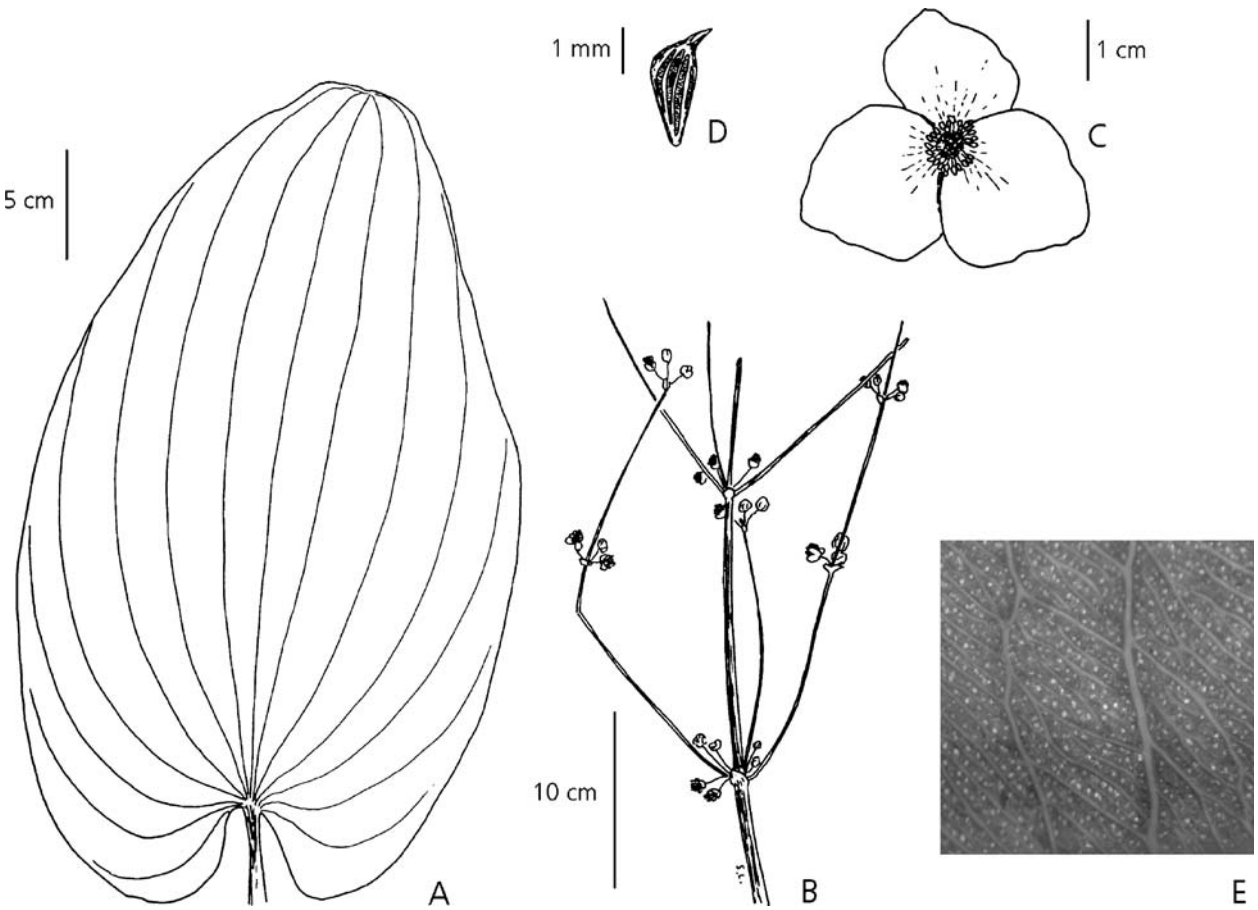


Fig. 6. *Echinodorus glaucus*. **A** leaf (*Thomas et al.* 4557, UNA!); **B** part of the inflorescence (*Hatschbach et al.* 63994, UNA!); **C** flower; **D** fruit (*Hatschbach et al.* 63994, UNA!); **E** enlargement of leaf illustrating absence of pellucid markings (*Thomas et al.* 4557, UNA!). DRAWN BY SAMULI LEHTONEN.

cordate leaves of *E. glaucus*, compared to the elliptic leaves with attenuate-truncate bases of *E. cylindricus*.

17. Echinodorus paniculatus *Micheli* (1881: 51); Buchenau (1903: 32); Hauman (1915: 314); Fassett (1955: 177); Rataj (1968: 402; 1970c: 22; 1975: 66); Haynes (1984: 10), Holm-Nielsen & Haynes (1986: 7); Haynes & Holm-Nielsen (1994: 59); Lot & Novelo (1994: 5); Rataj (2004: 124). Type: Guyana, *Schomburgk* 220 (lectotype K [digital image!], selected by Rataj 1968).

Echinodorus paniculatus Micheli f. *latifolia* Chodat & Hassler (1903: 1031). Type: Paraguay, Concepcion, *Hassler* 7229 (holotype G [digital image!]; isotype UC!) **synon. nov.**

Echinodorus paniculatus Micheli var. *brevifolia* Hauman (1915: 315). Type: Argentina, Santa Fe, *Venturi* 284 (holotype BA!).

Echinodorus paniculatus Micheli var. *dubius* Fassett (1955: 179). Type: Colombia, El Valle, Guanabanal, *Killip* 6218 (holotype US [digital image!]; isotypes GH, NY [digital image!], PH) **synon. nov.**

Perennial, from rhizomes, glabrous, to 200 cm. *Leaves* emersed, blades lanceolate, 5 – 7-veined, 8 – 30 cm long, 1 – 12 cm wide, pellucid markings absent, apex acute, base attenuate to truncate, petioles triangular in cross-section, 16 – 80 cm long, 8 mm diam., base with a sheath to 22 cm long. *Inflorescence* paniculate or racemose, of 4 – 11 whorls, each 5 – 21-flowered, erect or rarely decumbent, overtopping leaves, proliferating, to 40 cm long, 30 cm wide, rachis and peduncles triangular in cross-section, to 120 cm long, 7 mm diam., bracts lanceolate, shallowly connate at the base, coarse, shorter than pedicels subtended, 1 – 5.5 cm long, 4 – 8 mm wide, 8 – 15-veined, apex acuminate, pedicels spreading in flower and fruit, terete, 1 – 4 cm long, 0.5 mm diam. *Flowers* 3 – 4.5 cm diam., sepals and petals spreading, sepals c. 15-veined, c. 6 mm long, c. 4 mm wide, veins without papillae, petals white, not clawed, overlapping, c. 23 mm long, c. 17 mm wide, stamens 19 – 22, anthers versatile, c. 2 mm long, filaments c. 1.5 mm long, carpels numerous. *Fruit* oblanceoloid, 4 – 6 ribbed, keeled, eglandular, 1.5 – 3 mm long, 1 mm wide, beak terminal, erect, 0.1 – 0.8 mm.

DISTRIBUTION AND ECOLOGY. From Mexico to northern Argentina. Growing in various inundated habitats, including roadside ditches and other disturbed habitats. Flowering and fruiting year round. From sea level to 1400 m.

SELECTED COLLECTIONS. ARGENTINA. *Benitez et al.* 130 (UC!, CTES!), *Pedersen* 13387 (AAU!, C!, CTES!), *Venturi* 284 (BA!). **BOLIVIA.** *Baehock* 850 (AAU!, K!), *Beck* 5868 (AAU!, LPB!, UNA!), *Lehtonen* 168 (TUR!, LPB!), *Lehtonen* 200 (TUR!, LPB!). **BRAZIL.** *Glaziou* 14289 (K!), *Eiten & Eiten* 10175 (SP!), *Hatschbach & Scherer* 30438 (AAU!), *Gasparini* s.n. (CTES!), *Gardner* 2741 (BM!), *Pott et al.* 205 (UNA!). **COLOMBIA.** *Romero-Castañeda* 7583 (AAU!), *Smith* 2326 (BM!), *Smith* 4898 (BR!). **COSTA RICA.** *Lot et al.* 1239 (MEXU!), *Herrera et al.* 3868 (UNA!). **ECUADOR.** *Holm-Nielsen et al.* 2760 (AAU!, QCA!, UNA!), *Fraser* s.n. (BM!), *Lehtonen & Navarrete* 490 (TUR!, QCA!). **EL SALVADOR.** *Davidse et al.* 37342 (BM!, MEXU!), *Sidwell et al.* 690 (BM!). **GUYANA.** *Jansen-Jacobs et al.* 71 (AAU!) **MEXICO.** *Lot et al.* 1337 (MEXU!), *Novelo* 224 (MEXU!), *Orea* 188 (MEXU!), *Ramírez* 483 (MEXU!). **NICARAGUA.** *Nichols* 1057 (BM!), *Miller & Nee* 1363 (UNA!, MEXU!), *Atwood* 1009 (UC!), *Haynes* 8586 (AAU!, UNA!). **PANAMA.** *Barlett & Lasser* 16381 (CTES!). **PARAGUAY.** *Balansa* 572 (BM!, BR!), *Zardini* 23325 (UNA!), *Hassler* 7229 (UC!), *Parini et al.* 1112 (FCQ!), *Hassler* 294 (SI!), *Vanni et al.* 2385 (CTES!). **VENEZUELA.** *Gonzales & Wiersema* 2212 (UNA!, MY!), *Lehtonen & Pacheco* 471 (TUR!, VEN!).

NOTES. Haynes & Holm-Nielsen (1994) listed the following names as synonyms of *Echinodorus paniculatus*: *E. cylindricus* Rataj, *E. macrocarpus* Rataj (*E. pubescens*), and *E. glaucus* Rataj. These species are quite different from each other and readily distinguished from *E. paniculatus* by terete petioles and wax cover (*E. cylindricus* and *E. glaucus*) or pubescence (*E. pubescens*), so they are maintained as separate species.

Although *Echinodorus paniculatus* is easily recognised on the basis of its triangular petioles and peduncles, it has very variable leaf blades. Under full sunlight the blades are very narrow, but in shaded habitats blades become much broader, and occasionally almost cordate. These broad-leaved forms have been treated as different variations by some authors (Hauman 1915; Fassett 1955). Since the differences are purely ecological these variations are not accepted here.

18. Echinodorus uruguayensis *Arechav.* (1903: 66); Rataj (1970c: 36; 1975: 42), Haynes & Holm-Nielsen (1994: 16), Rataj (2004: 70). Type: Uruguay, Tacuarembo, Arroyo Cardoso, *Arechavaleta* 4238 (lectotype MVM!, selected by Alonso Paz 1986).

Echinodorus martii Micheli var. *uruguayensis* (Arechav.) Hauman (1915: 314). Type: Based on the type of *Echinodorus uruguayensis*.

Echinodorus aschersonianus Graebn. (1911: 433); Rataj (1970c: 25; 1975: 61), Haynes & Holm-Nielsen (1994: 62), Rataj (2004: 114). Type: Uruguay, Flores, Arroyo Grande, Paso Piedras, *Osten* 3249 (isotype MVM!) **synon. nov.**

Echinodorus osiris Rataj (1970a: 213 – 214; 1975: 44; 2004: 74). Type: Brazil, Paraná, Ponta Grossa, *Horeman* s.n. (holotype PR [photograph in AAU!]).

Echinodorus horemanii Rataj (1970a: 214 – 215; 1975: 43; 2004: 72). Type: Brazil, Paraná, Ponta Grossa, *Horeman* s.n. (holotype PR [photograph in AAU!]).

Echinodorus uruguayensis Arechav. var. *minor* Kasselm. (2001: 127). Type: Brazil, Paraná, Río das Flores, *Kasselmann* 501 (holotype B [digital image!]).

Perennial, from long rhizomes, glabrous, to 60 cm, rhizomes to 20 cm long, 5 mm diam. *Leaves* floating, emersed and submersed, floating blades elliptic-ovate, 5-veined c. 15 cm long, 4 – 6 cm wide, pellucid markings present as lines, apex round, base attenuate, petioles terete, 12 – 24 cm long, 3 mm diam., base with a sheath to 13 cm long, emersed blades lanceolate-elliptic, 3-veined, c. 7 cm long, 1.5 – 2 cm wide, pellucid markings present as lines, apex acute, base attenuate, petioles terete, 2 – 7 cm long, 2 mm diam., base with a sheath to 1 cm long, submersed blades linear, 3 – 5 pseudopinnate veins, 10 – 33 cm long, 1.5 – 4.5 cm wide, pellucid markings absent or present as lines, apex round, base attenuate, petioles triangular in cross-section, to 11 cm long, 4 mm diam., base with a sheath to 8 cm long. *Inflorescence* racemes, of 3 – 6 whorls, each 4 – 10-flowered, erect to decumbent, overtopping leaves, often proliferating, 10 – 30 cm long, 5 cm wide, rachis triangular in cross-section, peduncles terete, 20 – 40 cm long, 3 mm diam., bracts free, lanceolate, 0.7 – 6 cm long, 4 – 8 mm wide, 9 – 15-veined, apex acuminate, pedicels spreading in flower and fruit, terete, 1.5 – 5 cm long, 0.5 mm diam. *Flowers* 3.5 – 4.7 cm diam., fragrant, sepals erect, 8 – 14-veined, c. 7 mm long, c. 4 mm wide, veins without papillae, petals spreading, white, not clawed, overlapping, c. 18 mm long, c. 23 mm wide, stamens 18 – 22, anthers versatile, c. 1.5 mm long, filaments c. 2 mm long, carpels numerous. *Fruit* obovoid, 2 – 3-ribbed, glandular, c. 2 mm long, 0.6 mm wide, glands 2 – 3, separated by ribs, circular, beak terminal, erect, 0.2 – 0.7 mm.

DISTRIBUTION AND ECOLOGY. Uruguay, northern Argentina, southern Paraguay and South Brazil. Growing in small clear water rivers, most common in rapids. Flowering and fruiting from September to May. From sea level to 300 m.

SELECTED COLLECTIONS. ARGENTINA. *Niederlein* 1219 (BA!), *Krapovickas & Cristobal* 15634 (C!, CTES!, SI!), *Keller* 482 (CTES!), *Renvoize* 3186 (F!, K!, SI!), *Lehtonen et al.* 227 (TUR!), *Lehtonen et al.* 237 (TUR!). **BRAZIL.** *Smith & Reitz* 12591 (C!), *Hatschbach* 35188 (UC!), *Smith & Klein* 13120 (UC!), *Kasselmann* 502 (M!). **PARAGUAY.** *Marmori* 1137 (CTES!). **URUGUAY.** *Arechavaleta* 4238 (MVM!), *Osten* 3249 (MVM!), *Osten* 2984 (MVM!, W!), *Berro* 2408 (C!, MVFQ!), *Bogner* 2419 (M!), *Legrand* 3511 (MVM!), *Neiff* 902 (CTES!), *Lehtonen & Delfino* 364 (TUR, MVJB!), *Lehtonen & Delfino* 366 (TUR!, MVJB!).

NOTES. Rataj (1970a) divided the taxon into three species (*Echinodorus uruguayensis*, *E. horemanii* and *E. osiris*). While the descriptions of these taxa are slightly different (Rataj 1970a), the type specimens cannot be distinguished on the basis of the original species descriptions. Therefore all three taxa are considered to be conspecific.

Polyploid populations of this species have been placed in *Echinodorus osiris*. Both triploid and tetraploid populations are known from nature (D. Wanke pers. comm.). The phylogenetic analysis (Lehtonen & Myllys 2008) resolved a tetraploid specimen nested within *E. uruguayensis*. *E. osiris* has also been proposed to be of hybrid origin (Kasselmann 2003). Unfortunately the sequencing of chloroplast *matK* from the tetraploid specimen failed (Lehtonen & Myllys 2008). Therefore the possible contradiction between chloroplast and nuclear genome phylogenies remained unknown, and the hypothesis of hybrid origin could not be phylogenetically tested.

There has been some confusion regarding the type of *Echinodorus uruguayensis*. Rataj (1975) designated *Osten* 2984 (W!) as lectotype, although the specimen is not mentioned in the protologue of *E. uruguayensis*. Later he referred to the same specimen as neotype (Rataj 2004). Both typifications are incorrect. Arechavaleta (1903) did not mention any specimens in the protologue of *E. uruguayensis*, but included a photograph of one herbarium specimen. The corresponding specimen (*Arechavaleta* 4238, MVM!) was lectotypified by Alonso Paz (1986).

The type specimen of *Echinodorus aschersonianus* (*Osten* 3249, MVM!) was found to be an emersed growth form of *E. uruguayensis* (Lehtonen 2006), and the name is correspondingly synonymised here.

19. Echinodorus reptilis *Lehtonen* **sp. nov.** Herbae perennae, reptilis. Folia lanceolatae usque ellipticae, pellucido-lineatis. Inflorescentiae umbellatae vel racemae cum 2 – 3 verticilli, plerumque prolifer. Verticilli pauciflori. Pedicelli elongatis. Flores 2.5 – 4 cm lati. Stamina 15 – 22. Fructae biglandulosis. Typus: Paraguay, Misiones, Villa Florida, frente a la ciudad, 21 Dec. 2000, *Mereles, González Parini & López* 8512 (holotypus FCQ!).

Perennial, from short rhizomes, glabrous, to 40 cm, rhizomes to 5 cm long, 0.5 cm diam. *Leaves* emersed, blades lanceolate to elliptic, 3-veined, 3 – 10 cm long, 0.5 – 2 cm wide, pellucid markings present as short lines and dots, apex acute, base attenuate, petioles triangular in cross-section, to 8 cm long, 6 mm diam., base with a sheath to 2 cm long. *Inflorescence* consisting of umbels or racemes, of 1 – 2 (– 3) whorls, each 3 – 5-flowered, decumbent, overtopping leaves, often proliferating, 5 – 10 cm long, 4 cm wide, rachis terete to triangular in cross-section, peduncles terete, to 20 cm long, 1 mm diam., bracts free, lanceolate,

coarse with membranous margin, much shorter than subtended pedicels, to 8 mm long, 3 mm wide, c. 7 – 11-veined, apex acute, pedicels spreading in flower and fruit, terete, 3.5 – 6 cm long, 5 mm diam. *Flowers* 2.5 – 4 cm diam., sepals and petals spreading, sepals c. 11 – 14-veined, c. 5 mm long, c. 3 mm wide, veins without papillae, petals white, not clawed, not overlapping, c. 12 mm long, c. 12 mm wide, stamens 15 – 22, anthers versatile, c. 1.5 mm long, filaments c. 3 mm long, carpels numerous. *Fruit* oblanceoloid, 3 – 4-ribbed, keeled, glandular, c. 1.5 mm long, 0.5 mm wide, glands 2, separated by ribs, circular, beak terminal, erect, c. 0.3 mm. Fig. 7.

DISTRIBUTION AND ECOLOGY. Southern Paraguay, northeast Argentina, southern Brazil (Map 1). Growing on sandy riverbanks at c. 100 m elevation. Flowering and fruiting from October to January.

SPECIMENS EXAMINED. ARGENTINA. Corrientes: Capital, Route 12 and Arroyo Riachuelo, *Schinini & Crovetto* 12347 (CTES!, SI!); Misiones, Posadas, *Gerling* 10963 (BA!), *Mereyer* 5987 (UC!). **BRAZIL.** Porto Alegre, *Remeck & Gerrnak* 10961 (BA!). **PARAGUAY.** Misiones: Villa Florida, frente a la ciudad, *Mereles et al.* 8512 (holotype FCQ!); Villa Florida, Río Tebicuary, 26° 23′ 21.4″ S 57°07′ 31.1″ W, *Lehtonen & Burguez* 260 (TUR!, FCQ!), *Lehtonen & Burguez* 261 (TUR!, FCQ!), *Lehtonen & Burguez* 262 (TUR!, FCQ!), *Lehtonen & Burguez* 263 (TUR!, FCQ!), *Lehtonen & Burguez* 264 (TUR!, FCQ!), *Lehtonen & Burguez* 265 (TUR!, FCQ!), *Lehtonen & Burguez* 266 (TUR!, FCQ!).

CONSERVATION STATUS. Least concern (LC), area of occurence more than 20.000 km^2 (IUCN 2001).

ETYMOLOGY. This species is named for the prostrate and creeping habit, characteristic of this species.

NOTES. This species was referred to as *Echinodorus* sp. in Lehtonen (2006), and *E.* sp. 1 in Lehtonen & Myllys (2008). *E. reptilis* is distinctive in having a creeping umbelliform or racemose inflorescence of 2 whorls with only 3 – 4 flowers on long pedicels. Also, the plant is much smaller than most other species of the genus. The leaves are densely packed with short

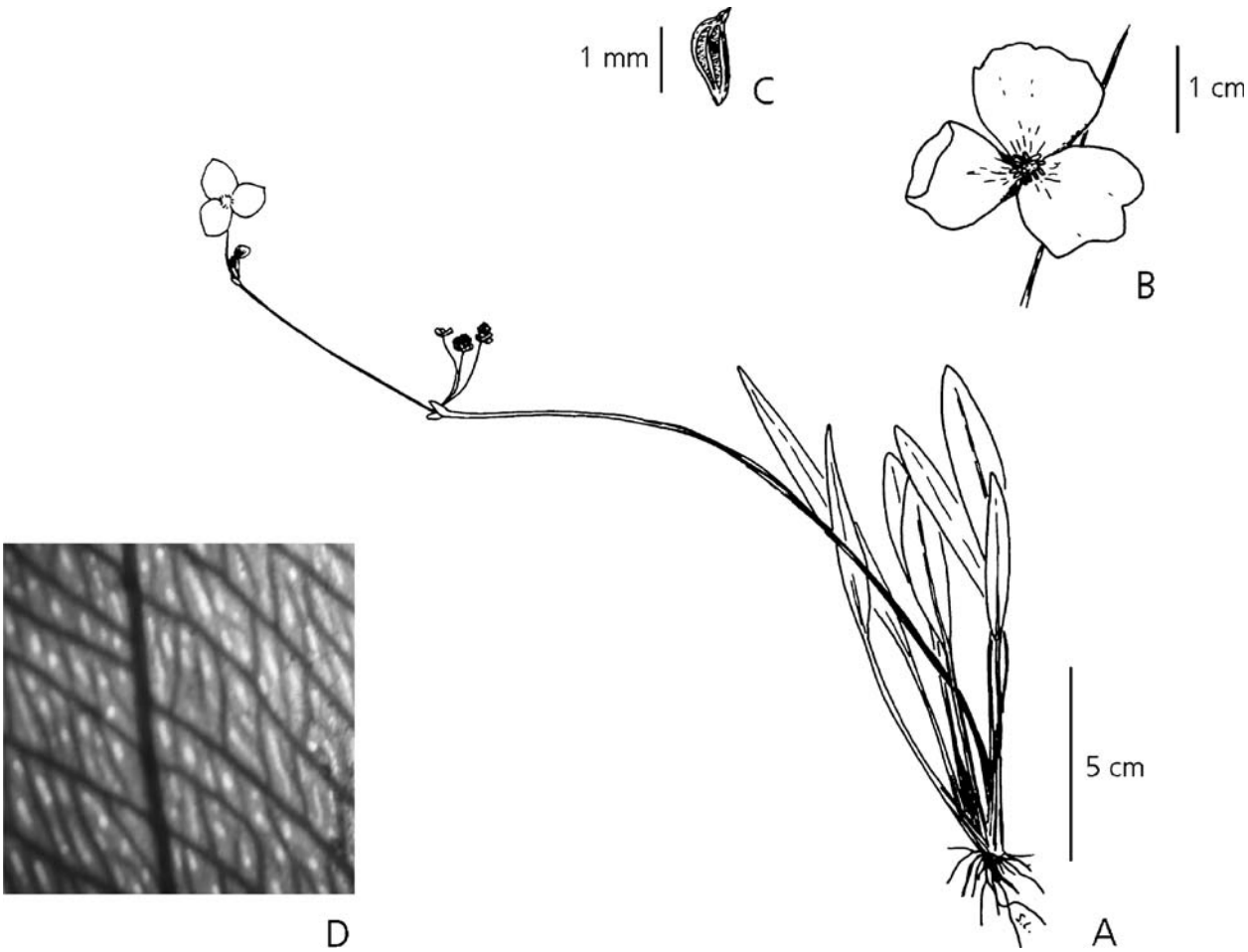


Fig. 7. *Echinodorus reptilis*. **A** habit (*Mereles et al.* 8512, FCQ!); **B** flower (*Lehtonen & Burguez* 264, TUR!); **C** fruit (*Lehtonen & Burguez* 264, TUR!); **D** enlargement of leaf illustrating pellucid markings present as short lines (*Mereyer* 5987, UC!). DRAWN BY SAMULI LEHTONEN.

pellucid lines. All known collections have been made on sand banks of rivers, which is a habitat usually avoided by the genus. Phylogenetically *E. reptilis* is close to *E. uruguayensis* (Lehtonen & Myllys 2008), and the emersed foliage of the former indeed resembles that of the latter. However, *E. uruguayensis* grows mostly in submersed conditions and only occasionally has emersed leaves, whereas *E. reptilis* grows emersed and does not seem to produce morphologically distinctive submersed foliage at all.

20. Echinodorus cordifolius (*L.*) *Griseb.* (1857: 257); Fassett (1955: 137); Rataj (1975: 54), Haynes & Holm-Nielsen (1986: 329; 1994: 41); Haynes & Hellquist (2000: 9); Rataj (2004: 98). Type: Based on the type of *Alisma cordifolia*.

Alisma cordifolia L. (1753). Type: Illustration from Morison (1699), t. 4, Fig. 6 (lectotype, selected by Haynes & Holm-Nielsen 1986).

Sagittaria cordifolia (L.) Lam. (1788: 504). Type: Based on the type of *Alisma cordifolia*.

Sagittaria radicans Nutt. (1835: 159). Type: USA, Arkansas, Sebastian Co., *Nuttall* s.n. (holotype PH [digital image!]).

Echinodorus radicans (Nutt.) Engelm. (1848: 460); Micheli (1881: 55); Buchenau (1903: 28); Britton (1905: 54); Small (1909: 47). Type: Based on the type of *Sagittaria radicans*.

Echinodorus ovalis Wright ex Sauvalle (1870: 564); Buchenau (1903: 31); Small (1909: 48); Fassett (1955: 174); Rataj (1975: 58); Haynes (1984: 9); Lot & Novelo (1994: 5); Rataj (2004: 104). Type: Cuba, *Wright* 3713 (lectotype GH; isolectotypes K [digital image!], NY [digital image!], selected by Rataj 1975).

Echinodorus fluitans Fassett (1955: 155); Rataj (1975: 60; 2004: 112). Type: Colombia, Magdalena, near Riohacha, *Haught* 4450 (holotype US [digital image!]; isotypes UC!, NY [digital image!]) **synon. nov.**

Echinodorus cordifolius (L.) Griseb. subsp. *fluitans* (Fassett) R. R. Haynes & Holm-Niels. (1986: 329; 1994: 42). Type: Based on the type of *Echinodorus fluitans*. **synon. nov.**

Perennial, from rhizomes, petioles and peduncles glabrous to scabrous, to 200 cm. *Leaves* emersed, blades ovate to oval, 5 – 9-veined, 7 – 30 cm long, 4 – 20 cm wide, pellucid markings absent or present as lines, apex acute to obtuse, base attenuate to cordate, petioles terete, 11 – 60 cm long, 5 mm diam., base with a sheath to 7 cm long. *Inflorescence* racemose or paniculate, of 3 – 8 whorls, each 6 – 22-flowered, decumbent, overtopping leaves, proliferating, to 75 cm long, to 45 cm wide, rachis terete to triangular in cross-section, peduncles terete, to 85 cm long, 5 mm diam., bracts free, lanceolate, coarse with membranous margin, shorter than pedicels subtended, 1 – 5 cm long, 2 – 5 mm wide, 9 – 16-veined, apex acuminate, pedicels spreading in flower and fruit, terete, 3 – 7.5 cm long, 1 mm diam. *Flowers* 2 – 3.5 cm diam., sepals and petals spreading, sepals 10 – 20-veined, c. 5 mm long, c. 5 mm wide, veins with or without papillae, petals white, not clawed, overlapping, c. 13 cm long, c. 14 mm wide, stamens 15 – 28, anthers versatile, c. 1.5 mm long, filaments c. 2 mm long, carpels numerous. *Fruit* oblanceoloid, 3 – 5-ribbed, keeled, glandular, 1.3 – 3 mm long, 0.5 – 1 mm wide, glands 1 – 3, separated by ribs, circular, beak terminal, erect, 0.2 – 1 mm.

DISTRIBUTION AND ECOLOGY. USA, Caribbean islands, states of Tamaulipas, Veracruz and Yucatan in Mexico, northern coastal area of Colombia and Venezuela, Pantanal area in Brazil and Paraguay. Growing in floodplains, flowering and fruiting from June to October. From sea level to 400 m.

SELECTED COLLECTIONS. BRAZIL. *Hatschbach et al.* 64532 (UNA!), *Pott et al.* 538 (UNA!), *Pott et al.* 4867 (UNA!). **COLOMBIA.** *Schmidt-Mumm* 216 (UNA!), *Haught* 4450 (UC!). **CUBA.** *Wright* 3713 (K!). **GUADELOUPE.** *Howard* 18602 (BM!). **MEXICO.** *Novelo & Martinez* 804 (MEXU!), *Rico-Gray & Ojeda* 651 (MEXU!), *Haynes* 7604a (UNA!), *Galeotti* s.n. (BR!), *Lehtonen & Ramírez-García* 417 (TUR!, MEXU!). **USA.** *Keener* 275 (UNA!), *Gattinger* 2741 (K!, M!, MEXU!), *Haynes* 6835 (C!, UNA!), *Radford et al.* 11455 (BR!, C!), *Radford et al.* 11455 (H!, MEXU!, UNA!). **VENEZUELA.** *Steyermark & Gonzales* 113775 (F!), *Trujillo* 11927 (MY!), *Trujillo* 13469 (MY!), *Trujillo* 14377 (MY!), *Tillet* 310–37 (MYF!), *Salazar* 25 (VEN!), *Jaase & Vareschi* 2797 (VEN!), *Steyermark & Braun* 94514 (VEN!), *Trujillo* 8811 (MY!), *Lehtonen* 457 (TUR!, VEN!).

NOTES. Confusion about the name and type of *Echinodorus cordifolius* was discussed by Fassett (1955) and Haynes & Holm-Nielsen (1986). Fassett (1955), Rataj (1975, 2004), Lot & Novelo (1994), and Mühlberg (2004) accepted the species *E. ovalis*, while Haynes & Holm-Nielsen (1986, 1994) did not. Mühlberg (2004) based his argument on morphological features: *E. ovalis* has relatively small ovate leaves with few veins, small flowers with 15 – 18 stamens, up to 200 cm long, thin inflorescence, long and thin pedicels and spreading sepals, in contrast to *E. cordifolius*, which has larger, broad, cordate leaves with more veins, larger flowers with 22 – 26 stamens, shorter, more robust and initially erect inflorescence, shorter and thicker pedicels, and erect sepals. According to Rataj (1975, 2004) *E. ovalis* is endemic to Cuba. However, specimens clearly matching the detailed description of *E. ovalis* by Mühlberg (2004) can also be found in Mexico and Venezuela. In addition, as mentioned by Haynes & Holm-Nielsen (1986), intermediate plants have been collected. The phylogenetic analyses by Lehtonen & Myllys (2008)

included one specimen (*Lehtonen & Ramírez* 417, TUR!, MEXU!) from Mexico with all the typical characters of *E. ovalis*: small ovate leaves with pellucid lines and dots, relatively small flowers with non-overlapping petals and 18 stamens, and a thin, creeping inflorescence. In the analysis this specimen was resolved between a North American specimen of typical *E. cordifolius* and a specimen of *E. cordifolius* collected from Venezuela. The population where this Venezuelan specimen (*Lehtonen* 457, TUR!, VEN!) was collected consisted of large plants with cordate leaves, pellucid lines and dots, large flowers with overlapping petals and up to 28 stamens, and creeping, paniculate inflorescences up to 200 cm long. Plants with intermediate characteristics between *E. cordifolius* and *E. ovalis* were observed nearby (*Lehtonen* 467, TUR!, VEN!). Since the total-evidence analysis (Lehtonen & Myllys 2008) placed the typical specimen of *E. ovalis* within specimens clearly representing *E. cordifolius*, I follow the conclusions made by Haynes & Holm-Nielsen (1986) and do not accept *E. ovalis* as a distinct species. Fassett (1955) and Rataj (1975, 2004) also accepted *E. fluitans*, treated as a subspecies of *E. cordifolius* by Haynes & Holm-Nielsen (1986, 1994). The imperfect type specimen is collected from Colombia, and differs from *E. cordifolius* only by the lack of pellucid markings. Similar specimens have been collected along the Venezuelan border, and the lack of pellucids is apparently related only to growing conditions. The phylogenetic analyses (Lehtonen & Myllys 2008) resolved *E. fluitans* within the *E. cordifolius*-*E. ovalis* clade. Therefore *E. fluitans* is also treated here as conspecific with *E. cordifolius*. Furthermore, the distribution of *E. cordifolius* seems to be much wider than usually thought. The main distribution of the species covers the Atlantic coastal plain and Mississippi valley in the USA, but the species is also present in the Caribbean Islands, in the states of Tamaulipas, Veracruz and Yucatan in Mexico, and in northern Colombia. It is widely distributed in northern Venezuela, and surprisingly present in Pantanal wetland in southern Brazil. Due to the wide geographical distribution, morphological variation is also large.

21. Echinodorus floribundus (*Seub.*) *Seub.* (1872: 113). Type: Based on the type of *Alisma floribundum*.

Alisma floribundum Seub. (1847: 109). Type: Brazil, *Gardner* 1860 (lectotype NY [digital image!]; isolectotypes BM!, G [digital image!], K [digital image!], NY, selected by Haynes & Holm-Nielsen 1994).

Echinodorus grandiflorus (Cham. & Schltdl.) Micheli α *floribundus* (Seub.) Micheli (1881: 58); Buchenau (1903: 33); Hauman (1915: 311). Type: Based on the type of *Alisma floribundum*.

Alisma pubescens Mart. β *claussenii* Seub. (1847: 107). Type: Brazil, Minas Gerais, *Claussen* 351 (holotype BR!; isotype K [digital image!]).

Echinodorus grandiflorus (Cham. & Schltdl.) Micheli var. *claussenii* Rataj (1969a: 324); Rataj (1975: 51). Type: Based on the type of *Alisma pubescens* β *claussenii*.

Echinodorus muricatus Griseb. (1858: 11); Small (1909: 48); Fassett (1955: 152). Type: Panama, *Duchassaing* s.n. (holotype GOET [digital image!], selected by Haynes & Holm-Nielsen 1994).

Echinodorus macrophyllus (Kunth) Micheli β *muricatus* (Griseb.) Micheli (1881: 50). Type: Based on the type of *Echinodorus muricatus*.

Echinodorus punctatus Micheli (1881: 59 – 60). Type: Brazil, province Saint-Paul *St. Hilaire Cat. C*^{2} no 1588 (lectotype P [digital image!]; isolectotype P [digital image!], selected by Haynes & Holm-Nielsen 1994).

Echinodorus grandiflorus (Cham. & Schltdl.) Micheli var. *aureus* Fassett (1955: 152). Type: Cuba, Habana, Rincón, *van Hermann* 540 (holotype F; isotype GH, NY [digital image!]).

Echinodorus grandiflorus (Cham. & Schltdl.) Micheli subsp. *aureus* (Fassett) R. R. Haynes & Holm-Niels. (1986: 330; 1994: 48). Type: Based on the type of *Echinodorus grandiflorus* var. *aureus* **synon. nov.**

Echinodorus grandiflorus (Cham. & Schltdl.) Micheli var. *longibracteatus* Rataj (1969a: 324 – 325; 1975: 50). Type: Brazil, Río Pardo, *Jürgens* 315 (holotype B [digital image!]; isotype B [digital image!]) **synon. nov.**

Perennial, from horizontal rhizomes, petioles and peduncles pubescent, to 300 cm. *Leaves* emersed, blades broad ovate, stellate pubescent on lower surface, 11 – 21-veined, 20 – 40 cm long, 16 – 40 cm wide, pellucid markings present as dots or rarely absent, apex retuse to obtuse, base cordate, petiole terete, stellate pubescent, to 90 cm long, 0.5 – 2.5 cm diam., base with a sheath to 22 cm long. *Inflorescence* paniculate, of 8 – 16 whorls, each 7 – 18-flowered, erect, overtopping leaves, occasionally proliferating, to 120 cm long, to 70 cm wide, rachis terete, peduncles terete, stellate pubescent, to 155 cm long, 2.5 cm diam., bracts lanceolate, coarse, 1 – 4 cm long, 4 – 11 mm wide, 11 – 24-veined, apex acuminate, pedicels spreading in flower and fruit, 1 – 4 cm long, 1 mm diam. *Flowers* 3 – 4 cm diam., sepals erect, 12 – 19-veined, 7 mm long, 5 mm wide, veins without papillae, petals spreading, white, not clawed, overlapping, c. 20 mm long, 18 mm wide, stamens 24 – 30, anthers versatile, c. 1.5 mm long, filaments c. 3 mm long, carpels numerous. *Fruit* oblanceoloid, 2 – 3-ribbed, glandular, 1.8 – 2.8 mm long, 1 mm wide, glands 2 – 3, separated by ribs, elongate, beak terminal, erect, 0.2 – 0.3 mm. Fig. 8.

DISTRIBUTION AND ECOLOGY. From Mexico and Cuba through Venezuela, Colombia, Peru and Brazil to

Bolivia, Paraguay and northern Argentina in south (Map 2). Growing in palm (*Mauritia flexuosa* L. f.) swamps, along lake margins, and in wet depressions in inundated savannas. Flowering and fruiting year round. From sea level to 1650 m.

SELECTED COLLECTIONS. ARGENTINA. *Lehtonen & Dematteis* 212 (TUR!), *Keller* 2015 (CTES!), *Krapovickas et al.* 26428 (CTES!), *Mroginski & Pire* 807 (K!), *Schwarz* 1514 (MVFA!), *Rodriguez* 634 (SI!). **BOLIVIA.** *Lehtonen* 161 (TUR!, LPB!), *Lehtonen* 165 (TUR!, LPB!), *Lehtonen* 188 (TUR!, LPB!), *Nee* 39349 (UNA!, LPB!), *Nee* 39372 (LPB!), *Pearce* s.n. (BM!). **BRAZIL.** *Marinoni* 133 (AAU!), *Warming* 157 (C!), *Bockermann* 297 (SP!), *Jürgens* 315 (B!), *Claussen* 351 (BR!), *Lindberg* 568 (BR!), *Vieira* 720 (UNA!), *Vieira* 723 (UNA!), *Löfgren* 1676 (C!), *Gardner* 1860 (BM!, G!), *Irwin* 2169 (UC!), *Dusen* 2981 (BM!), *Mexia* 4179 (UC!, BM!), *Hatschbach* 35769 (UC!), *Anderson et al.* 36211 (UNA!), *Hermogenes et al.* 33.270 (SP!). **COLOMBIA.** *De Escobar & Velásquez* 8158 (UNA!). **CUBA.** *Van Hermann* 540 (NY!). **HONDURAS.** *Haynes* 8445 (UNA!), *Meigs* 1592 (UNA!). **MEXICO.** *Kasselmann* 43 (C!), *Novelo & Ramos* 1599 (MEXU!), *Lot* 1630 (MEXU!), *Breedlove* 37821 (MEXU!), *Galeotti* s.n. (BR!). **NICARAGUA.** *Haynes* 8270 (UNA!), *Haynes* 8632 (AAU!, UNA!). **PANAMA.** *Folsom* 2147 (UNA!), *Hunter & Allen* 381 (BR!). **PARAGUAY.** *Soria* 6935 (FCQ!). **PERU.** *Barbour* 5561 (AAU!). **URUGUAY.** *Berro* 159 (C!, MVFQ!), *Neffa et al.* 458 (CTES!). **VENEZUELA.** *Lehtonen & Pacheco* 485 (TUR!, VEN!), *Alston* 5958 (BM!), *Davidse et al.* 18389 (UNA!, MEXU!), *Steyermark & Carreño* 111223 (K!, VEN!), *Delascio & López* 11706 (CAR!), *Trujillo* 12215 (MY!).

NOTES. According to Haynes & Holm-Nielsen (1986) this taxon is conspecific with *Echinodorus longiscapus* and *E. grandiflorus*, and it should be recognised only at the subspecific level (as *E. grandiflorus* subsp. *aureus*). Morphological data alone suggested non-monophyletic origins for these taxa (Lehtonen 2006), but in the total-evidence analysis they were resolved as a clade (Lehtonen & Myllys 2008). However, based on morphological differences I divide this clade into three species (*E. floribundus*, *E. grandiflorus* and *E. longiscapus*). All the species are resolved as clades in the total-evidence analysis, although DNA sequences used

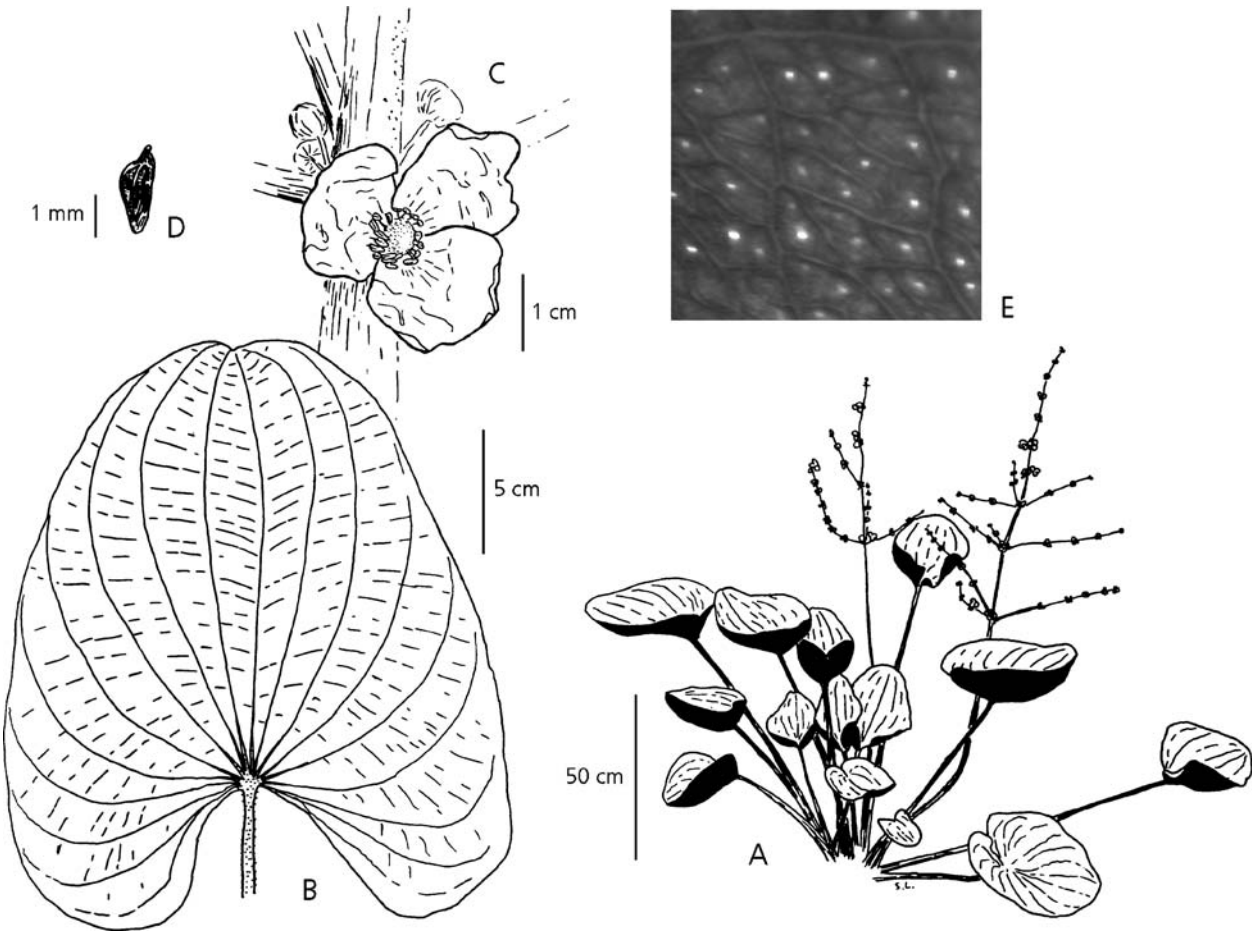


Fig. 8. *Echinodorus floribundus* (*Lehtonen* 161, TUR!). A habit; B leaf; C flower; D fruit; E enlargement of leaf illustrating pellucid dots. DRAWN BY SAMULI LEHTONEN.

in the analysis did not clearly define the species boundaries. *E. floribundus* can be recognised by its generally much larger size (1.5 – 3 m), almost round leaf blades with pellucid dots (rarely absent), and inflorescences which have several long and almost horizontal branches. *E. longiscapus* is much smaller (0.5 – 1 m), leaves are oval with pellucid lines and dots, and inflorescences are mostly without branches. *E. grandiflorus* is intermediate in size (1 – 1.5 m), leaves are long petiolate, with large oval blades and pellucid lines and dots. Petioles have node-like thickening below the leaf blades. Inflorescences are paniculate, but branches are short, few in number, and almost erect.

Rataj (1975) recognised these three different species as well (although he further split *Echinodorus grandiflorus*), but used incorrect names for two of them (*E. grandiflorus* for *E. floribundus*, and *E. argentinensis* and *E. pellucidus* for *E. grandiflorus*).

22. Echinodorus longiscapus *Arechav.* (1903: 67); Rataj (1969d: 183; 1970c: 32; 1975: 56; 2004: 100). Type: Uruguay, Tacuarembó, Arroyo Cardoso, *Arechavaleta* 4239 (lectotype MVM!, **selected here**).

Echinodorus grandiflorus (Cham. & Schltdl.) Micheli var. *longiscapus* (Arechav.) Hauman (1915: 311). Type: Based on the type of *Echinodorus longiscapus*.

Echinodorus sellowianus Buchenau (1903: 30 – 31). Type: Brazil, Brazilian meridionalis, *Sellow* 1659 (lectotype W, selected by Rataj 1969d).

Echinodorus sellowianus Buchenau var. *minor* Buchenau (1903: 30 – 31); Hauman (1915: 317). Type: Uruguay, Mercedes, *Osten* 2985 (lectotype MVM! selected by Troncoso 1964).

Echinodorus longiscapus Arechav. var. *minor* (Buchenau) Tronc. (1964: 626). Type: Based on the type of *E. sellowianus* var. *minor*.

Echinodorus sellowianus Buchenau var. *major* Buchenau (1903: 30 – 31). Type: Based on the type of *Echinodorus sellowianus*.

Echinodorus aschersonianus Graebn. var. *nulliglandulosus* Rataj (1970c: 25; 1975: 61). Type: Argentina, Santa Fé, Calchaqui, *Ragonese* 2105 (holotype BA!) **synon. nov.**

Perennial, from horizontal rhizomes, petioles and peduncles glabrous to sparingly pubescent, to 90 cm, rhizomes to 15 cm long, to 2.5 cm diam. *Leaves* emersed, blades oval to ovate, 5 – 11-veined, 6 – 15 cm long, 4 – 12 cm wide, pellucid markings present as dots and short lines, apex rounded to obtuse, base truncate to cordate, petioles terete, to 30 cm long, 3 – 5 mm diam., base with a sheath to 9 cm long. *Inflorescence* racemose or rarely paniculate with a few branches, of 4 – 10 whorls, each 5 – 15-flowered, erect or decumbent, overtopping leaves, proliferating, to 50 cm long, and 8 cm wide, rachis triangular in cross-section, peduncles terete, glabrous to stellate pubescent, to 50 cm long, 7 mm diam., bracts free, lanceolate, coarse, with 10 – 18 veins, 0.7 – 2.8 cm long, 3 – 8 mm wide, 10 – 18-veined, apex acute, pedicels spreading in flower and fruit, 0.5 – 3.5 cm long, 0.5 – 1 mm diam. *Flowers* 2.5 – 4 cm diam., sepals erect, 12 – 24-veined, c. 5 mm long, c. 3 mm wide, veins without papillae, petals spreading, white, not clawed, overlapping, c. 21 mm long and c. 17 mm wide, stamens 19 – 28, anthers versatile, c. 1.5 mm long, filaments c. 2.5 mm long, carpels numerous. *Fruit* oblanceoloid, 3 – 4-ribbed, keeled, glandular, 1.8 – 2.5 mm long and 0.7 mm wide, glands 2 – 4, separated by ribs, elongate, beak terminal, erect, 0.1 – 0.5 mm. Fig. 9.

DISTRIBUTION AND ECOLOGY. Argentina north of Buenos Aires, Paraguay, Uruguay, southern Brazil (Map 3). Growing usually in standing temporary waters, on swamps, ditches and inundated savannas. Flowering and fruiting from September to June. From sea level to 1300 m.

SELECTED COLLECTIONS. ARGENTINA. *Lehtonen & Dematteis* 204 (TUR!), *Lehtonen* 385 (TUR!), *Baez* 4 (SI!), *Auxiliar* 77 (BA!), *Venturi* 514 (BA!, SI!), *Petersen* 3009 (BR!, K!), *Schinini et al.* 12282 (CTES!, SI), *Castellanos* s.n. (BA!), *Hauman* 14998 (BA!), *Krapovickas et al.* 16561 (CTES!), *Renvoize et al. 3095* (K!), *Cabrera et al.* 279 (CTES!), *Krapovickas et al.* 16763 (BA!), *Krapovickas et al.* 16763 (CTES!). **BRAZIL.** *Pott et al* 385 (UNA!), *Da Cunha et al.* 2150 (UNA!), *Tessmann* 3667 (UNA!), *Hatschbach* 41908 (MEXU!). **URUGUAY.** *Lehtonen & Delfino* 334 (TUR!, MVJB!), *Lehtonen & Delfino* 341 (TUR!, MVJB!), *Anderson* 142 (BM!), *Alonso Paz* 316 (MVM!), *Bogner* 2388 (M!), *Berro* 2389 (MVFQ!), *Bogner* 2423 (M!), *Osten* 2985 (MVM!), *Arechavaleta* 4239 (MVM!). **PARAGUAY.** *Walter* 27 (BM!), *Mereles* 46 (CTES!), *Recalas* 71 (FCQ!), *Balansa* 571 (G-DC!), *Degen* 1760 (FCQ!, UNA!).

NOTES. Haynes & Holm-Nielsen (1994) treated this species together with *Echinodorus grandiflorus* as *E. grandiflorus* subsp. *grandiflorus*. In the total-evidence analysis of Lehtonen & Myllys (2008) these two taxa were recognised to have a sister relationship. The distribution of *E. grandiflorus* is mostly within that of *E. longiscapus*, but they have different ecological preferences and thus only rarely form mixed populations (pers. obs.). *E. grandiflorus* grows along rivers in permanently wet environments, whereas *E. longiscapus* favours temporarily wet depressions. Based on the phylogenetic evidence, widely overlapping distribution, and morphological and ecological differences I consider *E. longiscapus* and *E. grandiflorus* as separate species.

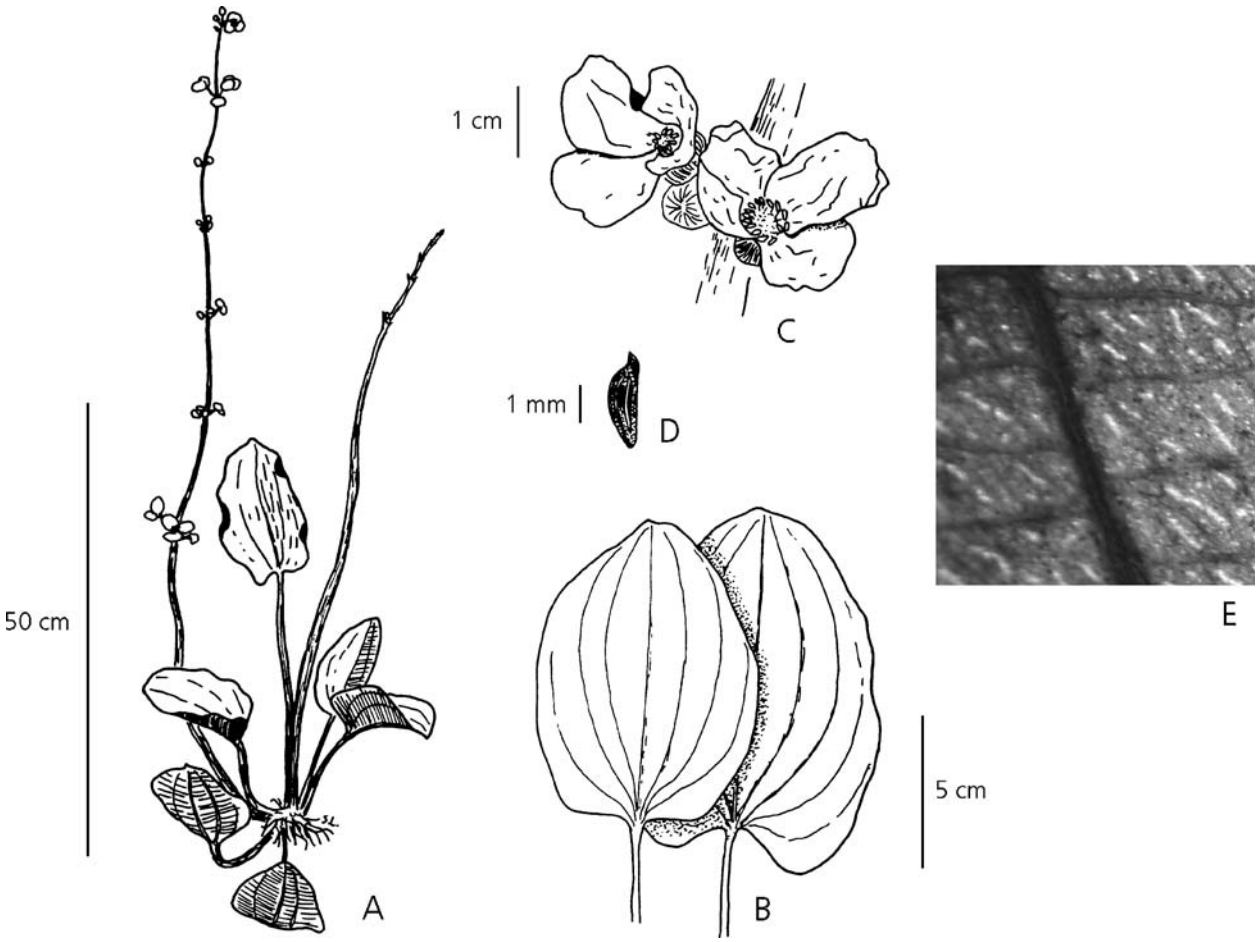


Fig. 9. *Echinodorus longiscapus*. A habit; B variation in leaf morphology (*Lehtonen* 384, TUR!; *Lehtonen & Delfino* 347, TUR!); C flowers (*Lehtonen & Delfino* 347); D fruit; E enlargement of leaf illustrating pellucid dots and lines (*Lehtonen & Dematteis* 204, TUR!). DRAWN BY SAMULI LEHTONEN.

Rataj (1970c) described *Echinodorus aschersonianus* var. *nulliglandulosus*, which is not conspecific with *E. aschersonianus* (i.e. *E. uruguayensis*), but instead it is in my opinion submersed *E. longiscapus*. Both the lack of pellucid markings and exceptionally long pedicels of the type specimen are common features of submersed *E. longiscapus*.

Arechavaleta (1903) did not mention any collection in the protologue of *Echinodorus longiscapus*. However, he included a photograph of the specimen *Arechavaleta* 4239 (MVM!) in the description. This specimen is here selected as the lectotype of *E. longiscapus*.

23. Echinodorus grandiflorus (*Cham. & Schltdl.*) *Micheli* (1881: 57 – 59); Buchenau (1903: 33); Haynes & Holm-Nielsen (1994: 42). Type: Based on the type of *Alisma grandiflorum*.

Alisma grandiflorum Cham. & Schltdl. (1827: 152 – 155). Type: Brazil, *Sellow* s.n. (lectotype LE; isolectotypes BM, BR!, E-GL, K [digital image!], MO [digital image!], selected by Haynes & Holm-Nielsen 1986).

Echinodorus grandiflorus (Cham. & Schltdl.) Micheli β *ovatus* Micheli (1881: 58). Type: Argentina, Buenos Aires, *Bâcle* 82 (lectotype G [digital image!]; isolectotypes G (3) [digital image!], G-DC [digital image!]).

Echinodorus argentinensis Rataj (1970c: 34 – 36; 1975: 59; 2004: 108). Type: Argentina, Concepción del Uruguay, *Lorenz* 1791 (holotype W!).

Echinodorus pellucidus Rataj (1975: 58); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 106). Type: Argentina, alrededores del Buenos Aires, Barracas al Sur, *Venturi* s.n. (holotype BA!) **synon. nov.**

Echinodorus floridanus R. R. Haynes & Burkhalter (1998: 180); Haynes & Hellquist (2000: 10); Rataj (2004: 138). Type: USA, Florida, Escambia, west edge of Pensacola, *Haynes & Burkhalter* 9717 (holotype MO [digital image!]; isotypes NY [digital image!], UNA!). **synon. nov.**

Map 3. Distribution of *Echinodorus longiscapus* (*black dots*), *E. scaber* (*grey dots*), *E. macrophyllus* (*triangles*) and *E. inpai* (*stars*), based on georeferenced herbarium material.

Perennial, from horizontal rhizomes, petioles and peduncles glabrous to pubescent, to 180 cm, rhizomes to 15 cm long, 3 cm diam. *Leaves* emersed, blades oval to ovate, glabrous to stellate pubescent on lower surface, 7 – 13-veined, 15 – 50 cm long, 5.5 – 30 cm wide, pellucid markings present as dots and short lines, apex acute to rounded, base attenuate to shallowly cordate, petiole terete, glabrous to stellate-pubescent, usually with a node-like thickening below the blades, up to 120 cm long, 0.3 – 2 cm diam., base with a sheath to 16 cm long. *Inflorescence* paniculate, of 5 – 13 whorls, each 7 – 19-flowered, erect, overtopping leaves, proliferating, to 55 cm long, and to 25 cm wide, rachis terete to triangular in cross-section, peduncles terete, glabrous to stellate pubescent, to 140 cm long, 1.2 cm diam., bracts lanceolate, coarse, 1.5 – 4.5 cm long, 6 – 14 mm wide, 10 – 20-veined, apex acuminate, pedicels spreading in flower and fruit, 1.5 – 6.5 cm long, 1 mm diam. *Flowers* 3.5 – 5 cm diam., weakly fragrant, sepals erect, 13 – 25-veined, 7 mm long, 5 mm wide, veins without papillae, petals spreading, white, not clawed, overlapping, c. 22 mm long, 20 mm wide, stamens 21 – 35, anthers versatile, c. 2 mm long, filaments c. 1.5 mm long, carpels numerous. *Fruit* oblanceoloid, 3 – 4-ribbed, glandular, 2 – 3 mm long, 1 mm wide, glands 2 – 3, separated by ribs, elongate, beak terminal, erect, 0.2 – 0.5 mm. Fig. 10.

DISTRIBUTION AND ECOLOGY. Coastal area from the mouth of Río Negro in Argentina through Uruguay to the state of Paraná in Brazil. An outlying population in Florida, USA (Map 2). Growing at sea level in flowing water along rivers and creeks, most common in river deltas. Flowering and fruiting from November to May in South America, from April to October in USA.

SELECTED COLLECTIONS. ARGENTINA. *Lehtonen* 390 (TUR!), *Lehtonen* 391 (TUR!), *López* 24 (BA!), *López* 55 (BA!), *Bâcle* 82 (G!, G-DC!), *Rodriguez* 133 (SI!), *Hurrell et al.* 1615 (SI!), *Tur* 1667 (SI!), *Lanfranchi* 1847 (SI!), *Burkart* 4511 (SI!), *Hurrell et al.* 5464 (SI!), *Burkart & Crespo* 22443 (SI!), *Eyerdam et al.* 23368 (UC!), *Burkart & Troncoso* 26118 (SI!), *Burkart & Troncoso* 27165 (SI!), *Faggi* 79014 (BA!), *Venturi* s.n. (BA!), *Daguerre* s.n. (BA!), *Castellanos* s.n. (BA!), *Castellanos* s.n. (BA!), *Venturi* s.n. (BA!), *Baffa* s.n. (BM!), *Lefebvre* s.n. (BR!), *Söyrinki* s.n. (H!), *Hicken*

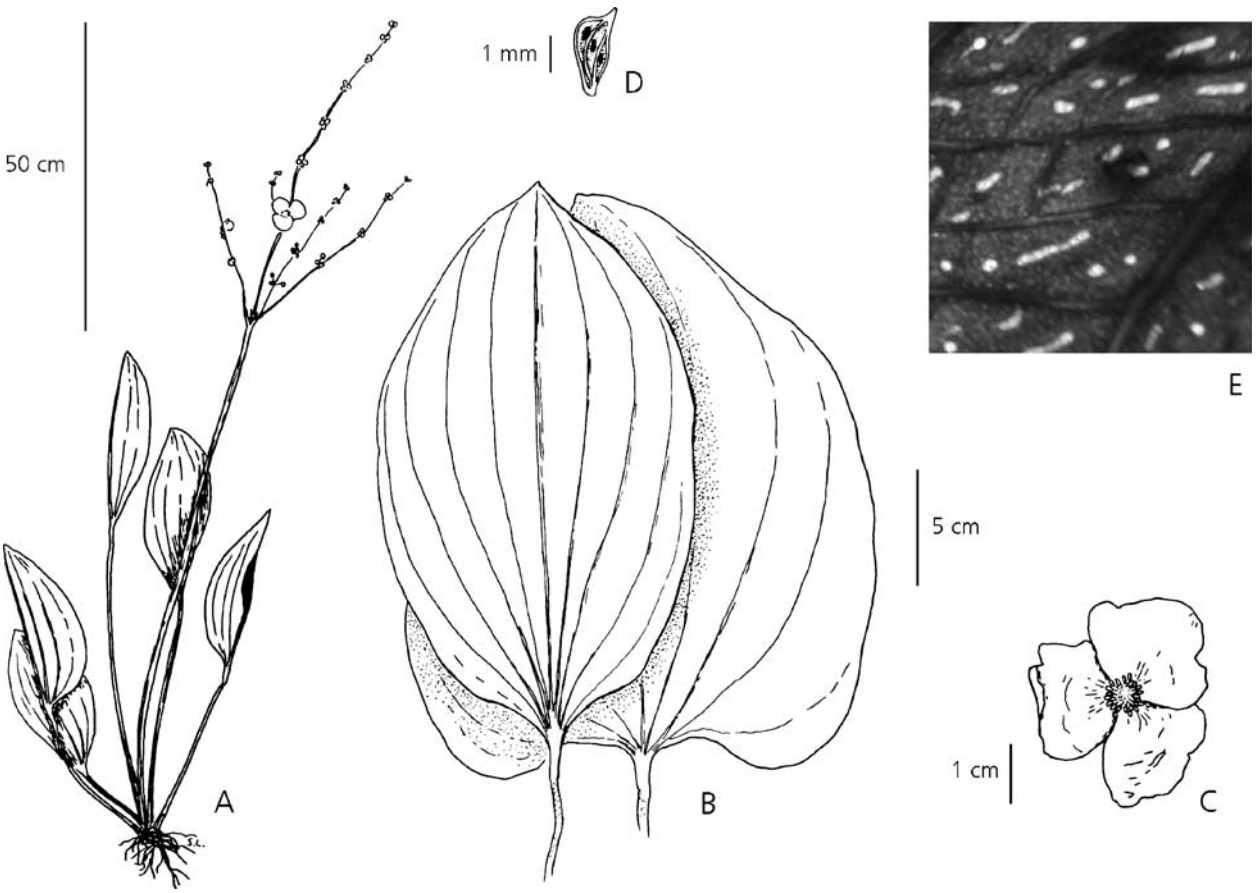


Fig. 10. *Echinodorus grandiflorus*. **A** habit (*Lehtonen* 386, TUR!); **B** variation in leaf morphology (*Lehtonen* 386; *Lehtonen & Delfino* 345, TUR!); **C** flower (*Lehtonen* 386); **D** fruit (*Abreu* 329, TUR!); **E** enlargement of leaf illustrating pellucid lines and dots (*Lehtonen* 383, TUR!). DRAWN BY SAMULI LEHTONEN.

s.n. (SI!), *Newton* s.n. (SI!), *Lorenz* 1791 (W!). **BRAZIL.** *Bueno* 292 (UNA!), *Abreu* 318 (TUR!), *Abreu* 329 (TUR!), *Abreu* 352 (TUR!), *Abreu et al.* 363 (TUR!), *Abreu et al.* 373 (TUR!), *Kummrow* 1233 (UNA!), *Kummrow* 2573 (UNA!), *Kummrow & Ribas* 2985 (UNA!), *Hatschbach et al.* 28167 (UNA!), *Hatschbach* 30982 (CTES!), *Hatschbach* 30982 (CTES!, M!, SI!, UC!), *Irgang* 35814 (CTES!), *Hatschbach & Barbosa* 67153 (UNA!), *Sellow* s.n. (K!, BR!). **URUGUAY.** *Lehtonen & Delfino* 358 (TUR!, MVJB!), *Aplin* s.n. (BM!), *Wright* s.n. (BM!), *Arrillaga et al.* 1925 (MVFQ!). **USA.** *Haynes & Burkhalter* 9617 (UNA!, NY!).

NOTES. Haynes & Burkhalter (1998) recently described a new species, *Echinodorus floridanus* from USA. They speculated on the possible close affinity of *E. floridanus* and *E. grandiflorus*, but without any phylogenetic evidence did not make further conclusions (Haynes & Burkhalter 1998). My morphological study (Lehtonen 2006) already indicated the conspecific status of these two, and this result is clearly confirmed in the combined phylogenetic analysis (Lehtonen & Myllys 2008). The origin of the population in USA is unknown, but is probably related to intense aquarium plant cultivation in Florida (see Ridings & Zettler 1973; Doyle 2001).

Haynes & Holm-Nielsen (1994) assumed, without studying the type specimen, that *Echinodorus pellucidus* would be a synonym of *E. uruguayensis*. However, after studying the type specimen with paniculate inflorescence and oval leaf blades I consider *E. pellucidus* to be conspecific with *E. grandiflorus*.

Doubtfully Accepted Species

Several species are known only on the basis of one or two collections. Since such material cannot provide any information on intraspecific variation I consider the species delimitation in these cases to be ambiguous. However, based on the available evidence these species cannot be rejected either, and are therefore accepted but considered to have uncertain status.

24. Echinodorus decumbens *Kasselm.* (2000: 5); Rataj (2004: 36). Type: Brazil, Piauhy, Rio Surubim, 1 April 1994, *Kasselmann* 205 (holotype INPA [photograph in AAU!]; isotypes B [digital image!], M!).

Perennial, from rhizomes, glabrous, to 100 (– 200) cm, rhizomes 1 cm diam. *Leaves* emersed, blades narrowly elliptic, 3 – 5-veined, 15 – 30 cm long, 1.8 – 4.5 cm wide, the pellucid markings present as short lines, apex acute, base attenuate, petioles channelled, ridged, to 30 (– 45) cm long, 5 mm diam., base with a sheath to 10 cm long. *Inflorescence* racemose or rarely paniculate, of 5 – 10 whorls, each 3 – 7-flowered, decumbent, overtopping leaves, proliferating, to 55 cm long, 3 cm wide, rachis triangular in cross-section, peduncles ridged, to 50 cm long, 3 mm wide, bracts slightly connate at the base, lanceolate, longer than pedicels subtended, to 5 cm long, 0.5 cm wide, c. 12-veined, apex long acuminate, pedicels spreading in flower and fruit, 0.5 – 1 cm long, c. 3 mm diam. *Flowers* c. 2 cm diam., sepals and petals spreading, sepals c. 15-veined, c. 5 mm long, c. 4 mm wide, veins without papillae, petals not claved, not overlapping, 10 mm long, c. 10 mm wide, stamens 12, anthers versatile, c. 1.5 mm long, filaments c. 2 mm long, carpels numerous. *Fruit* oblanceolate, 4-ribbed, glandular, 2 – 3 mm long, 1.2 mm wide, glands 1, circular, separated by ribs, beak terminal, erect, 0.9 mm. Fig. 11.

DISTRIBUTION AND ECOLOGY. Known only from the type locality (Map 1). Growing along rivers and in floodplains (Kasselmann 2000). Flowering and fruiting in April.

SELECTED COLLECTIONS. BRAZIL. *Kasselmann* 205 (B!, M!).

NOTES. Kasselmann (2000) considered this taxon to be closely related to *Echinodorus paniculatus*, while Rataj (2004) placed it close to *E. grisebachii*. Phylogenetic studies revealed a very close relationship with *E. subalatus* (Lehtonen & Myllys 2008). These species can be separated by the following set of characters: *E. decumbens* has a long creeping inflorescence with long internodes between relatively few whorls of few flowers, whereas *E. subalatus* has a relatively short and erect inflorescence with short internodes and many whorls with plenty of flowers. *E. paniculatus* and *E. grisebachii* have triangular, un-channelled petioles. Flowers of *E. paniculatus* are large with 19 – 22 stamens, and fruits lack glands. *E. grisebachii* has multiglandular fruits with short beak. *E. decumbens* is known only from the type locality, and more collections are needed to verify whether it is really a separate species or only a local ecological morph of *E. subalatus*.

25. Echinodorus inpai *Rataj* (1981: 20); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 56). Type: Brazil, Mato Grosso, Rio Aripuana *Rataj* s.n. (holotype INPA).

Perennial, from rhizomes, to 30 cm. *Leaves* emersed, blades elliptic, 3 – 5-veined, 8 – 20 cm long, 1 – 7 cm wide, pellucid markings present as lines, apex acute, the base acute, tapering along petiole, petioles triangular in cross-section, channelled, to 10 cm long, 3 mm diam., base with a sheath to 4 cm long. *Inflorescence* racemose or paniculate, of c. 6 whorls, each c. 7-flowered, erect, overtopping leaves, proliferating, 15 – 30 cm long, 2 cm wide, rachis triangular in cross-section, peduncles terete, to 17 cm long, 2 mm diam., bracts lanceolate, coarse, 0.6 – 1 cm long, 2 mm wide,

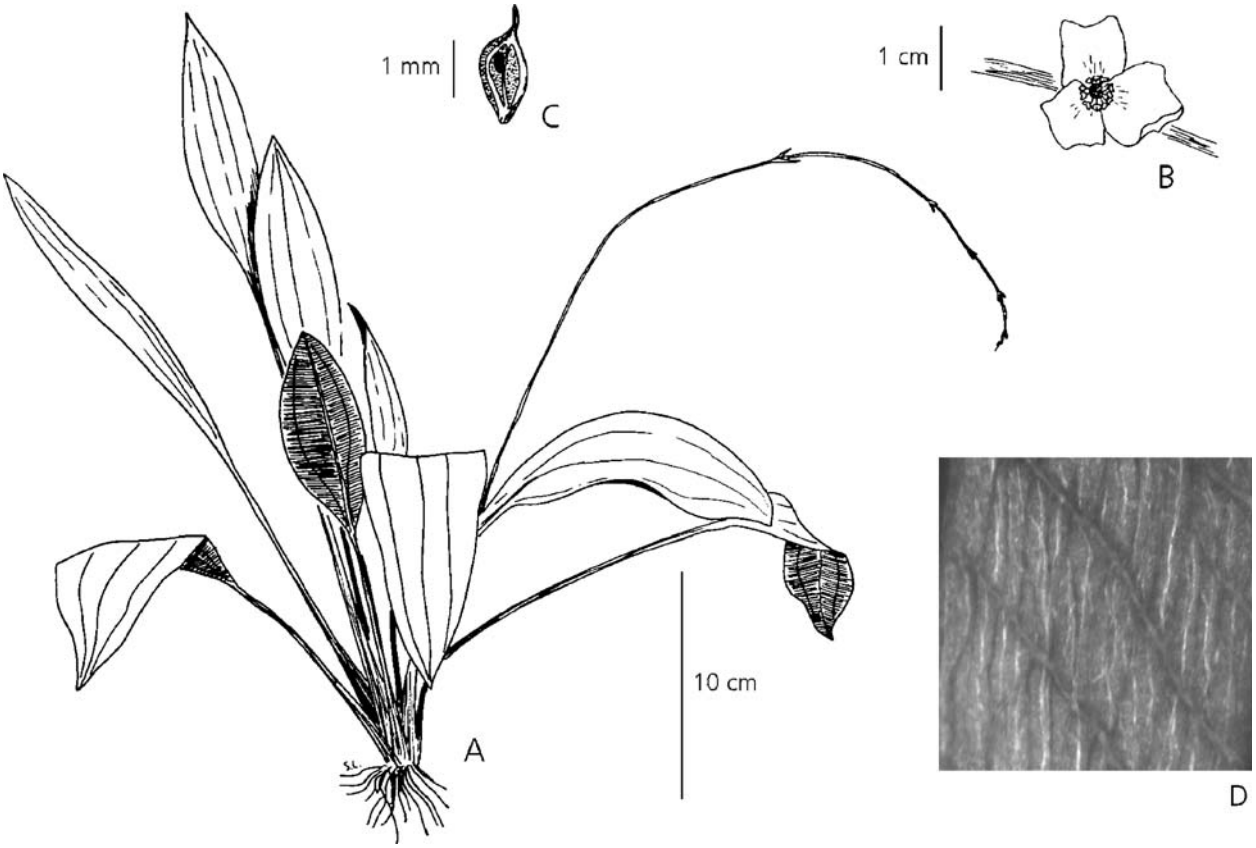


Fig. 11. *Echinodorus decumbens*. A habit; B flower; C fruit; D enlargement of leaf illustrating pellucid lines. DRAWN BY SAMULI LEHTONEN.

c. 6-veined, apex acuminate, pedicels spreading in flower and fruit, terete, c. 0.5 cm long, 3 mm diam. *Flowers* 0.8 – 1.2 cm diam., sepals and petals spreading, sepals c. 8-veined, c. 4 mm long, c. 2 mm wide, veins without papillae, petals white, not clawed, not overlapping, c. 1 cm long, c. 5 mm wide, stamens 12, anthers versatile, c. 1 mm long, filaments c. 1 mm long, carpels numerous. *Fruit* oblanceoloid, 3-ribbed, glandular, 1.3 – 1.5 mm long, 0.8 – 0.9 mm wide, glands 1 – 2, separated by ribs, circular, beak terminal, erect, c. 1.2 mm.

DISTRIBUTION AND ECOLOGY. Known only from the type locality (Map 3). Ecology unknown.

SELECTED COLLECTIONS. CULTIVATED. *Mühlberg* s.n. (TUR!).

NOTES. Haynes & Holm-Nielsen (1994) treated this taxon in synonymy under *Echinodorus subalatus*, but phylogenetic studies (Lehtonen & Myllys 2008) support its status as a closely related but separate species. However, the molecular evidence was based on cultivated material and therefore is not fully reliable. Furthermore, I have not been able to study the type specimen and therefore the application of the name is uncertain, although the cultivated material corresponded with the description of *E. inpai*.

26. Echinodorus heikobleheri *Rataj* (2004: 38). Type: Brazil, Roraima, Igarapé da Alemãoa, *Bleher* s.n. (holotype PR).

Perennial, from rhizomes. *Leaves* emersed and submersed, emersed blades elliptic, undulating, 3 – 5(?) pseudopinnate veins, 12 – 17 cm long, c. 1.5 cm wide, pellucid markings absent, apex acute to acuminate, base acute, petioles c. 5 cm long, submersed blades linear, undulating, pseudopinnate veins, 50 – 70 cm long, 1 – 1.5 cm wide, pellucid markings absent, apex acute, base attenuate. *Inflorescence* racemes, of c. 3 whorls, each c. 4-flowered, decumbent, overtopping leaves, proliferating, rachis triangular in cross-section, pedicels spreading in flower, c. 1 – 2 cm long. *Flowers* c. 1 cm diam., petals spreading, white, not clawed, not overlapping, stamens 9, carpels numerous. *Fruit* obovoid, 3 – 4-ribbed, glandular, glands 3 – 4, separated by ribs, circular, beak terminal, erect.

DISTRIBUTION AND ECOLOGY. Known only from the type locality. Growing submersed in creeks (Rataj 2004).

SELECTED COLLECTIONS. CULTIVATED. *Quester*, s.n. (TUR!).

NOTES. The status of this taxon as a separate species is questionable. It has some morphological apomorphies

(Rataj 2004), but molecular analysis resolved it within *Echinodorus grisebachii* (Lehtonen & Myllys 2008). However, the total-evidence analysis suggested a sister relationship with *E. grisebachii* (Lehtonen & Myllys 2008). *E. heikobleheri* is accepted here, but a more detailed analysis based on more collections covering the whole range of *E. grisebachii* group is needed.

27. Echinodorus lanceolatus *Rataj* (1968: 406; 1975: 68); Haynes & Holm-Nielsen (1994: 61); Rataj (2004: 126). Type: Brazil, São Paulo, *Burchell* 4158 (holotype BR!; isotypes BR!, K [digital image!]).

Perennial, from rhizomes, glabrous, to 160 cm. *Leaves* emersed, blades elliptic, 5-veined, c. 25 cm long, c. 3.5 cm wide, pellucid markings absent, apex acute, base attenuate, petioles terete, 50 – 68 cm long, c. 5 mm diam., base with a sheath to 10 cm long. *Inflorescence* racemose or paniculate, of 7 – 12 whorls, each 7 – 9-flowered, erect, overtopping leaves, not proliferating, to 60 cm long, 15 cm wide, rachis triangular in cross-section, peduncles terete, to 90 cm long, 8 mm diam., bracts shallowly connate at the base, lanceolate, coarse, 1 – 1.5 cm long, 5 mm wide, 11 – 13-veined, apex acute, pedicels spreading in flower and recurved in fruit, terete, 1 cm long, 0.5 mm diam. *Flowers* unknown. *Fruit* obovoid, 4-ribbed, glandular, 3 mm long, 1 mm wide, glands 5, circular, beak terminal, erect, c. 0.8 mm.

DISTRIBUTION AND ECOLOGY. Southern Brazil. Ecology unknown.

SELECTED COLLECTIONS. BRAZIL. *Burchell* 4158 (BR!, K!).

NOTES. No molecular data of this species was available for the phylogenetic studies, and morphological data is based only on holo- and isotypes (Lehtonen & Myllys 2008). Micheli (1881) listed the type specimen of *Echinodorus lanceolatus* (*Burchell* 4158, BR!, K!) under his description of *E. paniculatus*. Rataj (1968) noticed different fruit morphology of the specimen (multiple glands present, in contrast to eglandular fruits of *E. paniculatus*) and based his *E. lanceolatus* on that specimen. However, no more collections are known, and the species status cannot be ascertained at this time.

28. Echinodorus glandulosus *Rataj* (1969b: 336; 1975: 45); Haynes & Holm-Nielsen (1994: 24); Rataj (2004: 82). Type: Brazil, Pernambuco, Tapera, *Pickel* 64 (holotype BRG; isotype SP [digital image!]).

Perennial, from rhizomes, petioles and peduncles glabrous to pubescent, to 125 cm. *Leaves* emersed, blades ovate, 13-veined, c. 12 – 18 cm long, c. 13 – 18 cm wide, pellucid markings present as reticulate network, apex round, base truncate to cordate, petioles terete, c. 23 cm long, 5 mm diam., base with a sheath to 10 cm long. *Inflorescence* paniculate, of 12 whorls, each c. 24-flowered, erect, overtopping leaves, not proliferating, 35 cm long, 10 cm wide, rachis triangular in cross-section, alate, peduncles terete, bracts free, lanceolate, coarse with membranous margin, 1.5 cm long, 4 mm wide, apex acuminate, pedicels spreading in flower and fruit, terete, 1.5 cm long, 0.5 mm diam. *Flowers* c. 1.5 cm diam., sepals erect, 10 – 12-veined, c. 5 mm long, 4 mm wide, veins without papillae, petals not clawed, stamens c. 18. *Fruit* oblanceoloid, c. 4-ribbed, glandular, 2 mm long, 1.2 mm wide, glands 1, circular, beak terminal, erect, c. 0.6 mm.

DISTRIBUTION AND ECOLOGY. East Brazil. Ecology unknown.

SELECTED COLLECTIONS. BRAZIL. *Pickel* 64a (SP!).

NOTES. Rataj (1975) placed this species in his section *Longipetalii* with other species having reticulate pellucid markings, but he also hypothesised that *Echinodorus glandulosus* may be a hybrid between some species of *E. subalatus* and *E. horizontalis* groups (Rataj 1969b). The phylogenetic analysis (Lehtonen & Myllys 2008) placed this species in the same clade with *E. trialatus*, *E. scaber* and *E. emersus*, but no molecular data were available. Rataj (1975) mentioned only two collections of the species, and no more collections are known to exist.

Nomina Dubia

In the phylogenetic study of the genus, Lehtonen & Myllys (2008) mentioned two morphologically distinct populations (sp. 3 and sp. 4). Population sp. 3 has quite a distinct morphology (Fig. 12), but only one small population growing in an unusual habitat for the group (large plants submersed in a stream) was found from Paraguay. Population sp. 4 has a mixture of morphological characters of *Echinodorus longiscapus* and *E. floribundus* with a unique character state, a creeping inflorescence. Although these specimens could not be placed into any accepted species further collections are needed before the taxonomic status of these populations can be reliably ascertained.

Several species of *Echinodorus* have been described on the basis of cultivated material of unknown origin encountered in the aquarium trade, or sterile plants. Because natural species have been largely replaced by cultivars and hybrids produced for commercial purposes (Kasselmann 2003), species descriptions based on such material are dubious at best. Names that are considered to be dubious for these reasons are listed here.

Echinodorus africanus Rataj (1981: 20; 2004: 76); Haynes & Holm-Nielsen (1994: 65); Somogyi (2006: 381). Type. Cult. in Bot. Inst. CSAV Sumperk, 5 Oct. 1981, *Rataj* s.n. (holotype PR).

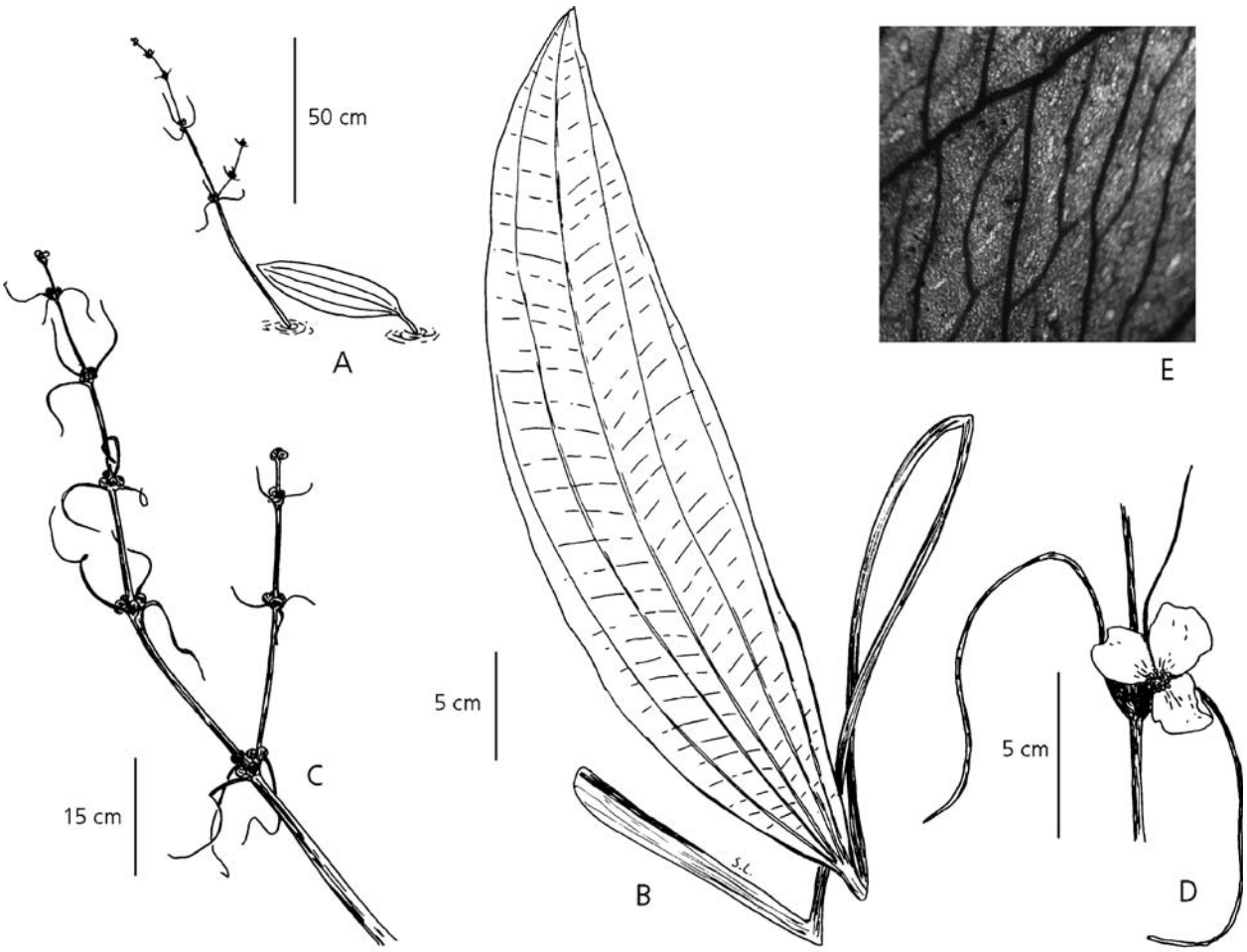


Fig. 12. *Echinodorus* sp. 3 (*Lehtonen & Burguez* 275, TUR!, FCQ!). **A** habit; **B** leaf; **C** inflorescence illustrating bracts up to 15 cm long; **D** enlargement of inflorescence illustrating flower with c. 20 stamens; **E** enlargement of leaf illustrating short pellucid lines. DRAWN BY SAMULI LEHTONEN.

Echinodorus barthii Mühlberg (1986: 368 – 369). Type. Cult. in Horto Botanico Halensi, 18 June 1986, *Mühlberg* s.n. (holotype HAL [photograph in AAU!]). Apparently hybrid (Kasselmann 2003).

Echinodorus gabrielii Rataj (1990: 14 – 15; 2004: 132). Type. Cult. In Bot. Inst. Praha, *Rataj* s.n. (holotype PR).

Echinodorus janii Rataj (1988: 30); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 67). Type. Cult. in Bot. Inst. Sumperk (Patria Paraguay?), 1 June 1988, *Rataj* s.n. (holotype PR).

Echinodorus maculatus Somogyi (2006: 382 – 383). Type. Cultivated in the Karel Rataj nursery in Sumperk, Czech Republic, 29 April 2005, *Somogyi* s.n. (holotype W [photograph in the original publication!]; isotypes BRA, M, PR, WU).

Echinodorus multiflorus Rataj (1989: 24); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 96). Type. Cult. in Bot. Inst. CSAV Sumperk, 16 Sept. 1987, *Rataj* s.n. (holotype PR).

Echinodorus opacus Rataj (1970a: 215 – 216; 1975: 70), Haynes & Holm-Nielsen (1994: 65), Rataj (2004: 134). Type. Brazil, Paraná, Ponta Grossa, 8 Nov. 1967, *Horeman* s.n. (holotype PR [photograph in AAU!]).

Echinodorus portoalegrensis Rataj (1970a: 216; 1975: 70); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 136). Type. Brazil, Rio Grande do Sul, Porto Alegre, 1967, *Bleher* s.n. (holotype PR [photograph in AAU!]).

Echinodorus pseudohorizontalis Rataj (2002: 30; 2004: 130). Type. Patria incognita, ex. cult. in hortulis, 10 April 2002, *Rataj* s.n. (holotype PR).

Echinodorus schlueteri Rataj (1981: 20); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 102). Type. Cult. in Bot. Inst. CSAV Sumperk, 12 Oct. 1981, *Rataj* s.n. (holotype PR).

Echinodorus veronikae Rataj (1988: 30); Haynes & Holm-Nielsen (1994: 65); Rataj (2004: 78); Somogyi (2006: 384). Type. Cult. in Bot. Inst. Sumperk

(Patria Cameroun), 20 May 1988, *Rataj* s.n. (holotype PR).

Echinodorus viridis Rataj (2002: 30; 2004: 80), Somogyi (2006: 384). Type. Cultivated plant, 15 April 2002 (holotype PR).

Acknowledgements

The directors and staff of all the mentioned herbaria are acknowledged. I thank Maarten Christenhusz for his generous help with the Latin diagnoses and many nomenclatural problems. The manuscript greatly benefitted from discussions with Hanna Tuomisto. I also thank Daniel Crawford, Jaakko Hyvönen, Pamela Soltis, Daniel Falck and two anonymous reviewers for their useful comments on previous drafts. The language was kindly checked by Mirkka Jones. This study was funded by the Jenny and Antti Wihuri, Turku University, Emil Aaltonen, and Oskar Öflund's Foundations.

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